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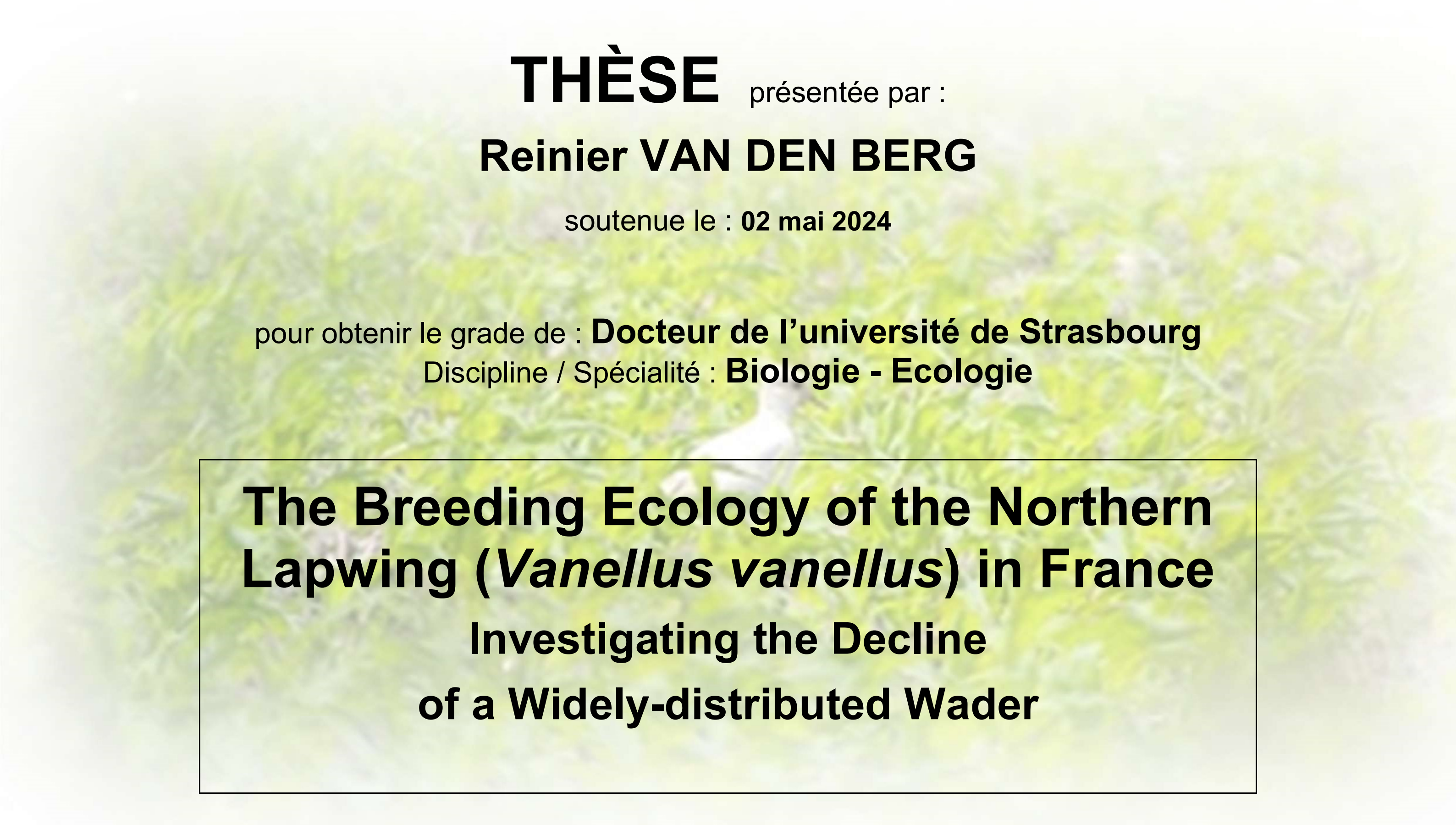

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The Breeding Ecology of the Northern Lapwing (*Vanellus vanellus*) in France

Investigating the Decline of a Widely-distributed Wader

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General Introduction

1) Avian Reproduction and Life History Strategies

The processes of natural selection have resulted in numerous species, which behave in different ways, with each individual organism the result of a consecutive set of processes that arose emergently from the billions of selection steps that preceded the current day (Skinner 1985). Some of the most impactful features that can be leveraged by natural selection are life history traits. When and where should an animal reproduce? How much should they invest in reproduction? Under which conditions should they skip an opportunity to reproduce? Should their bodies develop to support rapid reproduction, or should there perhaps be a pause between developmental maturity and reproductive activity (Becker *et al.* 2008, Horváthová *et al.* 2012, Bowers *et al.* 2016, Tavera *et al.* 2020)? A small change in how an individual of a species acts with regard to any of these questions can have serious consequences for their lifetime reproductive success. For example, Common Murres (*Uria aalge*) breed more successfully when they synchronise with their neighbours, and 50% of Common Murres will lay their eggs within a 7-day period (Murphy & Schauer 1996). An individual murre that always arrives at the breeding site three weeks late can be expected to produce, over its lifetime, much fewer offspring than the murres that synchronise with their conspecifics.

The particular set of physical and behavioural characteristics that define birds (Cl. *Aves*) as a group, have resulted in a potential for a large diversity of life history traits. Like other reptiles, birds provide all the nutrients needed for their embryos to develop when they lay their eggs. But like mammals, most birds will provide care for their embryonic offspring by ensuring they are kept at optimal conditions for development (Huggins 1941). Without this effort from the parent(s), bird embryos die rapidly (Webb 1987, Beissinger *et al.* 2005). Unlike for therian mammals, however, the offspring are external to the adult and can be abandoned if conditions at the breeding grounds suddenly take a turn for the worse (Guigueno & Sealy 2010). This provides birds with opportunities for unique reproductive strategies. For example, brood parasitism, whereby birds such as the Common Cuckoo (*Cuculus canorus*) will lay their eggs in other birds' nests, resulting in their chicks parasitising parental care from unrelated animals. This strategy would not be available without post-laying parental care, nor could it target animals that develop their offspring internally.

Where an animal chooses to reproduce can have a large impact on its reproductive success. Birds, being highly mobile animals, are in some ways spoiled for choice. Arctic Terns (*Sterna paradisaea*), for example, have been selected to be able to migrate across half the circumference of the earth (Egevang *et al.* 2010). Theoretically, a tern could breed at almost any point on the globe. However, we do not find Arctic Terns breeding in the middle of the Sahara Desert. Particular species will prefer to breed in particular habitats, to which their breeding habits and physiology are most adapted. If these places are unavailable, they may breed in alternative habitats, but will likely reproduce less efficiently (Cohen 2006, Chalfoun & Schmidt 2012). We may consider that for any species, there will be combinations of time and place that allow for successful reproduction, and other combinations that do not.

In many habitats, there is a periodic fluctuation in the suitability of the habitat for reproduction. As a result, the habitat may be suitable for breeding during a certain time window, but unsuitable otherwise. For example, food availability in some habitats may roughly follow a normal distribution around a particular point in the year, with an identifiable peak (McKinnon *et al.* 2012). Birds should time the beginning of their reproduction so that when the need for food is at its maximum, the breeding grounds will also provide their maximum amount of food (Martin 1987, McKinnon *et al.* 2012). This might mean that the optimal start of the breeding season will depend on environmental conditions which the birds may perceive, such as ambient temperature (Bowers *et al.* 2016), or the food availability at the breeding grounds (Svensson & Nilsson 1995). In addition, whole populations of birds can shift their migration patterns as a result of climatic change (Santangeli *et al.* 2018). When the start of reproduction is aligned with the expected optimum value based on resource availability at the breeding site, it may be considered “matched”, and when it is not it may be considered “mismatched” (Cushing 1969, Durant *et al.* 2007). At greater degrees of mismatch, we may expect lower reproductive success (Durant *et al.* 2007).

At the end of the breeding season, birds may stay in their breeding habitat or migrate to a different habitat to spend the non-breeding season, each of which a potential avenue to reproductive success, sometimes even within a single species (Grist *et al.* 2017). The population dynamics, then, will depend on the interactions between what happens on the breeding grounds and what happens on the non-breeding (wintering) grounds (Myers 1981, Gill *et al.* 2001). If particular individuals winter at higher quality sites, they might be expected, *ceteris paribus,* to reproduce more efficiently.

Similarly, the survival chances of new fledglings may be expected to differ based on their body condition (Maness & Anderson 2013), which can vary according to the quality of the breeding grounds on which they are raised (Galbraith 1988a). Of all chicks hatched, we expect a larger proportion of the ones from high quality breeding grounds to survive to reach the wintering grounds. The quality of the wintering grounds will partly determine their subsequent success at the breeding sites (see above). There are some species, like the Black-tailed Godwit (*Limosa limosa*) for which these two are linked: the individuals breeding at high quality breeding sites also end up at the higher quality wintering sites (Gunnarsson *et al.* 2005).

The length of time at the breeding grounds during which a particular individual may successfully breed then depends on the quality of the breeding and non-breeding sites, birds’ ages, their individual quality, and their migration schedules (Svensson & Nilsson 1995, Goutte *et al.* 2010, Descamps *et al.* 2011, Eichhorn *et al.* 2017). We might define the entire period over which an individual can successfully reproduce as a “favourable environmental window” for reproduction. When the favourable environmental window is sufficiently long, the opportunity arises for birds to “double-brood”: to raise two consecutive broods and produce fledglings from both (Phillips Jr *et al.* 1998). By contrast, if the favourable environmental window is short, then the success or failure of the breeding season as a whole will hinge on the success of the first and only clutch.

As birds will have limited resources available to them (see above), there must be a division in the allocation of these resources towards different aspects of the individual, where one necessarily precludes the other (a trade-off, Stearns 1989). One classic trade-off is the allocation of resources between adult survival and reproduction. Birds species are expected to be arranged in a spectrum between two extremes: those that invest heavily in survival and reproduce relatively slowly (slow pace of life), and those that reproduce fast and show low survival rates (fast pace of life, Sæther *et al.* 1996, Sæther & Bakke 2000).

Long-lived birds may compensate for failed breeding in one year by breeding successfully in following years (Chastel et al. 1993). The failure of any particular breeding attempt may then only have a small effect on lifetime reproductive success compared to the adults’ survival rates (Sæther & Bakke 2000). Thus, when a bird can expect to live through numerous breeding seasons, it can be expected to prioritise its own survival over that of its offspring of a particular year (Erikstad *et al.* 1998).

The amount of effort an individual bird should be expected to invest in one particular reproductive attempt further depends on external factors, like the suitability of its habitat for reproduction or availability of mates, and on intrinsic factors, like its expected remaining lifespan or current body condition (see above). On a species level, we expect species' life history trade-offs to be adapted to the expected conditions at their breeding sites (Sæther *et al.* 1996). Populations can reach evolutionary stable equilibria for these trade-offs, where a particular set of life history traits becomes dominant. For example, 77% of Eurasian Curlew (*Numenius arquata*) clutches contain exactly 4 eggs (Grant *et al.* 1999). On the other hand, in some species there has been a selection toward a certain degree of plasticity in reproductive investment. For example, House Sparrows (*Passer domesticus*) lay clutches of different sizes based on a combination of factors such as the number of clutches they have already laid that breeding season and their age (Westneat *et al.* 2009).

When the expected cost of continuing reproduction outweighs the expected benefits, birds may abandon their current breeding attempt in favor of future ones. Abandonment by one of the two parents occurs in species with biparental care as a result of a high chance to fledge chicks: one or both parents may assess that the parental care of the other alone will be sufficient to raise a brood. If their own chances of raising another clutch are sufficiently high, they may then abandon the brood and try to hatch another (Thomas *et al.* 2007). Parents may also abandon their breeding attempt because expected costs increase, for example because habitat becomes less suitable (Korner *et al.* 2024). One cost of reproduction which is tightly linked to a highly variable external factor is thermoregulatory effort.

2) Thermoregulation at the Nest

The typical bird's egg loses approximately 18% of its wet weight at time of laying through water loss (Rahn & Ar 1974). If conditions around the egg cause it to lose significantly more or less water than under normal incubation, this can result in high mortality rates for the embryos before they are able to hatch (Davis *et al.* 1988). Similarly, birds should keep the temperatures of their embryos within a range that allows for them to develop. Eggs' temperatures can fluctuate over time, with an average of around 34.3°C for attended nests in temperate North America, but with measured temperature extremes between 13.0°C and 45.8°C (Huggins 1941).

Hypothermia will slow down development, and eventually lead to the death of the embryo, while hyperthermia will lead the embryo to a much faster end, starting at around 41°C (reviewed in Webb 1987), with the potential for heat-adapted species to survive higher temperatures. Black-necked Stilts (*Himantopus mexicanus*) can survive egg temperatures to a maximum of 47.7°C (Grant 1982). Eggs will typically be laid in nests, which may be constructed in such a way that the combination of nest structure and parental attendance will promote optimal developmental conditions for the embryos, such as a higher-than-ambient vapour pressure (Vleck *et al.* 1983), or a more stable temperature (Mougeot *et al.* 2014). Egg temperatures will be tightly linked to adult body temperatures through regular direct contact between the two. In many bird species, direct contact is facilitated by a specialised patch of naked, highly vascularised, and oedemic skin called the 'brood patch' (Jones 1971, Lea & Klandorf 2002).

Birds are generally full-time homeothermic organisms, except for a few notable cases such as hummingbirds (Shankar *et al.* 2022). Although the insulative properties of feathers go a long way towards ensuring a stable core body temperature (Breitenbach & Baskett 1967), birds may find themselves in environmental conditions that require specific behavioural responses to maintain a stable temperature. As their clutch's development is linked to their ability to regulate their body temperature (Drent *et al.* 1970), it is of utmost importance during the incubation phase of the reproductive cycle that the adult thermoregulates very efficiently. Furthermore, the thermoregulatory capacity of birds' offspring is more restricted than their own, even for precocial species (Tazawa & Rahn 1986, Whittow & Tazawa 1991), which extends this relationship into the chick rearing phase.

To maintain body temperatures in cold conditions (and thus clutch temperatures), birds may show several adaptive responses: perching at warm locations (Zhou *et al.* 2017), shifting posture to minimize heat loss (Ryeland *et al.* 2017, Zhou *et al.* 2017), shivering thermogenesis (Randall 1943), muscle-related non-shivering thermogenesis (Pani & Bal 2022), and huddling together for warmth (Gilbert *et al.* 2006). During cold periods, birds may survive significant cold when they are well-fed (e.g. down to -40°C/F in Alberta, Canada, Rowan 1925), but can die quickly from cold when their fat reserves are low and they're unable to feed (Vepsäläinen 1968).

On the other end of the temperature spectrum, birds have been known to show several different behaviours to cool their bodies: panting, ptiloerection, wing drooping, belly / feather wetting, nest shading, and shade seeking (Randall 1943, Brown & Downs 2003, Amat & Masero 2004, Sharpe *et al.* 2021). In addition to their utility for the adult, feather wetting and nest shading also directly regulate the temperature and water loss of the bird's clutch (Grant 1982, Brown & Downs 2003, Amat & Masero 2004).

Many of these behaviours can increase evapotranspirative cooling rates of birds. Panting results in greater heat loss by directly increasing evapotranspiration through breath (Bouverot *et al.* 1974, Amat & Masero 2004, Sharpe *et al.* 2021). Ptiloerection, the erecting of the feathers, may result in greater gaps between feathers, allowing air to pass between the feather tracts more easily (Grant 1982, Amat & Masero 2004). Wing drooping, an extending of the wings from the resting position, increases the surface area of the bird which is exposed to the air, and thus over which wind may pass (Amat & Masero 2004, Smit *et al.* 2016). In some bird phyla, there is an *apterium*, (i.e. a spot with reduced or absent contour feathers), on the ventral side of the wing, which has been suggested to have a thermoregulatory function (George & Casler 1972), which may facilitate heat loss during wing drooping. Birds are also known to soak their feathers, particularly belly feathers, in water before returning to their nests (Grant 1982, Amat & Masero 2004). This allows eggs or chicks to replenish lost water and cool due to evapotranspiration (Grant 1982). Nest shading, or 'standing directly above the nest', is a behaviour exhibited by birds in warm habitats (Purdue 1976, Brown & Downs 2003, Amat & Masero 2004, Sharpe *et al.* 2021). It has been shown that Crowned Lapwing (*Vanellus coronatus*) adults are cooler when shading than when incubating. On the other hand, their eggs are cooler when being incubated than when shaded (Brown & Downs 2003).

Both cooling and warming behaviours can be stimulated by manipulating the bird's temperature directly (Randall 1943, Brummermann & Reinertsen 1991), but the potential for a clutch's temperature to affect the thermoregulatory behaviour of its parent is less clear. Grant (1982) considered that "egg temperature is not the proximate stimulus for belly-soaking", a cooling behaviour. The Black-necked Stilts he studied did not respond visibly to experimental heating of their clutches to a range of temperatures between 38.6°C and 48.0°C (Grant 1982). Drent (1970) experimentally heated Herring Gull (*Larus argentatus*) nests up to 50°C, and found they increased their thermoregulatory behaviours.

Finally, thermoregulatory responses may themselves influence other behaviours. It has been suggested that birds with simultaneous tendencies to leave and stay at the nest will preen as a form of displacement behaviour (Baerends 1959). This situation might occur when the bird is induced to shade the clutch, as it is simultaneously needed at the nest (to prevent the eggs from heating up) and should at the same time want to seek shade or a colder environment for itself (which involves leaving the nest).

3) Waders and the Northern Lapwing

Waders are a diverse polyphyletic group of species, consisting of the *Charadrii* and *Scolopaci* suborders of the order *Charadriiformes,* as well as three genera in the suborder *Lari* (**Figure 1**). Waders show a variety of mating and parental care strategies (Székely & Reynolds 1995). Different species of waders can be found breeding on every continent including Antarctica (gen. *Chionis*), and over a wide range of biomes. Thus, it is surprising that a great number of them are currently undergoing population declines.

A recent meta-analysis has found that 59% of 194 investigated wader species (of out 246 extant) show a population decline. More northerly breeding species show greater declines than southerly breeding species (Koleček *et al.* 2021). One such northerly species is the Northern Lapwing (*Vanellus vanellus*), a member of the family *Charadriidae* (**Figure 1**)*,* which can be found breeding across almost the full longitude of the palearctic: from north-western Morocco through western Europe into the steppes of Russia and beyond, to Mongolia (Cherkaoui & Hanane 2011, BirdLife International 2017a, Keller *et al.* 2020). The European population of lapwings is estimated at approximately 3,820,000, and is decreasing (BirdLife International. 2021).

The main causes for wader species' declines are most often identified as problems with the reproductive aspects of the species' population dynamics. These may be related to low fledging rates, loss of habitat, or degradation of remaining habitat (Wilson *et al.* 2004, Donald *et al.* 2006, Eglington *et al.* 2009, Leyrer *et al.* 2018, Roos *et al.* 2018). During the different stages of reproduction, the specific threats to reproduction may be different. For example, predators which frequently feed on chicks may only rarely feed on clutches (Teunissen *et al.* 2008).

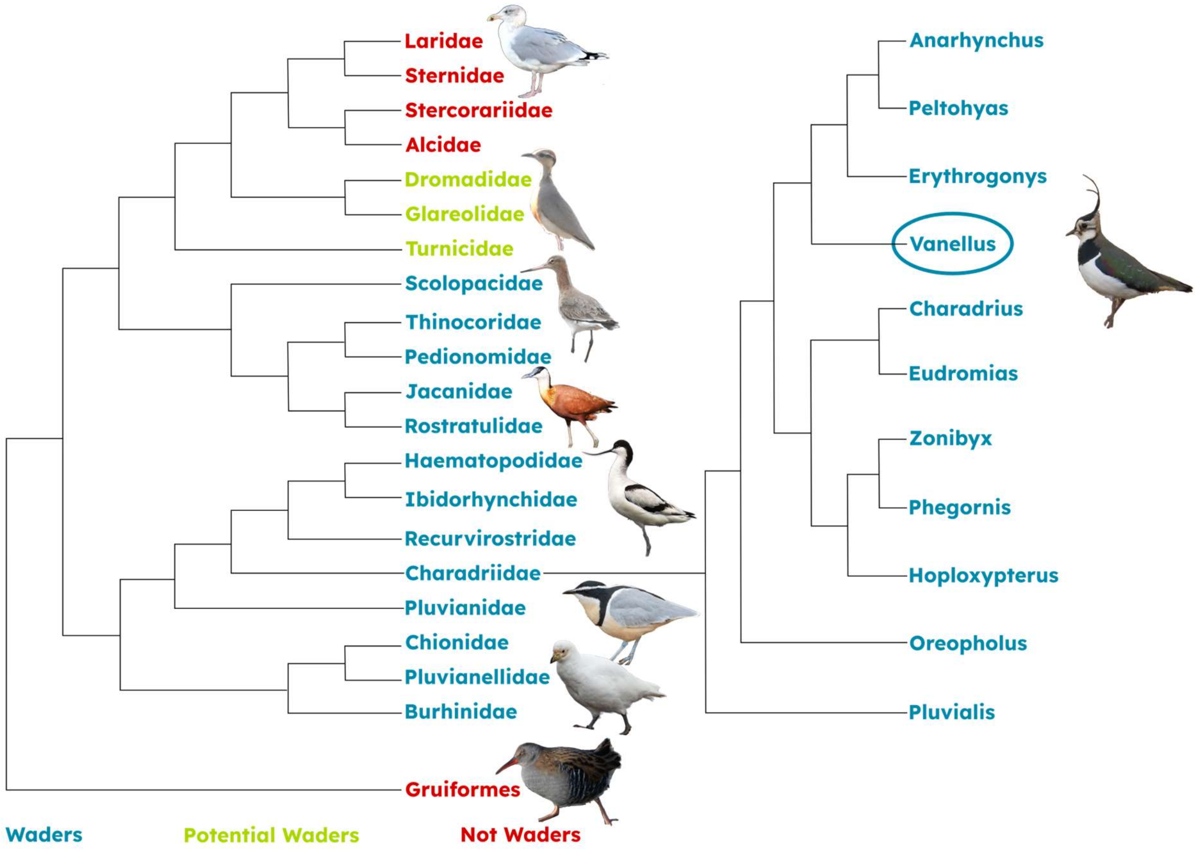

Figure 1: *Simplified phylogeny of waders following Kuhl et al. (2021) and of Charadriidae following Černý & Natale (2022). Branch lengths not to scale. Dromadidae, Glareolidae, and Turnicidae are not always considered waders. Photos by (top to bottom, left to right) Jørn Knudsen, scaramouche*, Stephen James McWilliam, Brian Fisher, P. S. Sivaprasad, Ricardo Rodero Henández, msr*, rimma_sych*; belvedere04*. * : Pseudonym*

3a) Distribution & migration

Northern Lapwings have been known to migrate thousands of kilometers over land (Potvin *et al.* 2016, Eichhorn *et al.* 2017), and may disperse over similar distances (Evans 1968, Mead *et al.* 1995), although many individuals do not disperse very far from their birthplace (Lislevand *et al.* 2009). Lapwing wintering grounds are found across western Europe, from Ireland through the United Kingdom, Belgium, and the Netherlands down to Spain and France (BirdLife International 2017b). France is the main destination for European lapwings, holding approximately 70% of the European breeding population in the wintering season (BirdLife International 2017b). Lapwings also winter in the eastern half of the Northern Mediterranean, including the Balkans and Türkiye, as well as further east to Armenia (BirdLife International 2017b). The Asian part of the population is much less studied, though see Khrokov (1998) for an overview of a population in Kazakhstan.

At their breeding grounds in Europe, lapwings are among the most well-studied wader species. Researchers in the United Kingdom, the Netherlands, Germany, Norway, Poland, Hungary, Czechia, and Belarus publish extensively on their migratory and breeding ecology (e.g. Liker & Székely 1999a, Eglington *et al.* 2009, Lislevand *et al.* 2009, Królikowska *et al.* 2016, Bertholdt *et al.* 2017, Brandsma *et al.* 2017, Düttmann *et al.* 2018, Kubelka *et al.* 2019, Kaasiku *et al.* 2022, Pilacka *et al.* 2023). Research effort is concentrated in countries hosting a large part of the population during the breeding season. However, information from the southern parts of the Northern Lapwing's breeding range, where lapwings breed in smaller numbers, is relatively scarce (though see e.g. Girard & Trolliet 1992, Triplet *et al.* 2004, Durant *et al.* 2008, Cherkaoui & Hanane 2011, Kotrošan *et al.* 2019, Korner *et al.* 2024).

3b) Breeding ecology

Lapwings arrive at their breeding grounds in late winter and early spring in migratory flocks, which settle down close to the breeding sites (Galbraith 2008). The exact date of arrival differs for each breeding site, with lapwings breeding further north arriving notably later than those breeding at lower latitudes. A difference of one month has been observed between lapwings arriving in Scotland (February 14th) and North Norway (Mar 28th, Barrett 2002).

The males claim their territories by performing characteristic flight displays, paired with their iconic calls (Klomp 1954, Dabelsteen 1978). Males will settle at their future breeding grounds earlier than females, who tend to arrive later than the males (Galbraith 2008). During pair formation, females will alight on the territories of the males. The male, noticing the female's arrival, performs a ground display that involves scraping at prospective nest sites while wagging his tail (**Figure 2: A, B**). If the female shows interest, the male exhibits a follow-up display behaviour, during which he holds his body tilted forwards at an approximately straight angle with the ground ("bowing"), while making a rasping call (**Figure 2: C**, Shrubb 2007, Byrkjedal *et al.* 2013).

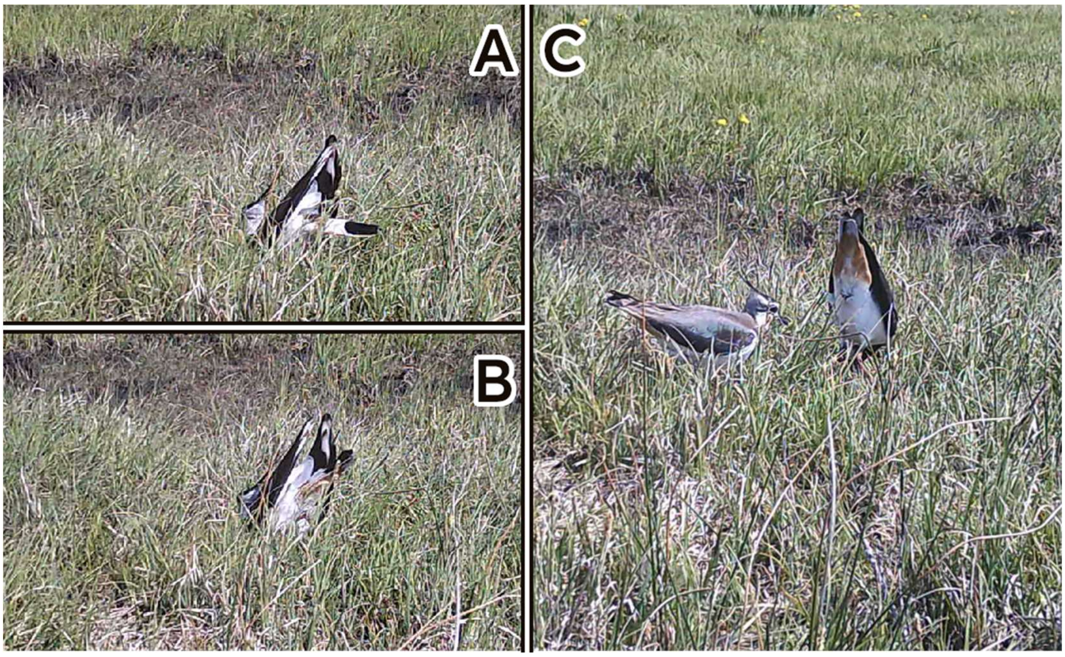

Figure 2: *Ground displays of the male lapwing during pair formation. **A & B**: scraping display at the nest site, with the tail wagging vertically. **C**: The female (left) approaches the nest while the male (right) bows forward, pecks at vegetation, and produces a raspy call.*

Female lapwings may visit multiple male territories before choosing a partner. In some cases, females can visit half a dozen nearby territories, each visit lasting only about 15 minutes (Byrkjedal *et al.* 2013). This high degree of female choice is usually paired with a high degree of female investment in the brood, as she will be responsible for the majority of the incubation effort (discussed below, Jongbloed *et al.* 2006, Sládeček *et al.* 2019).

Males may pair with several females on their territory, where each female will hold a sub-territory within the male's where they will not permit other females (Liker & Székely 1997, Byrkjedal *et al.* 2000). Polygynous males will tend to have larger territories, and territory size is negatively correlated with the number of close neighbours (nests within 100 m of primary female's nest, Berg 1993). Depending on suitable habitat and breeding density, lapwing colonies may be composed of up to 28 breeding pairs (colony: all nests within 200 m of any other nest, Berg *et al.* 1992), though single pairs are also found (MacDonald & Bolton 2008).

The male establishes his territory in an open habitat, where nest sites are ideally located far from woody plants (Bertholdt *et al.* 2017, Tamis & Heemskerk 2020). Nest depredation rates are higher close to trees (Berg *et al.* 1992, Kaasiku *et al.* 2022), which serve as hiding places and perches for predators. Popular breeding habitats range from wetlands, to grazed pastures or short meadows, to crop fields in the early stages of cultivation or fields planted with low-growing crops (Triplet *et al.* 1997, Henderson *et al.* 2002, Durant *et al.* 2008, Düttmann *et al.* 2018, Pilacka *et al.* 2023). A vegetation height below some 5 to 10 cm tall will be preferred (Siriwardena *et al.* 2016, Madsen *et al.* 2019).

Lapwings appear to have some ability to discern the likely future growth of vegetation at potential breeding sites. They avoid short vegetation that would grow tall later in the season (Klomp 1954). Nevertheless, lapwings are tolerant of taller vegetation when it is found close to surface water features showing variable water levels (Eglington *et al.* 2007, Durant *et al.* 2008). Changes in water levels can create zones of lower vegetation close to the water on previously flooded areas (Ausden *et al.* 2001). Waterlogged or flooded soils significantly impede plant growth (Yasumoto *et al.* 2011, Kaur *et al.* 2020). Corn fields, which grow very tall crops later in the season, are a preferred nesting habitat for lapwings (Saumer 1972). During the nest building period, these fields are still bare, freshly sown, or covered in young corn plants (widely-spaced), leading to lapwings preferentially building their nests on these fields (Korner *et al.* 2024). This results in some lapwings nesting in the middle of corn plants over a metre tall (pers. obs.). Some lapwings reportedly abandon their nests when surrounded by this type of vegetation (Korner *et al.* 2024).

A grass sward that has been left to grow ungrazed and unmown will elicit the same response from lapwings as other tall vegetation. Grasses at fertilized meadows can grow significantly taller than on unfertilized meadows, reaching above 10 cm before the end of May (Pavlů *et al.* 2022). Agricultural output across Europe has increased, through the mechanisation of agriculture and increased fertilizer use (Donald *et al.* 2001). This has transformed suitable lapwing habitat into unsuitable habitat (Taylor & Grant 2004), and resulted in declines of multiple farmland bird species (Donald *et al.* 2001).

Lapwings' preference for low vegetation likely relates to their nest survival strategy, which relies not only on nest crypsis but also on active defense of the nests by the adults (Elliot 1985a, Kis *et al.* 2000, Šálek & Cepáková 2006). Nest defense relies on mobbing behaviour characterised by swooping dives and fly-by's, which are often seen employed against avian intruders (Elliot 1985, Kis *et al.* 2000). Livestock may be warded away from the nest with an iconic "banner display", during which the lapwing raises both wings vertically and spreads them horizontally, increasing its apparent profile and showing the striking contrast between the white and black feathers of their wings and breast (Shrubb 2007).

Between 1 and 4 eggs are laid in the nest, though the overwhelming majority of clutches consist of exactly 4 eggs (Galbraith 1988). The majority of incubation is done by the female (Jongbloed *et al.* 2006, Sládeček *et al.* 2019). The amount of time males contribute to the incubation varies greatly among pairs. In lieu of incubating, males continue to perform display flights and often respond to predators throughout the incubation period (Liker & Székely 1999b, Lislevand *et al.* 2004, Sládeček *et al.* 2019).

Variation in males' incubation efforts are observed in both monogamous and polygynous pairings. Females that receive limited incubation help from males are unable to fully compensate for the lack of care (Sládeček *et al.* 2019). Greater nest attentiveness by the male shortens the incubation period (Grønstøl 2003, Lislevand *et al.* 2004), which should reduce nest predation risk.

In territories with one male and two females, the male will split his share of incubation effort between the two nests, but polygamous males do not increase their total incubation effort compared to monogamous males (Lislevand *et al.* 2004). This results in a greater incubation investment for both females (Grønstøl 2003). The first female who has settled at the territory typically receives a smaller amount of male’s help. Consequently, her incubation costs are considerably higher when compared to monogamous females (Grønstøl 2003).

The nest attendance rate of lapwings is not stable over time, with the female present almost 100% of the time during the night, while the time spent at the nest during the day varies (Lislevand *et al.* 2004, Sládeček *et al.* 2019). Incubation takes approximately 27 days (Hegyi 1996). Experimentally-created three-egg clutches hatch one day sooner than four-egg clutches, and similar five-egg clutches hatch one day later (Larsen *et al.* 2003).

Clutches may be lost due to agricultural procedures, depredation, flooding, livestock trampling, and abandonment (Hart *et al.* 2002, Kragten & De Snoo 2007, MacDonald & Bolton 2008, Eglington *et al.* 2009, Korner *et al.* 2024). If the nest fails before hatching, lapwings may lay replacement clutches (Hegyi & Sasvari 1998, Parish *et al.* 2001). Eggs in replacement clutches are usually smaller than those in the first clutch (Hegyi 1996). Egg and chick sizes are correlated, with smaller chicks being less likely to survive (Hegyi 1996). Females lose weight between the first and replacement clutches, and females with lesser body conditions do not appear to have the option of laying a replacement clutch (Hegyi & Sasvari 1998). Second replacement clutches after the loss of a first replacement clutch are less common, but may still hatch successfully (Parish *et al.* 1997).

After hatching, the chicks become mobile within a few hours, and will begin to feed themselves soon after. This places lapwing chicks on the precocial side of the altricial-precocial spectrum, which can be used to classify (avian) offspring on a spectrum from least developed at hatching (altricial) to most developed at hatching (precocial, Ducatez & Field 2021). Parents and chicks may continue to use their breeding territory as a chick rearing ground, or migrate up to several kilometers to reach higher quality grounds (Girard & Trolliet 1992, Grønstøl *et al.* 2013).

Chicks will take approximately 35 days to reach fledging (Pilacka *et al.* 2023). During this time they are vulnerable to predation, thermoregulation deficiencies, agricultural procedures, and starvation (Beintema & Visser 1989, Visser & Ricklefs 1993, Teunissen *et al.* 2008).

3c) Population dynamics

A common thread among lapwing literature from across Europe is the decline of the species, which is reflected not only on the breeding grounds but also on the wintering grounds (Deceuninck 2001, Taylor & Grant 2004, Wilson *et al.* 2004, Lislevand *et al.* 2021, Joyeux *et al.* 2022). The analysis of ringing data has indicated that the survival rates of adult lapwings are likely to be, on the scale of generation times, stable (Roodbergen *et al.* 2012, Souchay & Schaub 2016). Thus, we expect the causes for population decline to be primarily at the production level.

The estimated average number of fledglings a pair must produce per year to sustain a stable lapwing population has been estimated at 0.8 per pair per year (Galbraith 1988, Plard *et al.* 2020). If they survive their first year after fledging, for which survival rates have been estimated around 60%, adult lapwings can expect to live for another 3.5 years (Peach *et al.* 1994, Plard *et al.* 2020). Individual lapwings may live for well over 20 years (Catchpole *et al.* 1999). More than half of lapwings may be expected to breed in their first year, with some indications that females may be more likely to do so (Thompson *et al.* 1994, Lislevand *et al.* 2009). Based on these figures, an average female can be expected to survive through four breeding seasons (one as a yearling and three years after).

Studies in the UK, Netherlands, Germany, Switzerland, among others, show varying levels of reproductive success (**Table 1**). Hatching success ranges between all possible rates, with large differences between regions and years. Chick fledging rates vary almost as much as hatching rates, although they are almost always lower than hatching rates (**Table 1**). Underlying causes for poor lapwing reproduction vary on an inter-regional scale, but can be grouped into the same categories affecting waders as a whole: habitat loss and degradation, accidental destruction, and predation.

As agriculture progressively intensified during the 20th century, and many of Europe's wetlands were drained to make way for agriculture (Davidson 2014), lapwings have been increasingly restricted in terms of natural breeding habitat. Human-dominated breeding habitat has also become more restricted. Intensively managed and fertilised meadows are mown early and multiple times in a breeding season (Kleijn *et al.* 2010, Roodbergen & Teunissen 2014). In other places, grasslands have been replaced by crop fields (Krause *et al.* 2011). Broadly speaking, agricultural intensification has made European farmland less suitable for breeding birds (Donald *et al.* 2001).

In several regions, crop fields in their early stages of cultivation (ploughing, harrowing, tilling, sowing) provide numerous lapwing breeding sites (Krause *et al.* 2011). Surrounding grasslands may grow too tall for nest building, unless they are visited by grazers before or at the start of the breeding season (e.g. geese, Madsen *et al.* 2019). Autumn-sown cereals are less preferred for establishing territories compared to spring-sown cereals (Eggers *et al.* 2011), most likely also due to the vegetation height. Thus, the remaining breeding habitat for lapwings will consist of a mixture of extensively grazed pastures, fallow fields, spring-sown crop fields, and the remaining wetlands.

The quality of these breeding sites has deteriorated due to modern agricultural practices. Lapwing adults and chicks feed on invertebrates found on vegetation, and just below the soil or water surface (Khrokov 1998, Ausden *et al.* 2003). These invertebrates are susceptible to pesticides (Easton & Goulson 2013). The use of pesticides is also associated with declining insectivorous bird populations (Hallmann *et al.* 2014). Fields across Europe, even the ones that did not directly have pesticides applied to them, are contaminated with pesticides (Riedo *et al.* 2022), indicating that habitat degradation might be widespread across western Europe.

To be worked by machinery, crop fields should not be too wet (Rotz & Harrigan 2005). Intensively worked fields will likely have low moisture content, so machines can efficiently be driven across. However, this reduces lapwings' access to food because: 1) the soil will be harder for lapwings to penetrate by beak (Wiggers *et al.* 2015); 2) there will be fewer surface water features, which facilitate access to prey (Eglington *et al.* 2010). Compared to the chicks of altricial birds, which have food brought to their warm nest by their flight-capable parents, lapwing chicks must find their own food. This means they have to find enough food to: 1) thermoregulate; 2) move and find more food; 3) grow (Schekkerman *et al.* 2001). When food is scarce due to agricultural intensification, this may disproportionately impact precocial birds, whose chicks have these extra costs and can't readily source food from other habitats by flying to them.

Table 1: *A selection of studies reporting values for lapwing hatching/nest survival rates and fledging/chick survival rates. FPP: Fledglings per pair/female. '—': no value reported in this publication.*

Publication	**Location**	**Hatching rate**	**Fledging rate**
Blomqvist *et al.* 1997	Sweden	—	4% (small eggs) 35% (large eggs)
Seymour *et al* 2003	UK	38% (4 sites 1996) 60% (7 sites 1997) 95% (arable sites 1998) 23% (wet meadows 1998)	—
Schifferli *et al* 2006	Switzerland	95% (electric fence) 39% (unprotected)	0.80 FPP (2005) 0.25 FPP (2006)
Kragten & De Snoo 2007	Netherlands	54% (2005 organic farms) 39% (2006 organic farms) 67% (2005 conventional farms) 45% (2006 conventional farms)	—
Sheldon *et al* 2007	UK	68% (total rate) 53% (minimum, grasslands) 85% (maximum, AES fallow)	—
Bellebaum & Bock 2009	Germany	12% (minimum, 2000) 63% (maximum, 1998)	75% of hatched (wet) 31% of hatched (dry)
Schekkerman *et al.* 2009	Netherlands	—	14% (mean ± 8% SD)
Bolton *et al.* 2011	UK	31% (±4.4% SE, total rate)	0.07 – 0.95 FPP
Rickenbach *et al* 2011	Switzerland	—	24% (total rate fenced) 0% (total rate unfenced)
Grønstøl *et al.* 2013	Norway		55% (16-day survival)
Kamp *et al.* 2015	Germany	78% (industrial site) 45% (arable sites) 32% (pastures)	0.74 – 1.03 FPP (industrial) 0.15 FPP (arable) 0.40 FPP (pasture)
Plard *et al* 2020	Netherlands & Germany	44% (NL)	0.46 FPP (NL, unprotected) 0.54 FPP (NL, protected) 0.55 FPP(Schleswig-Holstein)
Pilacka *et al.* 2023	Belarus	—	54% (total rate 2006) 70% (total rate 2007)
Korner *et al.* 2024	Switzerland	66% (total rate)	37% (total rate)

In addition to a reduced food supply, modern fields also present an increased risk of nest destruction. In the early stages of cultivation, crop fields may be passed over multiple times by heavy machinery as the field is tilled, fertilized, sown, and sometimes mechanically weeded, potentially causing nest loss (Kragten & De Snoo 2007). On grasslands, mowing has long been recognised as dangerous to nests and chicks, and especially so on meadows for hay production as compared to grazed pasture (Baines 1990, Kruk *et al.* 1996).

Finally, predation rates on lapwing nests of over 50% have been reported in multiple studies spanning Europe (Baines 1990, Eglington *et al.* 2009, Bertholdt *et al.* 2017, Korner *et al.* 2024). Among mammalian predators, red foxes are one of the most common predators, but mustelids such as European badgers (*Meles meles*), weasels (*Mustela nivalis*), and stoats (*Mustela erminea*) may also feature, as well as golden jackals (*Canis aureus*, Bolton *et al.* 2007b, Teunissen *et al.* 2008, Rickenbach *et al.* 2011, Männil & Ranc 2022). Avian predators of eggs are often identified as gulls and corvids (Elliot 1985, Bolton *et al.* 2007b, Teunissen *et al.* 2008, Królikowska *et al.* 2016), whereas chicks appear to be taken more often by Grey Herons (*Ardea cinerea*) or raptors (Teunissen *et al.* 2008, Królikowska *et al.* 2016).

The precise rates of nest depredation usually differ between years, sites, and habitat types (Baines 1990), with some site-years clearly showing predation rates below 50% (Sheldon *et al.* 2007). Predation risk, then, can be a highly spatially heterogeneous phenomenon. This may be partially explained by predators' potential for remembering the breeding sites of ground-nesting birds between years (Sonerud & Fjeld 1987). Lapwings show high site fidelity, with 95% of breeding lapwings in the UK returning to the same or adjacent fields between years (Thompson *et al.* 1994), and Swedish lapwings breeding on average 960 meters from their previous nest sites between consecutive years (Berg *et al.* 2002). A predator that learns of a breeding site, then, is likely to be able to return to the same area over consecutive years to depredate nests.

Predation is also a major cause of chick mortality (Sheldon 2003, Sharpe *et al.* 2006, Teunissen *et al.* 2008, 2020, Schekkerman *et al.* 2009), though part of the predation risk may be confounded by chicks that are predated because they are starving or weak (Sharpe *et al.* 2006). This means that a certain portion of predation may not have occurred if food access, weather, or parental condition (and thus egg weight, and so chick weight, Hegyi 1996) would have been better.

Predation rates are also affected by the availability of other prey, as lapwing predators are generalists such as red foxes (Teunissen *et al.* 2008), which can feed on any number of alternative prey species. This means nest depredation rates may fluctuate with vole or lemming cycles, increasing as alternative prey becomes scarce (Ims *et al.* 2013).

3d) Conservation measures

To increase lapwings' reproductive output, several different conservation measures have been proposed and employed. One of the most extensively used methods is marking the nests, so that farmers may drive around the nesting locations of lapwings. Indicators consist of (painted) sticks, (bamboo) canes, or thin branches placed upright in meadows or crop fields, at some distance from the nest to prevent predators from directly associating the marking with the nest's location (Schifferli *et al.* 2006, Kragten *et al.* 2008, Zámečník *et al.* 2018).

Nest marking has been proven to reduce nest destruction by agricultural procedures (Kragten *et al.* 2008). However, the marked nests could be more affected by predation and desertion (Kragten *et al.* 2008). Nest survival rates decline with every visit to the nest, particularly in areas with high predation pressure (Goedhart *et al.* 2010). It has been suggested that the signs of human passage to the nest (Goedhart *et al.* 2010) or association learning between the marking object/human visit and the nest (Strang 1980, O'Donovan & Boyce 2021) may lead to increased vulnerability of the marked nests.

Another conservation measure aimed at reducing nest losses to agricultural practices is the implementation of delayed mowing schedules. At meadow breeding sites, delayed mowing can reduce rates of nest destruction and chick mortality (Kruk *et al.* 1996). However, reduced mowing also results in higher vegetation. This reduces the sites' suitability for breeding lapwings as described earlier and, consequently, may result in lower breeding densities in lapwings over time (Breeuwer *et al.* 2009). The corresponding equivalents for crop fields are the "lapwing plots". These are areas of up to 2 ha within a crop field which "remained fallow or were sparsely sown with a grass–clover mixture", combined with a marking procedure for nests found on the surrounding cropland (Buschmann et al. 2023).

In areas where ground-bound predators like foxes are the main predators of clutches and chicks, physical exclusion of those predators may improve reproductive success. This requires any agricultural procedures inside the barrier to be adapted to the breeding schedule (Korner *et al.* 2024). The exclusion can be achieved with a constructed barrier, which may be electrified (Verhoeven *et al.* 2022). Smaller and more nimble predators, such as mustelids, may still pass through such barriers (Verhoeven *et al.* 2022). Therefore, it's critical to assess which predators are locally responsible for depredations before putting costly barriers in place.

An alternative strategy to reduce predation risk for breeding lapwings has been lethal predator control. Targeted killing of predator species of waders — predominantly foxes and crows — has been studied, with mixed results even within single studies (Bolton *et al.* 2007b). In a successful case, lethal predator control on three moorland plots in the UK (between 9.3 – 14.4 km^2 each) achieved increased hatching success for ground-nesting birds, and an increased raptor abundance (Fletcher *et al.* 2010). This required a yearly lethal control of between 40 and 100 foxes, 80 and 400 crows, and 20 and 200 weasels per plot through year-round culling by a pair of game-keepers (Fletcher *et al.* 2010). Weasel activity was not affected by culling, but crow and fox abundances were reduced in years with control, and recovered on the plot where culling was halted (Fletcher *et al.* 2010). In another case, on a Northern-Irish island, removals of all ferrets (*Mustela furo*) and almost all territorial crows had no measurable effect on hatching or chick survival rates (Bodey *et al.* 2011).

Local predator control may result in knock-on effects to the predator community. In both island and mainland cases, predators may migrate to fill the empty territorial niches left by the deceased (Bodey *et al.* 2011, reviewed in Jiguet 2020). This wave of migrations can result in increased disease transmission (Jiguet 2020). Smaller predators may become emboldened when their larger rivals are lethally removed from the area (Brashares *et al.* 2010, Takimoto & Nishijima 2022), and local populations of small rodents may increase when predation pressure is reduced. These larger rodent populations may attract different predators, which can be dangerous for lapwings (e.g. the increase in raptors in Fletcher *et al.* 2010). Small rodents may compete with lapwings for access to soil invertebrates *(Abt & Bock 1998*, Ausden *et al.* 2003), reducing habitat quality.

To determine the correct response to observed depredation rates, the predators involved should ideally be identified to the level of species or individual. Several methods may be employed to accomplish this: 1) Inspection of egg remains for teeth or beak marks, 2) Timing of the predation with thermologgers, 3) Direct observations by researchers , 4) Direct observation of the event by means of a nest camera (Bellebaum & Boschert 2003, Bolton *et al.* 2007a, Teunissen *et al.* 2008).

Each of these methods has advantages and disadvantages. Inspection of egg remains is the least invasive, as it can take place entirely after incubation, but depredations often result in the complete absence of eggs (and thus evidence, Bellebaum & Boschert 2003). Timing depredations with thermologgers can determine the timing of nest depredations with a high degree of accuracy, which allows a distinction between nocturnal and diurnal predations (Bellebaum & Boschert 2003). Nocturnal depredations are almost entirely perpetrated by mammals (Teunissen *et al.* 2008). However, species-level determinations can't be made, and diurnal predators may be avian as well as mammalian (Bellebaum & Boschert 2003, Mason *et al.* 2018). Direct observations by researchers can provide reliable eye-witness evidence, but are too labour-intensive. Nest cameras can record depredations at a species level (Bolton *et al.* 2007a, Teunissen *et al.* 2008), but their effect on the behaviour of predators is uncertain: predators may be attracted to the nest site by the presence of a camera (O'Donovan & Boyce 2021), or show a neophobic response (Séquin *et al.* 2003). Other studies find no measurable effect of camera placement on nest survival rates (Galbraith 1987, Stien & Ims 2016, Zámečník *et al.* 2018, Salewski & Schmidt 2022). A further obstacle to accurate identification of predators is the problem of chronology: once the researcher shows up to the nest site, the depredation event has already occurred. It can't always be determined whether the depredation was preceded by nest abandonment. Similarly, nests apparently "lost to agricultural procedures" may have been depredated, before the relevant evidence subsequently disappeared under the machinery. Nest cameras, which can record the events leading up to a depredation as well as the event itself, are likely more accurate in this regard (Teunissen *et al.* 2008, Ellis *et al.* 2018).

As wet features and high water tables improve feeding efficiency for both adult and hatchling lapwings, the addition of new wet features at the breeding sites has been proposed as a habitat improvement measure (Eglington *et al.* 2010). Wet features may be achieved by pumped irrigation, landscape modification (digging), or water table control (as accomplished with sluices and ditches, Eglington *et al.* 2009a, Visser *et al.* 2017). However, a large-scale deployment of wet features in the Netherlands showed mixed effects on lapwings' productivity (Melman *et al.* 2020). The equivocal outcome was explained partially by a mixed effect on vegetation growth (vegetation growth slowed in some sites, but actually increased in others, Melman *et al.* 2020). Results may also have been affected by the presence of mustelids, which can easily cross water bodies to predate lapwing nests (Bellebaum & Bock 2009, Melman *et al.* 2020). While lapwings are clearly attracted to wet features when choosing nesting sites (Eglington *et al.* 2008), it is important to ensure that the habitat to which they are attracted remains suitable until fledging.

At fields with fast vegetation growth, the correct vegetation structure for breeding lapwings may be achieved by increasing grazing pressure (Franks *et al.* 2018). However, care should be taken regarding the densities of livestock due to the added risk of trampling (Sharps *et al.* 2017, Franks *et al.* 2018). Assuming inaction by the parents, cattle densities of only 1.5 head of adult cattle per hectare would result in 50% clutch loss (Sabatier *et al.* 2015).

In summary, there are multiple proven methods of increasing Northern Lapwing hatching and fledging success. However, whether applying any of those methods actually improves the situation, or whether it will instead be counter-productive, depends on the local situation. To determine the best course of action, it's possible to use data on vital rates to perform population viability analyses. These analyses can predict future population dynamics, and outline which vital rates should be improved through conservation action to improve the situation (Plard *et al.* 2020). Such an analysis can then be improved by making it spatially aware, using known information about available habitat and its quality, and adding an accounting of the cost of proposed measures (Buschmann *et al.* 2023). With such a model in hand, a clear message can be delivered to decision makers, on the basis of which they can take action. However, these models must rely on accurate information about the reproduction and survival of the species at the location of interest.

4) Outline of the Thesis

We have just learned that the Northern Lapwing is in population decline all over Europe, that it breeds over a wide area, in varied habitats, and that serious action has to be undertaken in order to halt or reverse the population decline. Conservation measures have to be adapted to fit the local situation. In some specific cases, the best thing for the population is to not intervene at all (Goedhart *et al.* 2010). The keystone of any effective conservation action is local knowledge.

In France, a lapwing population decline has been ongoing for several decades (Spitz 1964 *in Joyeux et al. 2022*, Dubois *et al.* 1991, Dronneau 2007, Caupenne & Trolliet 2015 *in Issa & Muller 2015*). Lapwings breed across the country, with the majority breeding north of a diagonal that runs roughly from Bordeaux in the south-west to Lyon in the south-east (Joyeux *et al.* 2022).

In this thesis, I set out to investigate the breeding ecology of Northern Lapwings in two regions of France, Alsace and Hauts-de-France. Alsace, an inland region, has been reported to hold one of the most important breeding populations of lapwings in France (Spitz 1964 in *Joyeux et al. 2022*, Joyeux *et al.* 2022), but has seen a drastic drop in the number of breeding pairs over the last decades (Dubois *et al.* 1991, Dronneau 2007). In Hauts-de-France, a coastal region, very low productivity has been reported on crop fields (Triplet *et al.* 1997). Furthermore, a reduction in surface area dedicated to cattle-grazed pastures may have contributed to a decline in the number of lapwing breeding in grasslands (Triplet *et al.* 1997, 2004).

My aim was to determine whether the local lapwing populations were reproducing at a rate sufficient to sustain their numbers, which I expected not to be the case based on the reported figures for population decline and low breeding success. I was interested in investigating which local factors might be limiting their breeding success, and whether there might be any special influences of the French meteorological conditions on their breeding success.

Chapter I. Effects of Weather and Inter-regional Differences on the Nest Survival of Northern Lapwings.

In the first chapter, we address the question of whether local conditions in Alsace and Hauts-de-France can explain local populations' hatching success rates. These two regions represent two ends of a coastal-continental climate gradient that runs across the longitude of mainland France (Planchon 2000). If nest survival rates are predictable over time or climate, or depend strongly on particular predators, this could inform effective conservation actions. The last two decades have been marked by continuing changes to lapwings' breeding habitat, including shifts in crop types, intensification of agricultural practices, and increasingly obvious consequences of climate change (Schott *et al.* 2010, Caubel *et al.* 2018, Mittelberger *et al.* 2024). These changes may have affected the reproductive success of local lapwings. Nest survival is the most straightforwardly measurable component of reproductive success as a whole, as a function of the required complexity and scale of fieldwork. Thus, the first section of the thesis is focused on quantifying the nest survival rates in these two regions as a function of their local conditions. To address this objective, we conducted weekly visits at lapwing nests in the two regions, placed nest cameras at a subset of nests to determine their outcomes with high accuracy, and left the others without a camera to assess the effect of camera placement on nest survival rates.

We expected to find reproductive success primarily limited by a combination of depredation and agricultural procedures, as is the case for lapwing populations breeding across Europe. We predicted that Alsace would show lower breeding success, as the population in the region has declined substantially in recent decades. We predicted that high temperatures and dry conditions would lead to increased nest failures, and that camera-equipped nests would show different nest survival rates from control nests.

Chapter II. The Response of Northern Lapwings to Human Disturbance at Their Nests Depends on Weather Conditions and Incubation Stage.

In the second chapter, we address the responses of lapwings monitored by nest cameras to the repeated visits of scientists at their nests, and how these responses relate to environmental conditions at the nest site. Over the course of the fieldwork for the first chapter, I became increasingly interested in the responses of the lapwings to the cameras placed close to their nests and the repeated visits to which they were subjected. In some cases, after placing cameras by their nests, lapwings returned within minutes and started to cautiously inspect the new addition to the environment. They might circle the nest and camera at a distance of <10 m for as long as we had the time available to observe them, or settle onto the nest relatively quickly. For those who will implement conservation measures in the field, it will be important to know the potential impact of their presence and their conservation measures on the lapwings' behaviour.

Thus, I investigated the durations of adult lapwings' absences from the nest after our weekly visits, and how they related to environmental conditions. We expected to find lapwings returning more quickly in the later stages of the clutches' development, faster returns later in the breeding season, and for lapwings to habituate to the repeated visits.

Chapter III. Thermoregulatory Behaviours of Northern Lapwings During Incubation in Warm Weather.

In the third chapter, we address lapwings' tolerances for high temperatures at the nest sites. Extreme weather events have become more common across Europe, including France (Brás *et al.*, 2021), with potential impacts on habitat suitability. These weather events are expected to occur more frequently and with greater amplitude in the future (Guerreiro *et al.*, 2018).

Over the course of this thesis, lapwings faced local air temperatures of up to 40°C in 2021, and the overall exceptionally dry and warm breeding season of 2022 (Mittelberger *et al.* 2024). These extreme weather events provided the opportunity to investigate how lapwings cope with high ambient temperatures at their nest sites during the incubation period. If lapwings reach the limits of their thermoregulatory capacity under current conditions, then we might expect a shift in breeding range or phenology when large parts of Europe continue to warm in coming decades (Rowell 2005). We expected lapwings to be more vulnerable to high temperatures and drought, showing more thermoregulatory behaviours at lower temperature limits than related species from more arid habitats (e.g. Snowy Plovers (*Anarhynchus nivosus*) and Crowned Lapwings, Purdue 1976, Smit *et al.* 2016).

Chapter IV. Synthesis.

In the final chapter of this thesis, I will consider how the results of my separate studies relate to one another, which future avenues of research into lapwing breeding ecology might be worth further investigation, and how much of my findings might be generalized to other species breeding in similar habitats. Finally, I will discuss perspectives on future conservation measures that might be undertaken in the two regions that have been the focus of this thesis, and potential implications for conservation measures elsewhere.

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General Material and Methods

1) Field Sites

Fieldwork for this thesis was performed in two regions of France: Alsace and Hauts-de-France. More accurately, fieldwork took place primarily on the coasts of the French departments of Somme (department number 80) and Pas-de-Calais (62), spread over an area of 596 km2. In Alsace, the fieldwork covered mostly the plains and rolling hills of the department of Bas-Rhin (67) and only the northern tip of Haut-Rhin (68), spread over an area of 1111 km2 (**Figure 3**).

During 2021, a single field team visited sites on both sides of France, as well as a third department (Ardennes). This resulted in field sites in Hauts-de-France being clustered around the southern coast of Pas-de-Calais for that year. During 2022, two separate field teams were active in Pas-de-Calais and Alsace, allowing for better coverage in both regions.

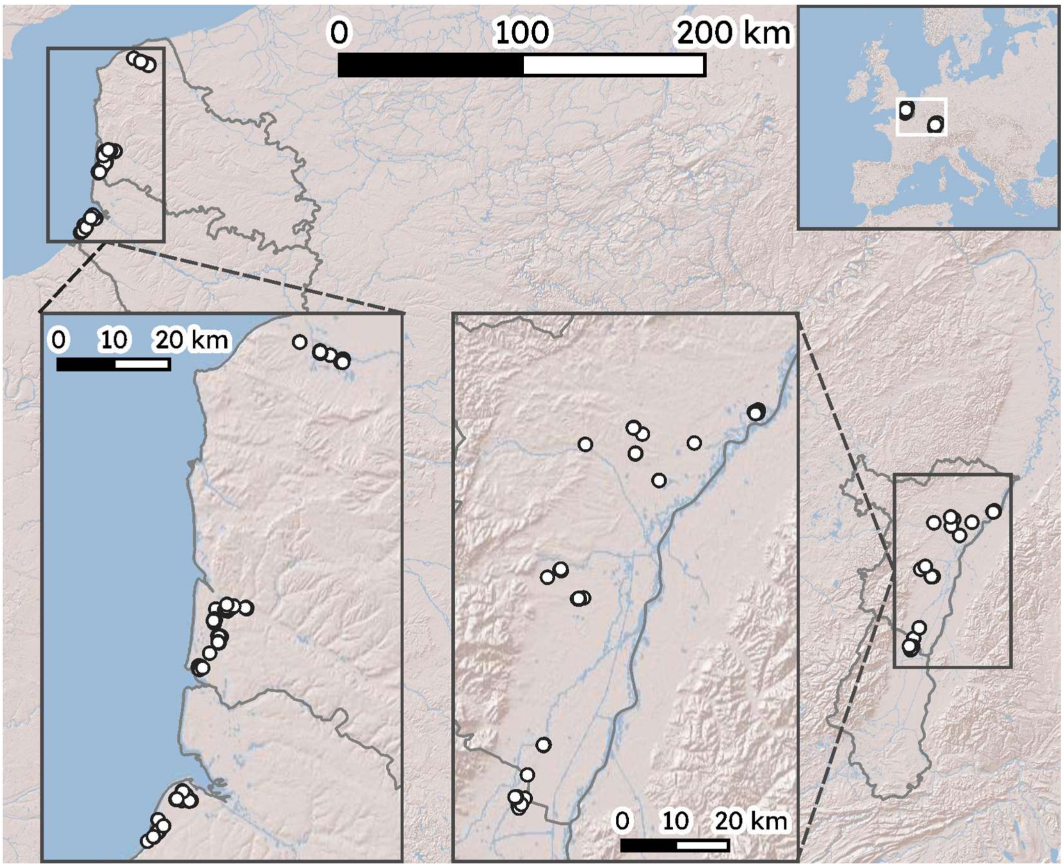

Figure 3: *Locations of monitored nests in France. Nests were not equally distributed over the total area of the departments (administrative regions). Map image tiles from the ESRI shaded relief map.*

In Alsace, we located potential lapwing nesting sites using three methods. First, we located nests using the online portal faune-france.org, which allows anyone to submit sightings of animal species including details such as location, behaviour, and likely breeding status. Based on historical as well as recent data, likely lapwing breeding sites were located and subsequently checked by the field team. Second, the local branch of the *Ligue pour la*

Protection des Oiseaux (LPO), a bird conservation NGO, is running a limited nest marking program in Alsace. They would occasionally provide locations of breeding lapwing, and cooperate on the field. Third, interested parties would occasionally remark about potential nesting sites (word of mouth).

In Hauts-de-France, we located lapwing nesting sites based on three methods as well. Similarly to Alsace, we located some nesting sites using faune-france.org. Second, the local hunters' associations of Pas-de-Calais and Somme lent their local connections among landowners to the project (facilitating access to the fields and to privately owned wetlands). Third, word of mouth tips from locals, including farmers, naturalists, and others. Occasionally, local naturalists would point to local farmers, who in turn pointed to colleagues, creating a chain of recommendations.

2) Monitoring Methods

After locating the nests on the fields, we followed nests using two methods. First, some nests were followed by visits only. This involved a unique identification code for the nest based on its region of origin and finding order, a record of its GPS coordinates, and a count of the number of eggs in the clutch. In 2022, we refined this protocol by additionally floating a single egg in each clutch for the first visit only (Van Paassen *et al.* 1984), to determine the age of the clutch when it was found. During the second field season we also took photos of every nest from a top-down angle at a height of 1.5 m for every week of monitoring (**Figure 4**).

Figure 4: *Top-down photo of a 4-egg lapwing clutch with reference object in a grassland habitat. Pictured also are the 1.5 m long reference stick which would ensure that the photo was taken at approximately the same height for every nest, and the author.*

The second monitoring method involved nest cameras. This method could only be applied on the subset of fields for which landowner approval was obtained. We placed the nest cameras (Victure HC300) at 2 m distance from the nests. Each camera was mounted on a pole 1 m tall and 6 cm in diameter, and each pole was topped with bird spikes to prevent perching by potential nest predators (**Figure 5**). Because of concerns that the sun passing directly in front of the camera would obscure midday and evening footage, we usually placed cameras facing between North-North-East and East. If we predicted that crops would grow in front of the camera before the end of incubation, we prioritised a clear field of view over sun-related concerns.

Figure 5: *Setup of a trap camera at a lapwing nest. Nest in the top-right with a color reference object. Camera posts featured anti-perching spikes to prevent use as perching spots by potential predators.*

Nest cameras came equipped with motion sensors, and we configured them to activate when these were triggered. We set cameras to take a photo and then record 30-second videos (**Figure 6**), because the initial response of a lapwing to a predator may be to quit the nest. Based on preliminary testing of the cameras, this would cause the camera to activate, and we estimated that 30 seconds would be long enough to capture a subsequent predation event. Data storage consisted of 128 GB memory cards, which we reformatted to work with the data storage compatibility of the nest cameras. This may have caused several cases of data corruption as the cameras were rated for a maximum storage of 32GB, but allowed us to visit the nests only 1/4th as many times as would have been needed with smaller memory cards. We replaced camera batteries on every visit, to prevent a degradation of the cameras' performance due to low voltages.

Figure 6: *Photo of a lapwing at its nest, which is obscured by vegetation. Photo taken by a nest camera at a wetland site in Hauts-de-France.*

Under both monitoring methods, monitoring continued until the nest's outcome could be clearly identified as hatched or failed. Because we did not observe all camera footage just after obtaining it, but usually many months afterwards, this meant that we followed some abandoned nests for several weeks after the parents halted incubation. We considered a nest as failed if the eggs disappeared with no obvious traces before the expected hatching date, or if the soil around the nest was disturbed by farming equipment. At nests where we found egg traces, we considered nests as hatched if the nest lining was littered with tiny egg shell pieces (Mabee *et al.* 2006, Thorup 2022). Large chunks of shell found close to the nest were considered sure signs of nest depredation (Bellebaum & Boschert 2003). Chicks observed in the nest cup were considered to have hatched inside. Chicks observed in the general area could not always be clearly assigned to a particular nest. For nests monitored by camera, we observed footage for signs of the nest outcome, including chicks in the nest cup or the appearance of known nest predators.

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Chapter I:
Effects of Weather and Inter-regional Differences on the Nest Survival of Northern Lapwings

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Abstract

Northern Lapwings (*Vanellus vanellus*) have been in a decades-long population decline in western Europe. A majority of field studies have shown that declines are more likely to be explained by low reproductive rates than by low adult survival rates. We assessed the most pressing threats to successful breeding of lapwings in their core breeding range in France, which hosts thousands of lapwing breeding pairs. We monitored nests of lapwings with nest cameras and weekly visits during the 2021 and 2022 breeding seasons in Alsace (an inland region of eastern France) and Hauts-de-France (along the English Channel coast in northern France). We compared nest survival rates between years and regions, and examined the effects of the microclimate at the nest on daily nest survival. Nest survival was high overall and at least 66% of nests successfully hatched and produced nestlings. We found that nest survival rates were lower in Alsace than Hauts-de-France, especially when wind speeds at the nest sites were lower. Nests equipped with pole-mounted cameras unexpectedly had higher rates of nest survival, particularly in Alsace. About a third of nests failed and the main causes of failure were damage by agricultural equipment (11%), abandonment (8.2%), and losses to predation (7.5%). Losses to agricultural practices were more common in Alsace than in Hauts-de-France. Where nest predators could be determined from camera images, mammals were responsible for all but one predation event. Our study suggests that reproductive success of lapwings in France could be increased by limiting losses due to agriculture practices through nest marking or by using fences or nest cages to reduce losses to mammalian predation.

Keywords: Agriculture, Camera trap, Hatching success, *Vanellus vanellus*, Waders

1) Introduction

Waders are an ecologically diverse group of birds in the order *Charadriiformes,* and about 59% of species show declining population trends (Koleček *et al.* 2021). Many waders are migratory and can breed over a large range. Thus, they are exposed to a variety of environmental conditions during both the wintering and breeding seasons, potentially increasing their vulnerability at a species level (Thomas *et al.* 2006). During the breeding season, waders can be found in various habitats including farmland (Jóhannesdóttir *et al.* 2018), which exposes them to human influences during their breeding season, particularly when agricultural practices demand frequent work on the fields (Kragten & De Snoo 2007, Sheldon *et al.* 2007). In terms of their population dynamics, adult survival rates appear to be relatively stable over time while reproductive rates are broadly assessed as insufficient to support their populations (Roodbergen *et al.* 2012, Souchay & Schaub 2016, Franks *et al.* 2017, Plard *et al.* 2020, Ewing *et al.* 2023). The most prominent causes of low reproductive rates have been identified as habitat loss (Leyrer *et al.* 2018), agricultural intensification (Donald *et al.* 2006), and depredation of eggs and chicks (MacDonald & Bolton 2008, Eglington *et al.* 2009).

In addition to anthropogenic and biotic factors, abiotic factors may also affect reproductive rates. In the warmer parts of their breeding range – which extends south to Morocco (Cherkaoui & Hanane 2011) – Northern Lapwings (*Vanellus vanellus*) may reach a temperature threshold, where costs associated with thermoregulation (Van De Ven *et al.* 2019) outweigh the fitness benefits of continuing a breeding attempt. If environmental conditions exceed the critical threshold, nests are predicted to be abandoned by the attending parents (Sharpe *et al.* 2019). Shorebirds can behaviourally compensate for higher temperatures using wet features of the environment (Ryeland *et al.* 2021), but access to water is not always available. In addition to water, wind can provide a source of cooling, as demonstrated by the Crowned Lapwings (*Vanellus coronatus*) of South Africa that stand above their eggs to cool down (Brown & Downs 2003). We can expect bird use of breeding sites to match a hypothetical optimal environmental niche (Hirzel & Le Lay 2008), outside of which breeding success is expected to be limited.

It is essential to understand local drivers of low reproductive rates to devise an optimal conservation strategy, because the biotic and abiotic drivers of demographic rates likely vary by location. In France, the size of the breeding population of Northern Lapwings (hereafter 'lapwing') has been reported as between 12,000 to 18,000 pairs in 2011 (Caupenne & Trolliet 2015 in Issa & Muller 2015), down from an estimate of 31,450 - 45,240 pairs in 1964 (Spitz 1964 *in* Joyeux *et al.* 2022). However, detailed information on reproductive success is not available. Environmental conditions have likely changed since the peak in population numbers during the 1960's. For example, surveys of red fox (*Vulpes vulpes*) populations in France indicated an increase in nation-wide population numbers between 2003 and 2013 (Ruette *et al.* 2015). France has also lost millions of hectares of grassland in the last decades, and continues to experience shifts in crop types and sowing dates (Schott *et al.* 2010, Caubel *et al.* 2018), which may lead to changing conflicts between nest construction by lapwings and the activities of farmers (Santangeli *et al.* 2018).

In this study, we conducted a detailed investigation of lapwing nesting success in two regions of France which represent a gradient across a coastal-continental climate spectrum. Lapwing populations have declined in the continental region of Alsace over the last decades (Dubois *et al.* 1991, Dronneau 2007), but trends are unclear for the coastal region of Hauts-de-France. Our three main objectives were to: 1) identify the primary causes of nest failure and estimate rates of nest survival in each region; 2) evaluate the potential effect of daily weather conditions on nest survival rates; and 3) assess the local impact of nest marking on nest survival rates. To address our objectives, we monitored nests with nest cameras and through repeated visits, evaluated local microclimatic conditions through modelling, and constructed nest survival models incorporating the effects of local conditions.

If the factors driving reproductive output in lapwings are similar to other waders nesting in agricultural systems, we predicted: 1) the majority of nest losses would be caused by a combination of predation and agricultural procedures, with a lower rate of nest survival in Alsace, where local populations have shown a decline (Dubois *et al.* 1991, Dronneau 2007); 2) a lower rate of nest survival on days without rain and days with high temperatures; 3) differences in the cause-of-loss for nest failures between nests equipped with cameras versus control nests. We expected that predators might either learn to associate nests with their markings, or conversely might avoid the novel objects in their habitat.

2) Materials & Methods

2a) Study species

The Northern Lapwing is a characteristic species of wader breeding in open habitats with short vegetation or bare ground in western Europe. Like many waders breeding on farmland, lapwing populations have been in a slow rangewide decline for multiple decades (Deceuninck 2001, Taylor & Grant 2004, Wilson *et al.* 2005, Lislevand *et al.* 2021, Joyeux *et al.* 2022). France is no exception to this trend, showing a decline in breeding pairs of up to 60% between 1964 and 2011 (Caupenne & Trolliet in Issa & Muller 2015, Spitz 1964 in Joyeux *et al.* 2022). At a regional level, some subpopulations decreased by as much as 90% between the 1960's and the 1980's, while in others the patterns of decline were more limited (Dubois *et al.* 1991). Surveys of breeding lapwings in the 1990's along the channel coast of northern France noted that crop fields were often used as nesting sites but showed low rates of fledging (Triplet *et al.* 1997).

Lapwings are semi-colonial breeders, with individual colony members participating in shared nest defence behaviour, particularly against avian predators (Elliot 1985). Lapwing eggs may be depredated by a variety of predators, including small mammals such as brown rats (*Rattus norvegicus*) and European hedgehogs (*Erinaceus europaeus*) or mesopredators such as red foxes, European badgers (*Meles meles*), and golden jackals (*Canis aureus*, Bolton *et al.* 2007b, Teunissen *et al.* 2008, Rickenbach *et al.* 2011, Männil & Ranc 2022). Avian predators of eggs during incubation include various species of gulls and corvids (Elliot 1985, Bolton *et al.* 2007b, Teunissen *et al.* 2008, Królikowska *et al.* 2016), whereas raptors are more likely to depredate chicks during the brood-rearing period (Teunissen *et al.* 2008, Królikowska *et al.* 2016).

2b) Field sites

We conducted regional surveys for nesting pairs of Northern Lapwings during the breeding seasons of 2021 and 2022 in two regions of France: the western region of Hauts-de-France (HdF) and the eastern region of Alsace (Alsace) (**Figure 7**). Surveys in Hauts-de-France occurred primarily in coastal flatlands whereas the Alsatian surveys occurred primarily in the Rhine river valley. Nests in Hauts-de-France were found in a 596 km^2 area (Minimum Convex Polygon (MCP) of nests found) whereas nests in Alsace were located within a 1111 km^2 area (MCP of nests found). The two regions are 500 km apart and separated by the Vosges mountain range. Surveys took place between 6th of April and the 20th of July in 2021 (106 days), and between 15th of February and 29th of June in 2022 (135 days).

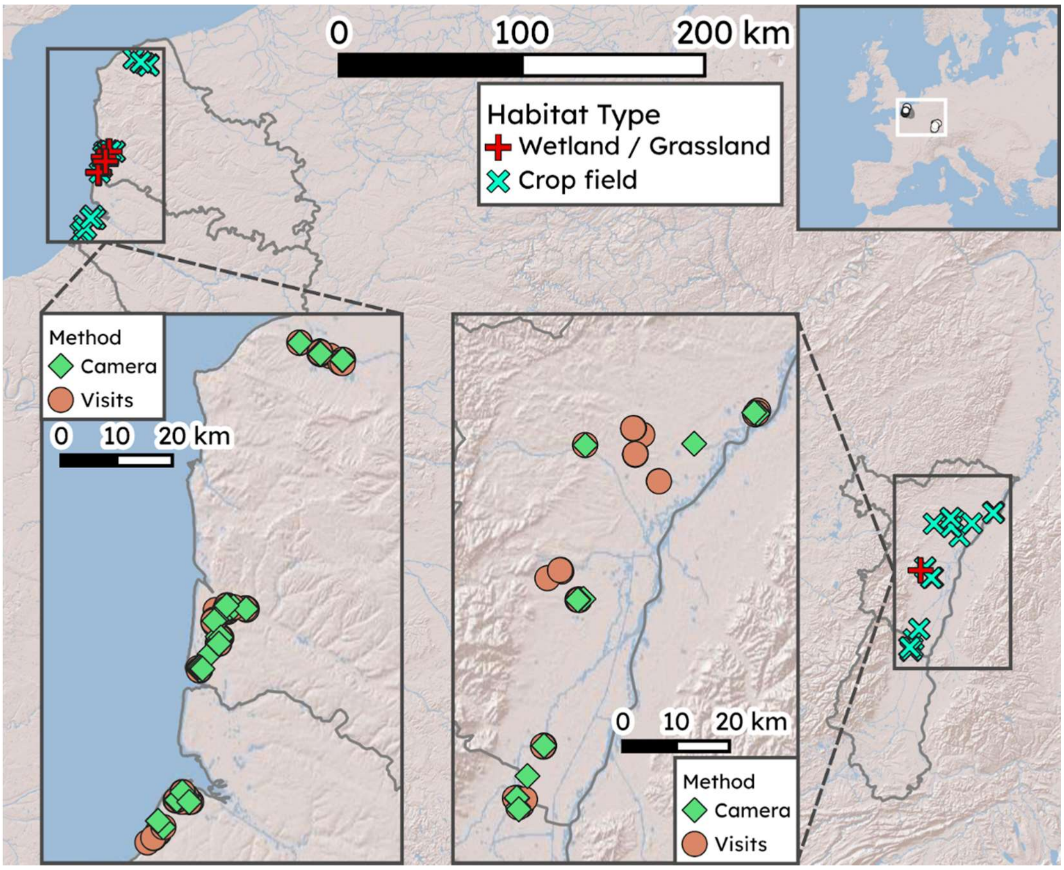

***Figure 7:** Locations, habitat, and monitoring method for lapwing nests in two regions of France, 2021-2022. Red pluses and cyan crosses indicate habitat type as wetland or croplands, whereas green diamonds and orange circles indicate whether the nest was monitored by camera or by visits only. Map image tiles from the ESRI shaded relief map.*

2c) Nest monitoring

Lapwings were located by observing birds with binoculars and a spotting scope, as well as naked eye observations and auditory cues. Birds' breeding status was assessed based on their behaviour: territorial males performing display flights and ground displays were used to locate the nesting sites (Rinkel 1940). Large flocks of densely spaced lapwings, on the other hand, were considered non-territorial groups.

Having approximately located habitats containing territories of breeding males, we then searched for lapwing nests within the territories. Potential nest locations were approached on foot for confirmation. At each identified nest, we recorded its GPS coordinates, the number of eggs in the clutch, and took a picture at a height of 1.5 m from a top-down perspective. Monitored nests were visited on a weekly basis to determine nest fate during the incubation period. Nest cameras (Victure HC300) were placed at 2 m distance from the nests with landowners' approval.

The cameras were configured to trigger based on motion, taking an initial photograph as well as a 30 second video. Photo and video footage was then used to verify nest fates. If footage was unavailable, we relied on direct observations of chicks around the nest cup as well as indirect assessments of nest fate. When small eggshell fragments were found in the nest lining, clutches were considered as successfully hatched (Mabee *et al.* 2006, Thorup 2022).

If at least one egg hatched and produced a chick, a nest was considered to be successful. A nest was considered to have failed if the eggs disappeared before the expected hatching date or if the soil around the nest was disturbed by farming equipment. Clutches of lapwings were monitored until the outcome of the incubation attempt could be established as either failed or hatched.

2d) Weather parameters

To obtain information on local weather conditions, we used the R package *NichemapR* (Kearney & Porter 2017), which uses a combination of historical satellite weather data and geographical data to estimate weather conditions over time for any given location on Earth. The estimates are provided on an hourly basis, using weather parameters interpolated from 6-hourly source data. We relied on the ERA5 dataset for our microclimate modelling (Hersbach *et al.* 2020), as implemented through the function *micro_era5* of the R package *NichemapR* (Klinges *et al.* 2022), which itself relies on functions from the package *microclima* (Maclean *et al.* 2019).

We estimated weather conditions for every nest over the entire span of the breeding season. For our analysis of nest survival, we used five different variables: i) air temperature at 1 cm above soil surface, ii) soil surface temperature, iii) wind speed at 1 cm above surface, iv) daily rainfall, and v) solar irradiance. The last two variables were not hourly but were extracted as daily totals. We extracted daily means, maxima, and minima for each variable where available, for use as potential daily covariates in a nest survival model.

2e) Statistical analysis

Statistical analyses were performed in *R version 4.2.2* (R Core Team 2022). We compared the available environmental variables between our two regions, by modelling each variable in a linear model featuring the region and progress into the year as fixed variables and the date as a random variable.

2e.1) Incubation failure causes

To determine whether there were any differences in nest fates between regions, we ran a pair of Fisher's Exact Tests from the base R package *stats* (R Core Team 2022). We ran the analysis for the full dataset and again for the subset of nests that were monitored by camera. The camera dataset provides direct information on failure causes, while the causes of failures for "visits only" nests were inferred from signs at the nest site.

We assessed any determined differences on a category-by-category basis using Holm-Bonferroni-corrected post-hoc tests using the function *row_wise_fisher_test* from the package *rstatix* (Kassambara 2023).

Potential differences in the timing of nest fates were estimated with a gaussian linear regression from the base R package *stats* (R Core Team 2022), modelling the day the clutch was last observed active as a function of its fate. We calculated post-hoc contrasts using the package *emmeans* (Lenth 2023).

2e.2) Nest survival modelling

For our analyses of daily nest survival, we used the MARK implementation of nest survival models (Dinsmore *et al.* 2002), using the R package *Rmark* as an interface (Laake 2013). The method allowed us to model daily nest survival rates based on the number of 'exposure days' over which they were monitored: the number of days during which we may consider the nests at risk of failure.

Nests were considered at risk of failure from the first day they were discovered with eggs (*i*). We then recorded the last day on which the nest was known to be active (*j*), and the final day that the fate of the nesting attempt was confirmed to be completed (*k*). In the case of a successful nesting attempt, *j* and *k* were identical (observation of hatched chicks), whereas in the case of unsuccessful nests, *j* was lower than *k* (nest last observed in a state of failure). For failed nests, the probability of being destroyed within the interval between *j* and *k* is accounted for in our estimate of exposure as '*1 - probability of surviving between j and k'*, as a single estimate, while the period of known survival between *i* and *j* is handled identically for successful and failed nests as the product of the probability of surviving each consecutive day (Dinsmore *et al.* 2002).

We also assigned each nest its environmental variables, which could be dynamic and different for each day of the breeding season, or static if they remained the same for the entire breeding season, such as the region and year.

Nest survival modelling proceeded in four steps: variable selection, model building, model selection, and parameter estimation. During variable selection, we used pairwise comparisons to test for collinearities among available microclimate variables such as mean soil temperature, maximum soil temperature, and mean wind speed. We considered relationships as correlated strongly enough to warrant exclusion at r values greater than |0.65| (Dormann *et al.* 2013). When two or more variables were strongly correlated, we chose to include the variable which we judged to be most directly ecologically relevant.

We used a model building procedure where we simulated every model that was nested within the top-level (global) model. We defined the top-level model as the model predicting daily survival rates (S) from all grouping variables and the selected environmental variables (**Formula 1.1**), as well as potentially ecologically relevant interaction effects. We considered five grouping variables: habitat type (crop fields / other), year (2021 / 2022), region (Alsace / Hauts-de-France), clutch size (<4 / 4 eggs), and monitoring method (camera / visits).

In addition to the main effects, we considered three possible interactions among the factors that were relevant to our study system. We expected there might be an interaction between mean soil temperature and mean wind speed if the convective cooling effect of higher wind speeds was more important for birds experiencing higher (soil) temperatures, and vice-versa for lower temperatures (Bakken *et al.* 2002, Reid *et al.* 2002).

We considered an interaction effect between region and wind speed because there might be overall climatic differences between the two regions: our exploratory analysis showed that the correlation between wind speed and soil temperature was different for the two regions.

Last, we considered an interaction between the monitoring method and the region of origin as nests without a camera might be exposed to different baseline risks depending on the region. Our global model for nest survival was given by the following expression:

Formula 1.1:

Nest Survival ~ Habitat Type + Year + Eggs in Clutch + Daily Rainfall + Total Solar Irradiance + Mean Daily Soil Temperature*Mean Daily Wind Speed + Region*Mean Daily Wind Speed + Previous Day's Mean Daily Soil Temperature + Previous Day's Mean Daily Wind Speed * Mean Daily Wind Speed + Region*Monitoring Method + Days Into the Season

Model selection was initially based on the differences in AICc scores ('*Akaike Information Criterion',* Sugiura 1978, Akaike 1998) among the candidate models. For interpreting whether individual parameters inside models might be uninformative relative to the rest of the model we relied on 95% Confidence Intervals of each separate variable within a model on the logit scale. Program MARK does not provide p-values for coefficients of the nest survival models, instead we considered parameters as weakly predictive of our response variable if the confidence interval of the estimated effect overlapped 0. The test could be considered as equivalent to a p-value relative to a "no-effect" null hypothesis above 0.05 (Tan & Tan 2010). In a model for which every variable's CI overlaps 0, each individual variable was at best weakly predictive of our response variable. Thus, we excluded any models for which the 95% confidence intervals for the variable estimates of all variables overlapped 0. We did not exclude models with at least one 'significant' predictor (95% confidence interval of the estimated effect does not overlap 0).

Of our remaining models, we considered the best-fit model to be the model with the lowest AICc score, indicating the best balance between explanatory power and variable count. Models within 2 ΔAICc of the best-fit model were considered 'candidate models' and checked for parsimony improvement over the nominal 'best-fit' model. All alternative candidate models within 2 ΔAICc of the best-fit model included at least one additional parameter, and were rejected due to reduced parsimony over the best-fit model (**Table 2**). We used only our best-fit model for inference, excluding from our interpretation the models which differ from the min-AICc model by adding one uninformative parameter (Arnold 2010).

Table 2: *All models within 2 AICc of the best-fit model, and the intercept-only model. Values in columns 2 through 12 indicate variables included in the models, in which case the slope estimate is provided on the logit scale, or its absence from the model (NA). Bolded values followed by an asterisk (*) indicate variables for which the 95% confidence interval does not include 0 ('Informative variables'). Variables include: whether a camera was placed at the nest (Camera), whether the region in which the nest was found was Alsace or Hauts-de-France (Region), an interaction effect between Camera and Region, soil surface temperature in degrees celsius (Soil Temperature), wind speed at 1 cm above surface in m/s (Wind Speed), daily rainfall in mm (Rainfall), progress into the breeding season in days (Season), solar irradiance at the surface in* Wm^{-2} *(Solar Irradiance), the interaction effect between soil temperature and wind speed (Temperature:Wind), and an interaction effect between Region and Wind speed. The final five columns indicate the degrees of freedom in the model (df), log-likelihood of the proposed model (logLik), AICc score (AICc), difference in AICc score between the proposed model and the best performing model (Delta), and model weight relative to all proposed models (Weight). Model weights were calculated on the full exhaustive model list before removing uninformative or collinear models from consideration, and so is considerably deflated. None of the top model candidates included the categorical variables 'Number of eggs in the nest', 'Habitat type', or 'Year'.*

Model	Intercept	Camera	Region	Soil Temperature	Wind Speed	Yesterday's Temperature	Yesterday's Wind Speed	Rain	Season	Solar Irradiance	Camera : Region	Region : Wind	Wind : Yesterday's Wind	df	logLik	AICc	Delta	Weight
Top fitted	-1.013	**1.931***	**1.700***	NA	1.905	NA	**7.732***	NA	NA	NA	**-1.708***	NA	**-5.741***	7	-165.626	345.309	0	0.198
2	-0.918	**1.965***	0.347	NA	0.825	NA	**9.438***	NA	NA	NA	**-1.737***	3.020	**-8.119***	8	-164.935	345.942	0.634	0.144
3	-1.043	**1.889***	**1.655***	NA	1.639	NA	**7.839***	0.060	NA	NA	**-1.658***	NA	**-5.597***	8	-165.126	346.326	1.017	0.119
4	-2.093	**1.894***	**1.604***	0.037	2.694	NA	**8.391***	NA	NA	NA	**-1.657***	NA	**-6.543***	8	-165.128	346.329	1.020	0.119
5	-1.833	**1.877***	**1.597***	NA	2.200	0.031	**8.403***	NA	NA	NA	**-1.640***	NA	**-6.159***	8	-165.207	346.488	1.179	0.110
6	-0.945	**1.914***	**0.284***	NA	0.600	NA	**9.542***	0.060	NA	NA	**-1.679***	3.077	**-8.089***	9	-164.421	346.933	1.624	0.088
7	-1.120	**1.884***	**1.649***	NA	1.960	NA	**7.780***	NA	0.003	NA	**-1.656***	NA	**-5.805***	8	-165.573	347.219	1.910	0.076
8	-2.152	**1.840***	**1.553***	0.038	2.455	NA	**8.510***	0.062	NA	NA	**-1.595***	NA	**-6.434***	9	-164.579	347.249	1.940	0.075
9	-0.860	**1.925***	**1.701***	NA	1.826	NA	**7.714***	NA	NA	-0.00002	**-1.701***	NA	**-5.666***	8	-165.613	347.299	1.990	0.073
Null model	**3.678***	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	1	-197.431	396.863	51.554	<0.001

We calculated the estimated probability of surviving the full average incubation period (27 days, Larsen *et al.* 2003) by combining daily survival rates for nests laid in either region (Alsace or Hauts-de-France) during either breeding season (2021 or 2022), under either monitoring method (Camera present / absent). We averaged values of mean daily wind speed for each combination of region and year, providing unique hypothetical average weather conditions for each day. We generated expected mean daily survival rates for these hypothetical weather conditions with our best-fit model. With the means and standard errors of these estimates we created 1000 bootstrap replicates for every day of the breeding season, for every combination of region and year (and only for the days where we followed nests in those combinations).

The chance to survive the full incubation period for a hypothetical nest that begins incubation on a particular day was then calculated from the product of the daily survival rate of its day of completion and the following 26 days (for a total of 27 exposure days), which results in a survival estimate which takes into account dynamically varying daily survival rates (Weiser 2021). Thus, we calculated estimates for every day until the 27th-to-last day for which we had followed nests in a particular combination of region and year. We used parametric bootstrapping based on 1000 iterations to obtain the variance and confidence intervals of the estimate. Bootstrap distributions were corrected by subtracting the difference between the mean of the bootstrap distribution from the expected mean based on the source data. Our 95% confidence intervals for the estimated mean probability of surviving incubation were the 2.5% – 97.5% interquantile-ranges of the corrected bootstrap distributions.

3) Results

3a) Nest monitoring

Of 184 nests found with eggs, we used 145 for our analysis. For 39 remaining nests (21% of nests), we could not accurately determine nest fate either due to a lack of the landowner's permission for observations or the absence of clues to determine the nest fates reliably. Of our 145 nests, 37 were located in Alsace (20 with a camera and 17 monitored by visits only) and 108 were located in Hauts-de-France (72 with a camera and 36 monitored by visits only). Of the nests in Hauts-de-France, 30 were found in the 2021 breeding season (26 with a camera and 4 with visits only) and 78 were found in the 2022 breeding season (46 with a camera and 32 with visits only). Of the nests in Alsace, 10 were found in the 2021 breeding season (6 with a camera and 4 with visits only) and 27 were found in the 2022 breeding season (14 with a camera and 13 with visits only). Over both regions and years, 92 nests were monitored by camera and 53 nests were monitored by visits only. The median monitoring duration for all nests was 14 days (interquartile range (IQR): 8 - 22).

3b) Environmental differences

We found that there were small differences in environmental variables between the two regions, while controlling for the day of the year and progress into the year (**Table 3**). Air temperatures were 1-3℃ higher in Alsace than Hauts-de-France. The same was true for soil surface temperatures. Minimum, maximum, and mean wind speeds were 0.2-0.4 m/sec higher in Hauts-de-France than Alsace. Temperature ranges within single days were 2.4℃ greater in Alsace, while wind speed ranges were 0.17 m/sec greater in Hauts-de-France. Daily rainfall was 0.4 mm more in Alsace, and 31% of all nest-days were dry. Mean solar irradiance was 6 W/m^2 higher in Hauts-de-France, but maximum solar irradiance did not differ between regions.

Table 3: *Estimated marginal means of environmental variables for each exposure day of every nest, grouped by region (n=2087 nest-days, 367 in Alsace and 1720 in Hauts-de-France). Air variables were calculated at 1 cm above soil surface. P-values indicate the estimated significance of the independent effect of region in a linear model predicting the environmental variable (x) as a function of the region (r) and progress into the year (days), and controlling for the random effect of date (date) in the form: x ~ r + days + (1 | date).*

Model	Estimate Alsace (Mean ± SE)	Estimate Hauts-de-France (Mean ± SE)	P-value in linear mixed model	Magnitude of difference
Mean Air Temperature (°C)	15.8 ± 0.288	13.9 + 0.268	**< 0.001**	1.9 °C
Maximum Air Temperature (°C)	24.6 ± 0.616	21.3 + 0.580	**< 0.001**	3.3 °C
Minimum Air Temperature (°C)	8.65 ± 0.231	7.70 + 0.214	**< 0.001**	0.95 °C
Mean Soil Temperature (°C)	17.2 ± 0.355	15.5 + 0.332	**< 0.001**	1.7 °C
Maximum Soil Temperature (°C)	30.7 ± 0.924	27.4 + 0.870	**< 0.001**	3.3 °C
Minimum Soil Temperature (°C)	8.13 ± 0.234	7.26 + 0.216	**< 0.001**	0.87 °C
Mean Wind Speed (m/s)	0.33 ± 0.022	0.64 + 0.020	**< 0.001**	0.31 m/s
Maximum Wind Speed (m/s)	0.53 ± 0.027	0.91 + 0.025	**< 0.001**	0.38 m/s
Minimum Wind Speed (m/s)	0.16 ± 0.019	0.37 + 0.017	**< 0.001**	0.21 m/s
Air Temperature Range (°C)	16.0 ± 0.642	13.6 + 0.607	**< 0.001**	2.4 °C
Soil Temperature Range (°C)	22.6 ± 0.968	20.2 + 0.914	**< 0.001**	2.4 °C
Wind Speed Range	0.37 ± 0.021	0.54 ± 0.019	**< 0.001**	0.17 m/s
Rain (mm)	2.63 ± 0.344	2.23 ± 0.320	**0.015**	0.4 mm
Mean solar irradiance (W/m^2)	217 ± 5.62	223 ± 5.32	**0.007**	6 W/m^2
Maximum solar irradiance (W/m^2)	668 ± 14.9	667 ± 14.1	0.802	1 W/m^2

3c) Causes of nest failure

The observed nest fates were unevenly distributed across regions (Fisher's Exact Test, n = 145, $p < 0.001$, **Table 4, Figure 8**). Alsatian nests were less likely to hatch than nests in Hauts-de-France (35% of nests vs. 76% of nests, odds ratio 0.174, Pairwise Fisher's Test with HB-correction, n = 145, adjusted $p < 0.001$), and they were more likely to be lost to agricultural procedures (30% of nests vs. 5% of nests, odds ratio 8.54, Pairwise Fisher's Test with HB-correction, n = 145, adjusted $p < 0.001$). When we considered only camera-monitored nests, we found no difference in nest fates between regions (Fisher's Exact Test, n = 92, p = 0.194).

Table 4: *Nest fate for Northern Lapwings nesting in two regions of France, 2021-2022. The significant differences between two regions are indicated in bold (adjusted p < 0.001, Pairwise Fisher's exact test with HB correction, n = 145).*

	Hatched	**Lost to agriculture**	Depredated	Abandoned	Unknown & Flooding
Alsace (n = 37)	**13 (35%)**	**11 (30%)**	6 (16%)	5 (14%)	2 (5%)
Hauts-de-France (n = 108)	**82 (76%)**	**5 (5%)**	5 (5%)	7 (6%)	9 (8%)
Total (n = 145)	*95 (66%)*	*16 (11%)*	*11 (8%)*	*12 (8%)*	*11 (8%)*

Apart from agricultural practices, causes of nest failure were approximately equally distributed. Nests that were lost to unknown causes could have failed for any reason, but were likely depredated in most cases because eggs were removed from the nest cup and the surrounding soil was undisturbed. Predators were identified from camera footage at nine nests during two field seasons, five nests were depredated by red foxes, two by beech martens (*Martes foina*), one by a European badger, and one by carrion crows (*Corvus corone*). Two additional nests were clearly depredated based on eggshell remains, but the predator could not be identified. Other failed nests were either abandoned, or lost to flooding or other unknown causes (**Figure 8**). Under the assumption that all nest losses to unknown causes were lost to depredation (and excluding confirmed abandonments and losses to environmental hazards), we found no difference in the number of apparent depredation events between nests monitored by cameras (11%) and nests monitored by visits only (20%, odds ratio 1.96, Pairwise Fisher's Test with HB-correction, n = 130, adjusted p = 0.205), nor between our two regions (odds ratio 2.1, Pairwise Fisher's Test with HB-correction, n = 130, adjusted p = 0.157).

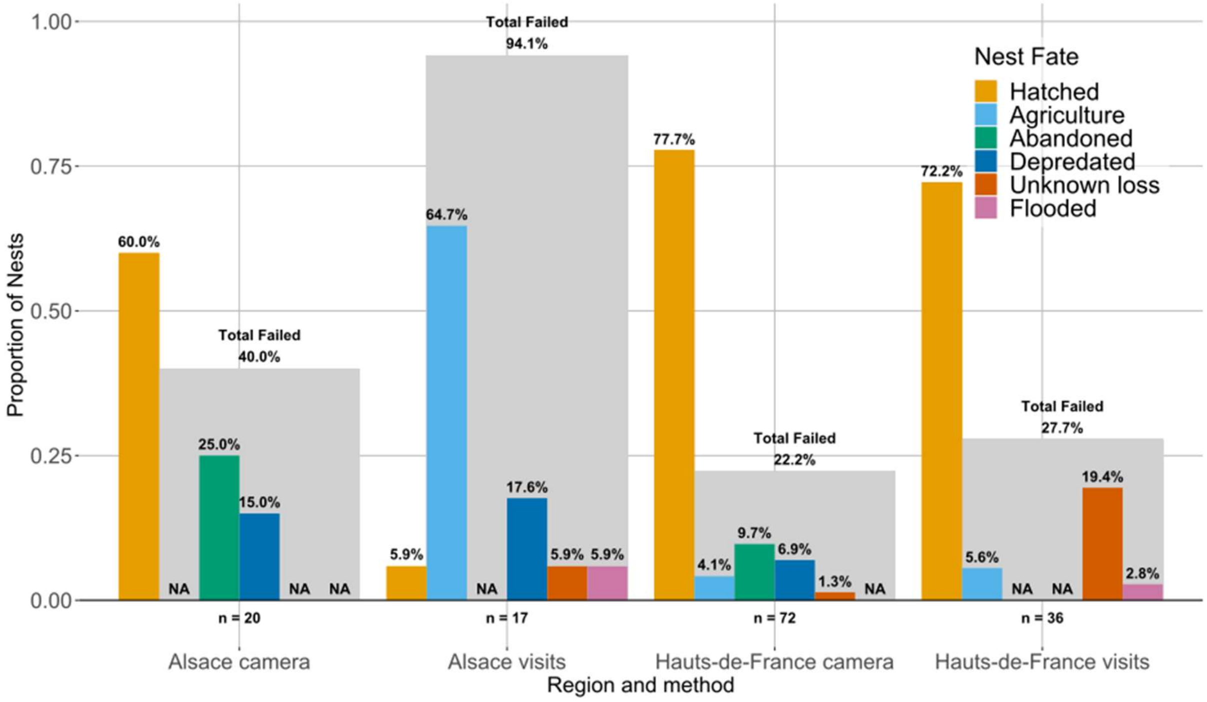

Figure 8: *Observed proportions of nest fates for each combination of region and nest monitoring method in two regions of France, 2021-2022. Nests for which nest fate could not be clearly determined are not shown (n = 39). The shaded grey bar indicates the total proportion of unsuccessful nests.*

We found that nests lost to agriculture were last observed on average 24 to 33 days earlier in the season when compared to any other nest fate (Tukey's HSD, p < 0.003 for four pairwise comparisons, **Figure 9**). The other nest fates did not occur at significantly different times from each other (Tukey's HSD, p > 0.432 for six pairwise comparisons, **Figure 9**). Only two nests were lost to floods, both in the same year.

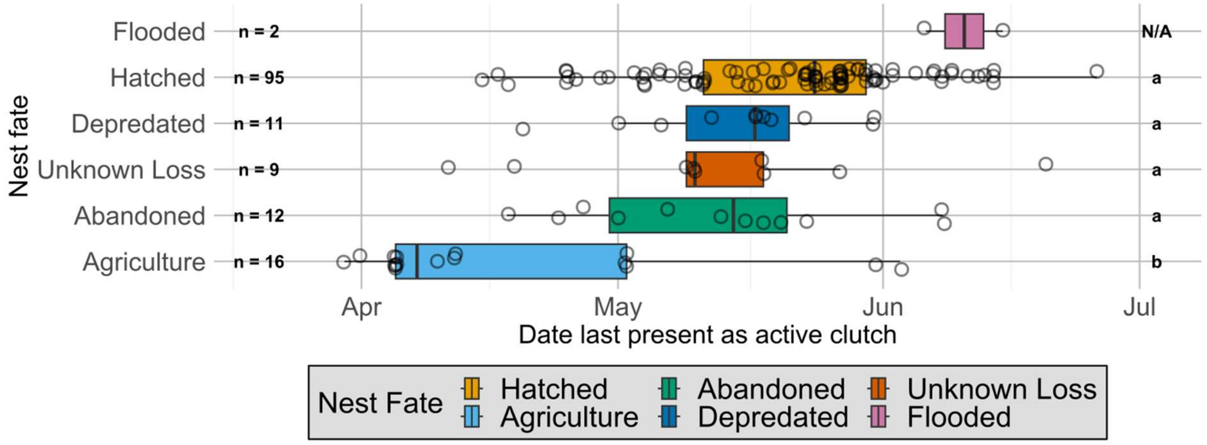

Figure 9: *Observed timing of nest fate summed between both regions and both breeding seasons 2021-2022. Nests for which hatching or failing could not be clearly determined are not shown (n = 39). Points indicate individual clutches.*

3d) Nest survival

Survival rates for a nest on any given day were best explained by a combination of six factors: 1) the region in which the nest is present; 2) the monitoring method; 3) an interaction effect between monitoring method and region; 4) the mean wind speed on a given day; 5) the mean wind speed on the day prior; and 6) the interaction effect between wind speed on the day itself and the day prior (**Formula 1.2**, **Table 5, Figure 10**).

Formula 1.2:

Daily Nest Survival ~ Region * Monitoring Method + Mean Daily Wind Speed * Yesterday's Mean Daily Wind Speed

Table 5: *Estimated effects for each variable of the best-performing model, and the associated standard errors (SE), lower-, and upper 95% confidence intervals. All numbers presented on the logit scale. The effect of wind speed, for which the confidence interval overlaps 0, is considered uninformative for estimating nest survival rate when considered separately but contributes positively to the accuracy of the entire model as compared to a model that excludes it.*

Variable	Estimate	SE	Lower CI	Upper CI
Intercept	-1.013	0.915	-2.807	0.781
Region: Hauts-De-France	**1.700**	**0.565**	**0.591**	**2.808**
Monitoring Method: Camera	**1.931**	**0.470**	**1.009**	**2.852**
Mean Wind Speed	1.905	1.900	-1.820	5.630
Yesterday's Mean Wind Speed	**7.732**	**2.097**	**3.621**	**11.843**
HDF + Camera	**-1.708**	**0.626**	**-2.933**	**-0.481**
Wind Speed : Yesterday's Wind Speed	**-5.741**	**2.533**	**-10.706**	**-0.777**

We used the variable effect estimates from the top-level model to estimate daily survival rates for lapwing nests. The best-fit model showed that daily nest survival rates were higher in the region of Hauts-de-France, and were only moderately reduced at low wind speeds (Without camera: median DSR = 0.987, IQR 0.978–0.991. With camera: median DSR = 0.989, IQR 0.982 – 0.993, **Table 6, Figure 10**). Nest survival rates were high in Alsace for higher wind speeds, but were reduced by low wind speeds or factors related to low wind speed, especially when cameras were absent (Without camera: median DSR = 0.842, IQR 0.777 – 0.924. With camera: median DSR = 0.967, IQR 0.949 – 0.981, **Table 6, Figure 10**).

Deployment of a camera at a nest was associated with increased nest survival rates (**Table 6**). The mean daily survival rate estimate for camera-equipped nests in Hauts-de-France was estimated to be 0.003 higher per day than for those without a camera. The difference resulted in a 17% reduction in the estimated daily chance of failure (complement of daily survival rate), because of the high survival rates in either condition. The mean daily survival rate estimate for camera-equipped nests in Alsace was estimated to be 0.13 higher per day than for nests without equipment. The difference resulted in a 78% reduction in estimated daily chance of failure.

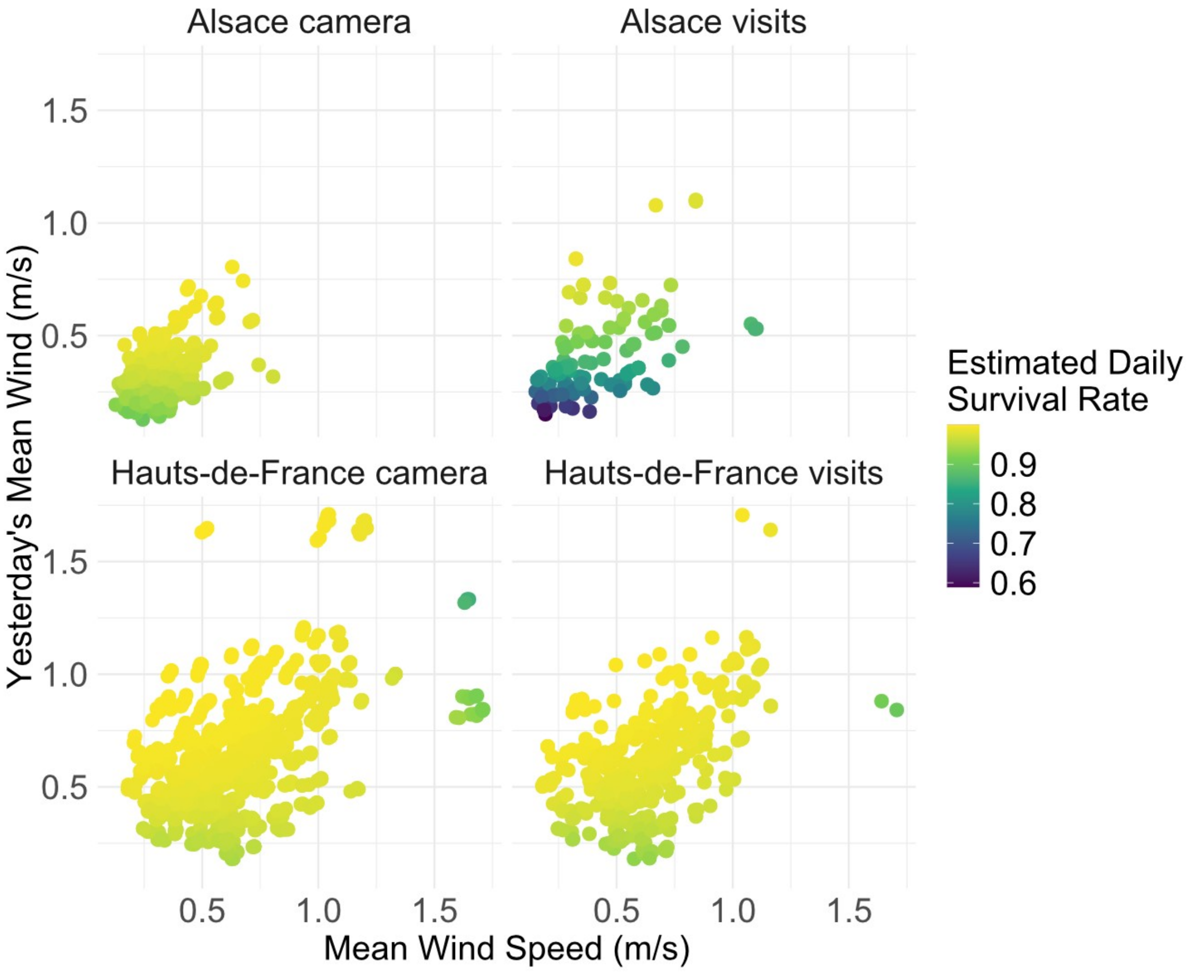

Figure 10: *Estimates of the daily survival rate of nests as a function of the region, nest monitoring method, local mean daily wind speed, and mean daily wind speed of the previous day.*

Table 6: *The mean predicted nest survival rates for all nests over their exposure days, and associated interquartile ranges. For each region and monitoring method grouping, the average of the mean daily wind speed of all nests is provided.*

Region	Monitoring method	Median daily survival rate	Interquartile range	Mean of mean daily wind speed (m/s)
Alsace	Camera	0.967	0.949 – 0.981	0.335
Alsace	Visits	0.842	0.777 – 0.924	0.426
Hauts-de-France	Camera	0.989	0.982 – 0.994	0.652
Hauts-de-France	Visits	0.987	0.978 – 0.991	0.624

The mean estimated probabilities to survive a full incubation period were greater in Hauts-de-France as compared to Alsace (**Figure 11**). Hypothetical nests in Hauts-de-France (1000 bootstrapped replicates each for 173 days over 2 years) had a mean estimated probability to survive incubation of 0.656 (bootstrapped sd = 0.051) when monitored by a camera and a probability of 0.592 (bootstrapped sd = 0.057) when not monitored by camera. Hypothetical nests in Alsace (1000 bootstrapped replicates each for 151 days over 2 years) had a mean estimated probability to survive incubation of 0.428 (bootstrapped sd = 0.035) when monitored by camera and a probability of 0.007 (bootstrapped sd = 0.003) when not monitored by camera.

Seven variables were not present in the best-fit model. The grouping variables of year, habitat type, and number of eggs in the clutch were not included in any of the model candidates within 2 AICc score of the best-fit model (**Table 2**). The numeric variables of daily rainfall, mean daily soil temperature, solar irradiance, progress into the season, and the interaction effect between region and wind speed featured in some of the top candidate models, but not the top-fitted model (**Table 2**).

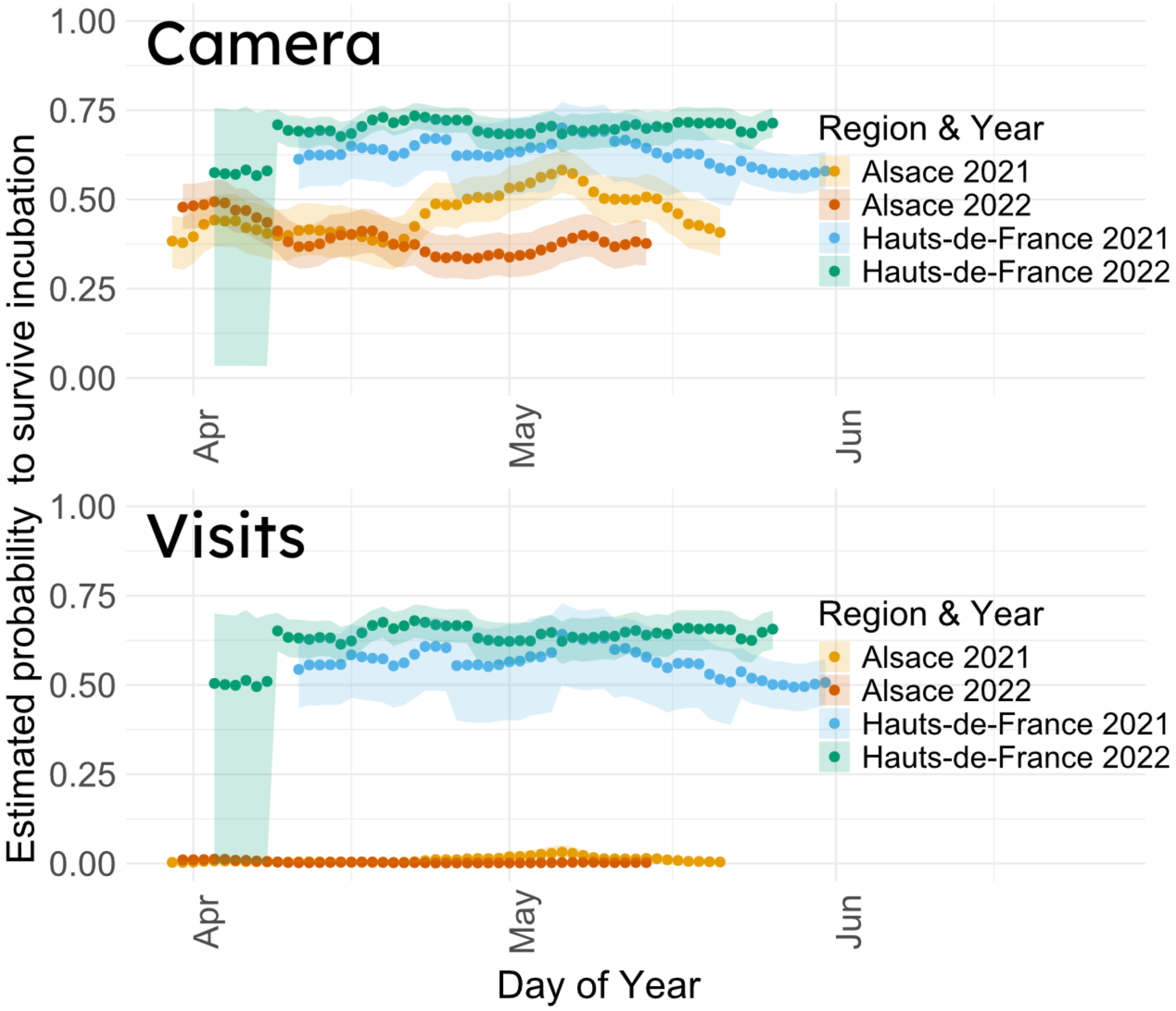

Figure 11: *Estimated probabilities for a nest to survive incubation (27 days) as a function of the day on which the clutch is completed, grouped by the region and year in which it's constructed. Shaded bands indicate the bootstrap-based 95% confidence intervals. Nests followed by Camera (top) show higher probabilities to survive incubation than nests followed by visits only (bottom), particularly in Alsace.*

4) Discussion

In this field study, we investigated factors affecting the nest success of Northern Lapwings in coastal and inland breeding sites in France, where the majority of lapwings were found breeding on crop fields. Our new information on nest survival and causes of failure may inform conservation decisions for lapwings in France, where the species has been in a nationwide decline (Joyeux et al. 2022), and potentially provide insights that would generalise to other ground-nesting birds in agricultural habitats. Through monitoring lapwings during the incubation stage of their reproductive cycle, we produced three main results. First, nest survival differed between regions and may result in source-sink dynamics or even local extinctions if the observed pattern holds into the future. Second, local weather conditions affected nest survival rates, with the lowest survival under low mean wind speed conditions. Last, deploying cameras at the nests resulted in a net-positive effect on nest survival rates, potentially due to neophobia among the nest predators. Few predations were documented by our nest cameras but a majority of confirmed nest depredations were caused by mammals.

4a) Nest fates

The majority of monitored nests hatched (66%). In the Netherlands between 2002 and 2005, of 15 site and year combinations investigated, only 2 site-years had rates of nest success >60% (Teunissen et al. 2008). Similarly, in North Yorkshire, UK, between 1996 and 1998, of 17 site and year combinations investigated, 7 had rates of nest success >60% (Seymour et al. 2003). However, nest success was not equally distributed between our two investigated regions. We found that Northern Lapwing nests in Alsace were less likely to hatch and more likely to be lost to agricultural processes than nests in Hauts-de-France.

In agreement with available information for waders nesting in grasslands from other parts of Europe, a combination of confirmed predations and agricultural procedures represented the majority of all nest losses (56%). Compared to other regions of Europe with a longer history of marking nests for their protection, our observed levels of predation were lower, but losses to agricultural procedures were greater (Schifferli et al. 2006, Bellebaum & Bock 2009).

In contrast to the relatively low predation rates, abandonment rates for nests equipped with cameras (25% and 9.7% of nests with known fates in Alsace and Hauts-de-France, respectively) were above rates previously reported for lapwing nests with nest cameras or nest cages placed in close proximity (2.5% and 8.1%, Bolton et al. 2007a, Isaksson et al. 2007). We could not establish whether a difference in monitoring methods, regional differences, or other factors were responsible for these rates of abandonment, because we had difficulties identifying abandonment at nests which were monitored through visits only.

Nests lost to agriculture made up the greatest proportion of nest losses (32% of confirmed nest failures), and losses occurred significantly earlier in the breeding season compared to other nests. Similar to lapwings nesting on Norwegian crop fields between 1988 and 1990 — where over 80% of nest losses occurred due to farming activities, a majority of which on untilled fields (Berg et al., 1992) — most losses to agriculture appear to arrive early in the French growing season. A difference in the start of the growing season between the two regions investigated in this study might explain the disparity in nest losses to agriculture between them. Such a difference in timing might be driven by the coastal climate in Hauts-de-France (Planchon 2000). A similar effect has already been noted at Polish crop fields, showing a 30-day gradient in sowing dates at a national scale (Marcinkowski & Piniewski 2018). To further understand the timing of nest losses due to agricultural procedures, it is necessary to compare lapwings' breeding phenology and agricultural schedules for each suitable crop type in each region more closely.

We predicted that predation, being a major driver of nest failure for lapwings breeding across Europe (Isaksson et al. 2007, MacDonald & Bolton 2008, Bellebaum & Bock 2009, Eglington et al. 2009, Bodey et al. 2011, Düttmann et al. 2018), would feature as one of the most common causes of nest loss, and be a potential driver of differences in nest survival rates between regions. Unexpectedly, we found no differences in rates of predation between regions or between monitoring methods, potentially related to the relatively low number of observed predations. Apparent depredation rates for our two study regions (ca. 8% - 20%) were below nest predation rates reported for lapwings in many other parts of Europe (ca. 30-60%, Isaksson *et al.* 2007, MacDonald & Bolton 2008, Bellebaum & Bock 2009, Eglington *et al.* 2009, Bodey *et al.* 2011, Düttmann *et al.* 2018). Most predation events at our nests were attributed to mammalian predators where a species-level determination was possible.

4b) Weather impacts

Our best-fit nest survival model predicted much lower nest survival rates in Alsace than in Hauts-de-France. The difference was in line with our prediction that Alsace would show lower rates of nest survival given its historical population decline (Dubois et al. 1991, Dronneau 2007), and may be expected based on the differences in nest fates outlined above.

In contrast to our predictions, we found that nest survival rates were not negatively impacted by dry weather and high temperatures. Instead, the best-fit model indicated a positive relationship between daily mean wind speeds and survival. At higher wind speeds, odours at the nest are more readily dispersed, while convective heat loss of both birds and eggs increases (Bakken et al. 2002, Reid et al. 2002, Conover 2007). Birds may abandon their nests at high temperatures, likely as a result of increasing thermoregulatory costs (Sharpe et al. 2019). We might expect the risk would be reduced if greater heat loss is enabled through convection at higher wind speeds, and vice-versa at lower wind speeds. A reduced need for panting may also reduce bird movements at the nest. At higher temperatures, birds will lose more water to thermoregulation (Eto *et al.* 2017). To prevent dehydration, lapwings would have to take incubation breaks more often, as nests in our study sites were often found some distance from surface water. Reduced nest attendance would result in a lower average number of lapwings in the breeding colony at any one time, and lower numbers of lapwings in a colony are associated with reduced anti-predator responses (Elliot 1985).

Additionally, as the presence of an active shorebird at its nest may serve as a cue for predators to locate its clutch (Engel et al. 2020), we might expect repeated movements between the nest site and a water source to serve as a cue for predators. Additionally, the thermoregulatory behaviour may increase the potential for visually oriented predators to detect the nest if lapwings assume a standing posture more often and for longer periods of time, as found for other species (Purdue 1976, Brown & Downs 2003). While standing, the parent's profile is raised and concealment by surrounding habitat features which would otherwise limit predators' sight lines (Hancock *et al.* 2023), will be reduced. The shadow of attending birds is also lengthened, the birds move, and the visually striking features of their plumage – the white belly feathers in particular – are held off the ground.

The potential for olfactory predators to detect the nest may be lower when wind speeds are higher, as higher wind speeds allow for odours to be dispersed more quickly (Conover 2007). Lapwings breeding at high temperatures may thus experience a three-fold benefit from higher wind speeds. A reduced thermoregulatory cost through convective cooling, a reduced risk of detection by predators due to less visual cues at the nest, odours dispersed more quickly, and stronger anti-predator responses with a higher proportion of birds expected at the colony. The combination of these effects may potentially explain why we find more support for an effect of daily mean wind speed on nest survival rates, and not our expected effect of daily temperatures.

We found that an interaction between wind speed and the wind speed of the previous day explained part of the nest survival rates of our nests. Survival rates were lower at the extreme low end of daily wind speeds, but also when wind speeds were very fast. It's possible that this relates to stormy weather, multi-day inclement weather as represented by high mean wind speeds on both the day of survival rate estimation as well as the day prior may be especially dangerous. In combination with the effect of monitoring method and region (**Figure 10**), it seems that differences between regions might affect the impact of the wind conditions at the nests. The accessibility of surface water features may provide alternative sources of cooling (Ryeland *et al.* 2021) and mitigate the need for a cooling breeze at the nest site. In addition, there may be differences in the cooling potential of the prevailing wind, which blows West to East from the English Channel in Hauts-de-France, but from SSW to NNE along the Rhine valley in Alsace (Davis *et al.* 2023). A sea breeze may be more effective at cooling than a land-based south-western wind. Future analyses might consider the interaction between wind speed and direction at nesting sites, or some measure of the expected cooling effect, as well as the availability of surface water for cooling and drinking.

4c) Monitoring methods

We observed higher daily survival rates for nests equipped with cameras than reference nests monitored with visits only. Additionally, there was an interaction effect between region and camera, such that cameras greatly increased nest survival in Alsace, but not in Hauts-de-France.

Previous studies have found varied effects of visiting nests of ground-nesting birds, or marking the nest with a human object, on subsequent survival or predation rates. For some species and locations, marking nests does not appear to result in reduced nest survival (Galbraith 1987, Zámečník et al. 2018, Salewski & Schmidt 2022), whereas other studies report site-specific negative or positive effects (Teunissen *et al.* 2008). Some studies have found no effect of the placement of a camera but a negative effect of visiting the nest (Stien & Ims 2016), while other studies have found no effect of frequent visitation when nests are left unmarked (Fletcher et al. 2005). Marking nests may be expected to reduce losses to agricultural procedures (Kragten & De Snoo 2007, Zámečník et al. 2018), and so we were unsure whether to expect net-positive or net-negative effects on nest survival at our study sites if marking for nest protection is combined with an unpredictable effect on predation rates.

Our net-positive effect of camera placement on nest survival rates might be explained by local conditions at our study sites. First, there have been no nest marking programs at our study sites using a setup similar to the one used in our study. Foxes and corvids often show some degree of neophobia (Miller et al. 2022, Morton et al. 2023), and the local novelty of our marking setup may have contributed to neophobic responses from predator species. Second, the majority of our nests were found on crop fields, and the majority of these crop fields were planted with maize. Proposed mechanisms for increased predation risk following human visits have included deposited scent trails or trails of disturbed vegetation (Teunissen et al. 2006). As maize crops, in the early stages of their development, can be traversed with minimal physical contact between researchers and crops, local conditions may have limited trail deposition at the majority of our study sites.

Potential future marking programs at the same nesting sites should monitor nest outcomes to determine whether predators learn to associate, over time, the marking method with the presence of nests.

4d) Improving nest survival

Our best-fit model provided estimates for the chance to survive incubation in Alsace that indicate considerable risks for nests in this region. The primary risk appears to be nest destruction through farm work. As a measure to prevent nest losses by agricultural processes, nests could be marked so they are visible to farmers. By contrast, nests in Hauts-de-France appeared less at risk of destruction. If agricultural processes are no issue and the majority of failures are due to clutch depredation, then nest marking may be detrimental to fledging outcomes (Goedhart *et al.* 2010). In those cases, excluding predators from the nesting and breeding areas may improve survival rates and reproductive rates when agricultural procedures are appropriately managed (Verhoeven *et al.* 2022), though in some situations it may be best not to intervene at all (Goedhart *et al.* 2010). From our data, it appears that predation is responsible for a low proportion of reproductive losses under current conditions.

5) Conclusion

To counteract low rates of nest success in Alsace, local efforts to mark lapwing nests should be encouraged and supported. Marking and protection of lapwing nests has been supported by national agricultural programs elsewhere in Europe (Zámečník et al. 2018). As nest success was high in Hauts-de-France, extensive efforts to reduce nest losses may not be a productive investment of time and resources. Instead, where we have evidence of relatively high rates of nest survival, available resources may be better spent to investigate the subsequent survival of the chicks and resulting fledging rates. Continued observations may bear out whether the breeding seasons of 2021 and 2022 in Hauts-de-France were extraordinarily good for nest survival, or whether these are usual conditions. As more information on local demographic rates becomes available, a model-based population viability analysis, as was performed for lapwings in the Netherlands and Germany (Plard *et al.* 2020), may shed light on future population viability.

As the majority of nests lost to agriculture are lost in the early growing period, nest marking efforts in crop fields should be coordinated with local farmers and focus on the early part of the growing season. In France, the key period would have been the first two weeks of April, but each year's "focus period" should depend on farmers' schedules in combination with that year's arrival dates of lapwings and weather conditions.

The effects of climate change may lead to increased periods of drought and heat waves during the breeding season (Gudmundsson & Seneviratne 2016, Guerreiro *et al.* 2018). As potential cooling sources may become more limiting for successful breeding, we might find that the breeding success of lapwings becomes more dependent on the availability of sources of surface water or, as implied by our results, prevailing cooling winds (e.g. in coastal regions like Hauts-de-France). Conservation entities managing inland sites hosting breeding meadow birds may consider securing access to wet features, not only for their reported benefits to chick foraging (Eglington *et al.* 2010) and for attracting breeding pairs (Bertholdt *et al.* 2017, van der Winden *et al.* 2017), but also as potential cooling resources, which may allow for a more successful breeding season under warming conditions.

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Chapter II:

The Response of Northern Lapwings to Human Disturbance at Their Nests Depends on Weather Conditions and Incubation Stage

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Abstract

Northern Lapwings (Vanellus vanellus) are one of many ground-nesting bird species breeding in open habitats, where they face the competing demands of self-maintenance, nest thermoregulation, and anti-predator behaviours. We monitored nesting lapwings with motion-activated nest cameras, and recorded the time between our visits to the nests and the lapwings' subsequent return, during the 2021 and 2022 breeding seasons in France. We investigated whether lapwings modulated their responses according to environmental variables, the duration they had been monitored, and the stage of incubation of their clutch. Among the 98 nests monitored, lapwings showed a surprising amount of variability in the lengths of their absences: some birds returning within minutes of a disturbance, while others stayed away for hours. A considerable part of this variation could be explained by a combination of the number of times a nest camera was triggered, an interaction effect between monitoring duration and incubation stage, and a three-way interaction between soil temperature, wind speed, and time of day at the time of the visit to the nest. Lapwings were observed to return more quickly (shorter return latencies) when the nest camera was triggered by motion more often, the longer they had been monitored, and when their clutches were closer to hatching. Absences were shorter in the mornings and when temperatures were higher, but were longer when dusk approached and when wind speeds were higher in the afternoon. Conversely, higher wind speeds were associated with faster returns in the mornings. These results suggest that lapwings may adapt their risk-taking behaviour in accordance with the thermoregulatory needs of their clutch, resulting in faster returns to the nest after quitting the nest involuntarily at conditions unfavourable to embryonic development.

Keywords: Camera monitoring, Human disturbance, Ground-nesting birds, Risk-taking behaviours, Thermoregulation

1) Introduction

Most birds provide substantial parental care for their offspring, incurring significant costs to provide thermoregulatory, antipredatory, and nutritional benefits. During the incubation stage, bird embryos rely on the nutrients contained within the egg, while parents have to ensure a thermally and hydrologically optimal nest environment and prevent the nest's depredation.

Ground-nesting is the presumed ancestral condition of all birds, originating before their split from the other theropod dinosaurs (Fang *et al.* 2018). Early birds may have covered their nests with piles of vegetation, as currently practised by species in the family *Megapodiidae* (Harris *et al.* 2014), while nesting strategies depending on successively greater parental investment evolved later (Mainwaring *et al.* 2023). Many species in the order *Charadriiformes* (waders, gulls, and auks) build open ground nests, which leave their clutches exposed during parental absences (Fang *et al.* 2018) and provide varying degrees of uni- or bi-parental care for their offspring depending on species (Székely & Reynolds, 1995). The surrounding environment may strongly affect the visibility of nests placed on the ground, where the contents of such nests may be spotted from dozens of metres away by flying predators (Hancock *et al.* 2023) and allow for direct insolation of the unshaded clutch.

The unaltered thermal properties of an open nest with no cover from the sun are most likely highly variable over time, as their temperatures will trend quickly towards the ambient temperature when they are unattended (Schneider & Mcwilliams 2007, Mougeot *et al.* 2014). Temperatures near the ground are also more variable than those higher in the air column (Pfister *et al.* 2017, Sigmund *et al.* 2017). This means that parents may be required to incubate all through cold nights (Sládeček *et al.* 2019), while in hot environments clutches may need to be kept cooler than ambient temperatures during the day (Mougeot *et al.* 2014). Differences in wind speed or humidity may additionally modify thermoregulatory costs over short timescales (Chappell *et al.* 1989, Van Dyk *et al.* 2019).

Environmental conditions are likely to evolve over the breeding period, often towards warmer temperatures as spring turns to summer. The thermoregulatory needs of the clutch also develop over time, with more developed embryos having stricter thermal requirements (Tazawa & Rahn, 1986), requiring a greater investment from parents. The further the ambient temperature is from the temperature that would keep the eggs at their developmental optimum, the more effort we could expect from the incubating parents (Conway & Martin, 2000). Conversely, during optimal environmental conditions, parents may be temporarily freed from thermoregulatory duties (Yom-Tov *et al.* 1978). These factors make the cost of 'perfect' thermoregulation highly variable over time for any particular breeding attempt.

At times, the demands of thermoregulation and anti-predatory strategies are directly opposed. When potential predators approach the nest site, it may be advantageous for an incubating bird to leave the nest area and rely on nest crypsis to prevent the clutch from being discovered (Šálek & Cepáková, 2006). However, this leaves the clutch exposed to potentially deleterious environmental conditions. Vice-versa, a parent staying at the nest to ensure optimal conditions may serve as a cue to potential predators (Engel *et al.* 2020).

Predation risk is unequally distributed over time. Depending on the local predator community, the majority of clutch predation risk may be experienced during the day (from avian predators, Teunissen *et al.* 2008), or during the night (from mammalian predators, Berg *et al.* 1992). As alternative prey become more numerous or unavailable, predators can shift their diet toward or away from (ground-nesting) birds' clutches (Beintema & Muskens, 1987), leading to differential predation pressure over the breeding season.

Different predator species are associated with different anti-predator strategies and energy expenditure: avian predators can often be chased off by mobbing behaviour (Kis *et al.* 2000), while larger-bodied predators such as foxes might only be distracted away from nests instead of being directly chased or threatened off (Elliot, 1985). This means that at different times of day, at different locations, facing different environmental challenges, theoretically optimal anti-predator strategies will be different.

The Northern Lapwing (*Vanellus vanellus*) is a ground-nesting wader breeding in open habitats across temperate Eurasia (Birdlife International, 2017), with a small foothold in North-Africa (Cherkaoui & Hanane, 2011). The species finds itself in a gradual population decline across western Europe, due to insufficient reproductive output (Roodbergen *et al.* 2012, Plard *et al.* 2020). Investment in incubation behaviour is variable between individuals (Grønstøl, 2003, Sládeček *et al.* 2019), and may be impacted by body condition (Hegyi & Sasvari, 1998). Unsuccessful breeding in one year may be compensated by successful breeding in following years, and lapwings can be expected to reduce investment in their current breeding in favour of future ones when conditions become unfavourable (Gustafsson & Sutherland 1988, Nilsson & Svensson 1996). We may then expect a complicated relationship between various external conditions (predator risk, weather conditions, food availability, development of the clutch), internal conditions (body condition, personality), and the trade-offs incubating birds make between current and future breeding success.

Using nest cameras to monitor activity around bird nests has seen wider use in recent decades. Nest cameras can provide species-level information on nest predators with a high degree of accuracy (Bolton *et al.* 2007, Teunissen *et al.* 2008). However, the presence of the camera may have an effect on the behaviour of local animals. On the one hand, the camera's presence may attract or repel predators (Séquin *et al.* 2003, O'Donovan & Boyce 2021). On the other hand, placing cameras next to nests may also increase rates of nest abandonment (Pietz & Granfors 2000).

In this study, we investigated the responses of breeding lapwings to a repeated encounter with a potential predator (visit by a scientist) and how these responses depend on varying environmental conditions, in the context of a trade-off between incubation behaviour and anti-predator responses. Our main objectives were: 1) to relate lapwings' absence from the nest directly following a visit by a scientist to weather variables indicating conditions that necessitate thermoregulation; 2) to determine whether lapwings habituate to repeated nest visits apart from expected differences based on environment and clutch development. To investigate this, we determined the length of the lapwings' absences from their nests using footage from motion-activated nest cameras and related these to weather variables as well as nest-specific information such as incubation stage.

We expected lapwings to return to their nests more quickly at the extreme ends of the local temperature spectrum, and slower at intermediate temperatures. We predicted we would find shorter absences in the mornings and longer absences closer to sunset, coinciding with the activity patterns of diurnal avian predators, which can be mobbed away from the nest site. This may encourage increased presence at the nest during the day. Lapwings should return faster later in the clutch's development, reflecting increasingly strict thermoregulatory needs of the embryos. If reduced opportunities for laying replacement clutches encourages investment in the current clutch, we would also find returns to be faster in the later parts of the breeding season. Finally, we expected lapwings to return progressively faster over their monitoring duration, controlling for other variables, due to habituation to the monitoring method.

2) Materials & Methods

2a) Nest monitoring

We monitored Northern Lapwing nests to determine incubation outcomes during the 2021 (6 April - 20 July) and 2022 (15 February - 29 June) breeding seasons in two regions of France, the coastal region of Hauts-de-France and the inland region of Alsace (**Figure 12**, **Chapter 1**). In the Alsace region all monitored nests were located on crop fields. In the Hauts-de-France region, in addition to crop fields, we had access to three wetland sites: 1) a grassland interspersed with numerous shallow ponds of 0.28 km^2, 2) a single pond surrounded by horse-grazed grassland of 0.04 km^2, and 3) a patchwork of circles of peat approximately 15 m in diameter surrounded by reed beds, of 0.11 km^2.

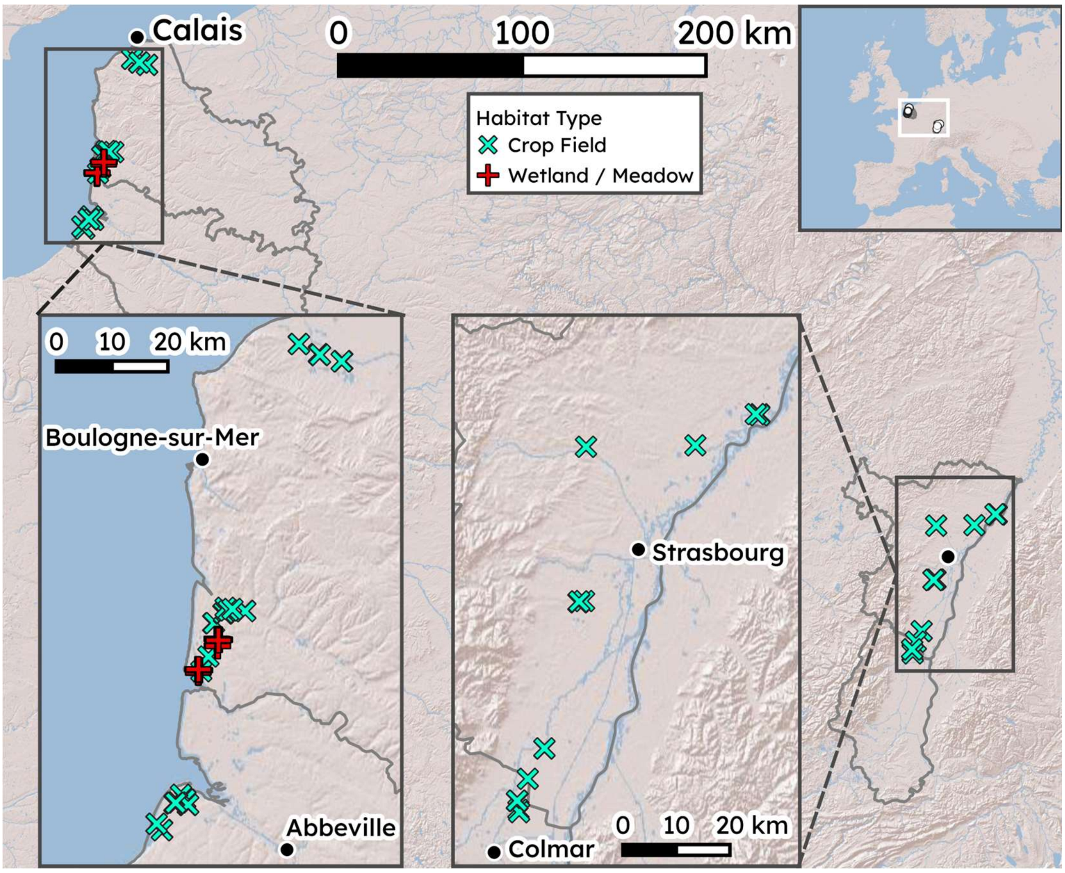

Figure 12: *Map of the nests in crop fields (cyan '**X**' signs) and in wetlands/meadows (red '+' signs) monitored with nest cameras.*

We located nests as described in **Chapter 1**, using binoculars and spotting scopes and then approached them on foot for confirmation. Nests found in close proximity to each other (within sight of each other and not separated by roads or water bodies more than 3 m wide) were assigned to the same cluster or 'site'. We placed motion-activated cameras (Victure HC300) next to the nests to monitor the nests' statuses, parental behaviour, and the presence of other animals around the nests. The cameras were placed on 6 cm diameter wooden poles 1 m above ground. The poles were put 2 m away from the nests. Bird spikes were added to the poles to prevent avian predators from perching on top.

Following the initial placement, cameras were visited weekly to change their batteries and SD cards. We defined the **latency to return to the nest, 'Return Latency',** after a particular nest visit as the time between the end of a visit by a scientist and the first time a lapwing is seen showing incubation behaviour or brooding chicks at that nest on subsequent camera footage. In this context, incubation behaviour is either sitting on the eggs or standing directly above them (Sládeček *et al.* 2019). The initial placements of cameras took a median of 9 minutes (IQR 7 - 11 min), while follow-up visits took a median of 5 minutes (IQR 4 - 7 min).

We placed cameras at 98 nests during the 2021 and 2022 breeding seasons. Twenty-three cameras were located on wetlands and meadows, and 63 were on crop fields. The majority of crop fields were corn fields, others were fields of potatoes, soybeans, peas, and chicory root cultures.

Nests were monitored until the nest fate could be established as described in **Chapter 1**. To establish nest fate, we used direct evidence (camera footage) or circumstantial evidence (eggshell fragments and signs of agricultural activity). A lack of return to the nest between two visits (6.1 ± 1.8 days, mean ± SD), as determined from available camera footage, was considered nest abandonment.

Of all 420 nest visits to 98 nests, parents were seen to return to their nest in 233 cases. The other 187 visits (where parents did not return) included 122 visits to empty nests after hatching or predation (58 nests), 19 visits to empty nests of an unknown fate (10 nests), and 46 visits to nests with eggs after a confirmed abandonment (12 nests).

2b) Weather conditions

Weather conditions around the nests were modelled using the *NichemapR* and *microclima* R packages (Kearney & Porter 2017, Klinges *et al.* 2022, Maclean *et al.* 2019), with climate data from the ERA5 dataset of the Copernicus institute (Hersbach *et al.* 2020). The ERA5 dataset operates on a 0.25° grid, providing grid squares with a maximum size of 27.5km x 27.5km (at the equator). The elevation data is provided on a 30m x 30m scale, allowing highly localised adjustments based on the ambient climate. Soil temperatures were extracted at surface level to simulate conditions relevant to unattended eggs. Relative humidity and wind speed were modelled at 1 cm above ground level, the level at which they would impact the clutch. The vapour pressure potential was calculated from the air temperature at 1 cm above ground level and the relevant relative humidity, as the available water vapour pressure that could evaporate into the air at that time.

All weather variables were modelled for every hour for every nest over the entire breeding season, then for every visit the whole-hour value was extracted such that a visit at 11:45 is accompanied by the weather conditions estimated at 11:00. Changes in soil temperature were assessed relative to the preceding full hour, which for our example would be at 10:00, on the assumption that lapwings could sense changing conditions in the past. The time of day used to model our weather conditions was based on clock time.

The analysis of lapwing behaviour was based on solar time variables, which correspond closely with lapwings' activity patterns (Brynychová *et al.* 2020). The solar time variables used in the analyses were hours since dawn (sun 6° below the horizon and rising), hours distance from solar noon (sun at zenith), or hours until dusk (sun 6° below the horizon and setting).

2c) Statistical analysis

Of the 233 visits which were followed by a parent's return, we retained only those visits where we knew the date of the end of incubation exactly, and which occurred before that end of incubation. This excluded nests for which the outcome was entirely unknown, and visits to nests after chicks already hatched or were hatching (and the parent subsequently returned to brood the chicks, which happened for all hatched nests). After accounting for these filters, 216 visits to 86 nests remained for analysis. The 86 nests were located on 24 fields (median: 8 nests/field, IQR 4.75 - 11.25 nests).

Because we expected non-linear relationships to be heavily involved in the relationships between our explanatory variables and **return latency**, we chose to construct Generalized Additive Models (GAMs) using the R package *mgcv* (Wood, 2017). We implemented random variables by modelling them as penalised regression terms within the GAM model structure as developed by Wood (2008). Non-random explanatory variables were modelled using thin-plate regression splines. We constructed our models using the Gamma model family rather than Gaussian because our response variable, **return latency**, can't have negative values.

We considered the following explanatory variables: the number of days until the determined nest outcome; the number of days since a camera had been placed at the nest; the interaction between the number of days with a camera and the number of days until the nest outcome; the number of times the nest camera was triggered by motion in the 24 hours following the end of the nest visit; the soil surface temperature; the wind speed, vapour pressure potential, and relative humidity at 1 cm height (as separate variables, and as interaction effects between each other and soil surface temperature up to three-dimensional effects); the hours since dawn, hours until dusk, or hours difference from solar noon. We used nest identity as a random variable to control for multiple measurements.

We followed a stepwise forward process for building our models, starting from the intercept-only model and introducing new variables one at a time (Gorman & Toman, 1966). This method is mathematically suboptimal (Gorman & Toman, 1966), but justified in this case because any analysis of a model containing all possible variables will be overparameterized. We evaluated for improved explanatory power using Akaike's Information Criterion (AIC, Akaike, 1998), while avoiding concurvity between model variables (equivalent to collinearity avoidance in linear modelling). The selected best model outperformed other models in terms of AIC scores (the lowest score) with a caveat to selection: during the final comparison between models, if the best-fit model differed by less than 2 ΔAICc from a nested model that excluded one of its factors, we preferred the simpler model (Arnold, 2010).

We verified whether the resulting model produced predictions that showed biassed residuals across the dataset by using the residual analysis package DHARMa (Hartig, 2017). We accepted a certain level of inaccuracy for our model as we expected to find an imperfect prediction of behavioural responses. However, we ensured there was no bias in model residuals as a factor of any variable potentially to be included in the models, or other potentially confounding variables like the day of year, or visit order (Zuur & Ieno, 2016).

We report median values and interquartile ranges (IQR), because the expected distributions of many of the variables involved in our analysis are non-normal. To illustrate the predicted effects of our model variables in the figures, we show the relationship of the variable of interest at “typical conditions”. The typical conditions were defined as the median values for all observed numeric variables, as if they were observed at the nest with the median effect of nest identity.

3) Results

Lapwings showed a median return latency of 1.04 hrs (IQR: 0.45 – 3.75 hrs). Visits to the nests occurred at a median temperature of 22.98°C (IQR: 18.90 – 30.92°C). Lapwings returned after a mean temperature change of -1.95°C (SD: 7.02°C) between the end of the scientists' visit and their return. 29.2% of returns occurred at a temperature difference of at least 5°C, and 11.6% of returns occurred at a temperature difference of at least 10°C. Out of 98 nests followed by camera, 7 nests were potentially abandoned directly after the placement of the camera, while 5 nests were abandoned during the course of the monitoring period (after 2, 12, 20, 28, and 33 days of monitoring, respectively).

The best-fit model involved the following variables, listed in order of decreasing F statistic (**Formula 2.1**): the log-transformed 24-hour activation rate (F = 35.327, edf = 2.816); an interaction effect between the number of days a nest had a camera placed at it and the number of days until the end of incubation at that nest (F = 16.737, edf = 6.740); a three-dimensional effect combining soil temperature, wind speed at 1 cm height, and hours difference from noon (F = 3.997, edf = 6.211); and the random effect of nest identity (F = 1.442, edf = 49.314). All variables were estimated using thin-plate regression splines, except for the random effect of nest identity, as mentioned above.

Formula 2.1: Return Latency ~ *log(ActivationRate)* + *(DayswithCamera * DaysUntilEnd)* + *(SoilTemperature * WindSpeed * HoursFromNoon)* + NestIdentity

The following variables were evaluated for their predictive value, but could not explain lapwings' return latencies better than the best-fit model: number of eggs in the nest, vapour pressure potential, relative humidity, time since dawn, time before dusk, days into the breeding season, the number of videos between the end of the visit and the return of the lapwing.

Weather conditions and time of day were significant predictors of the lapwings' return latencies (**Figure 13**). At higher temperatures, lapwings returned to their nests faster, especially when those temperatures were expected to result in lethal overheating for the clutch (above 41 degrees C). Visits before noon generally resulted in faster returns than visits after noon for similar temperature values. Increasing wind speeds were related to longer expected absences in the afternoon, but shorter ones in the mornings for similar temperature values. Our dataset did not include high wind speeds in combination with high temperatures.

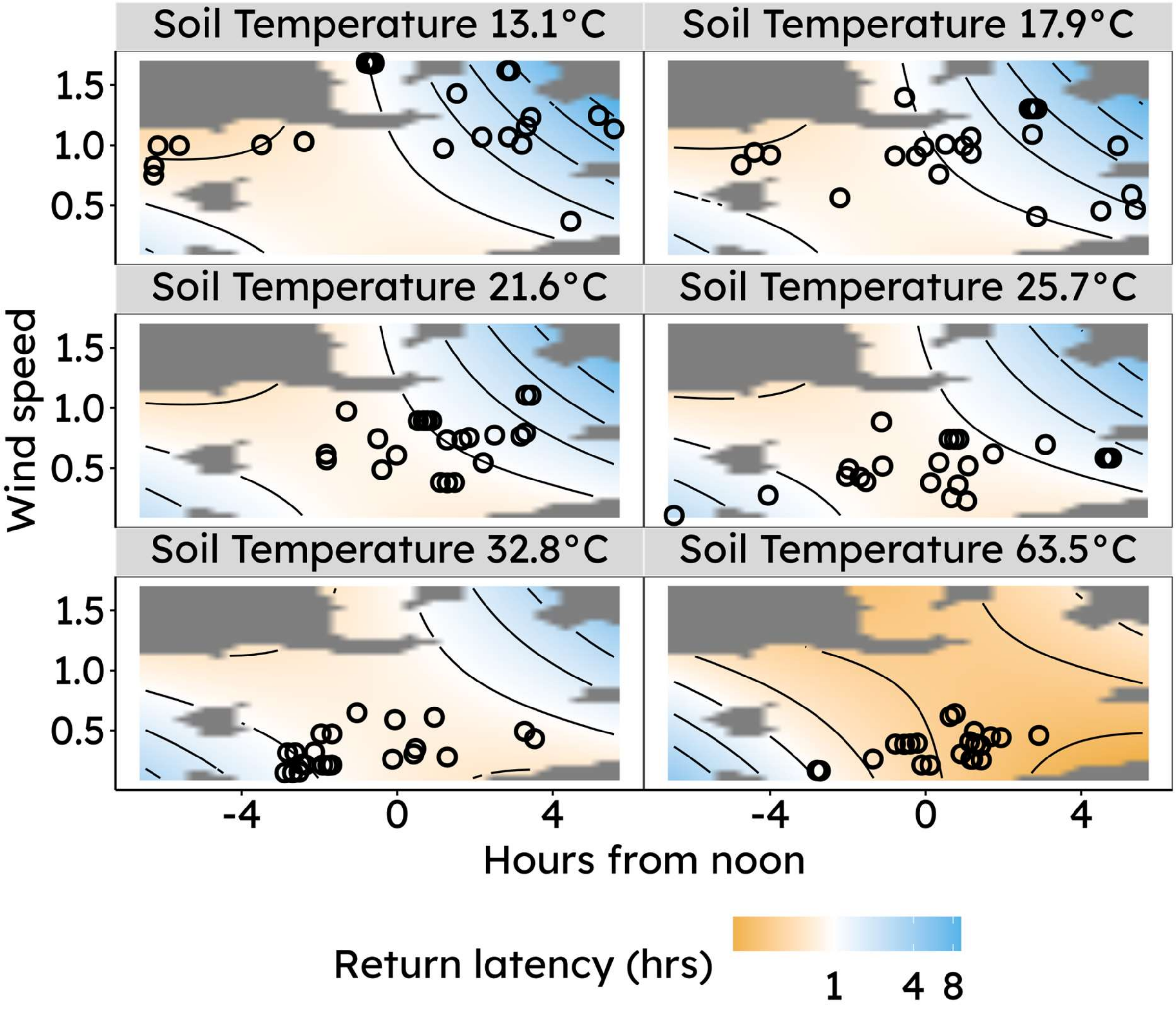

Figure 13: *The expected return latencies on the response scale as a function of the hour difference from noon, wind speed, and soil temperature. Each plotted slice shows the quantile of source data closest to the relevant temperature value, with expected return latencies shown as a colour gradient. The first and last temperature slices indicate the minimum and maximum soil temperatures during our visits.*

Lapwings showed longer return latencies when the nest was monitored for a shorter period of time (**Figure 14a, Figure 15**). On the day of the camera's deployment, the median observed return latency was 2.78 hours (n = 81, IQR 1.32 — 12.88 hrs). For visits where the camera had been present for at least 14 days, the median observed return latency was only 0.67 hours (n = 34, IQR 0.38 — 0.96 hrs). Moreover, for a given number of days a camera has been at a nest, lapwings tended to return faster if the clutch was closer to the end of its incubation period and vice versa (**Figure 14b**). For visits during the last 7 days of incubation, the median observed return latency was 0.68 hours (n = 83, IQR 0.40 — 1.50 hrs), while for earlier visits the median observed return latency was 1.67 hours (n = 133, IQR 0.52 — 5.87 hrs).

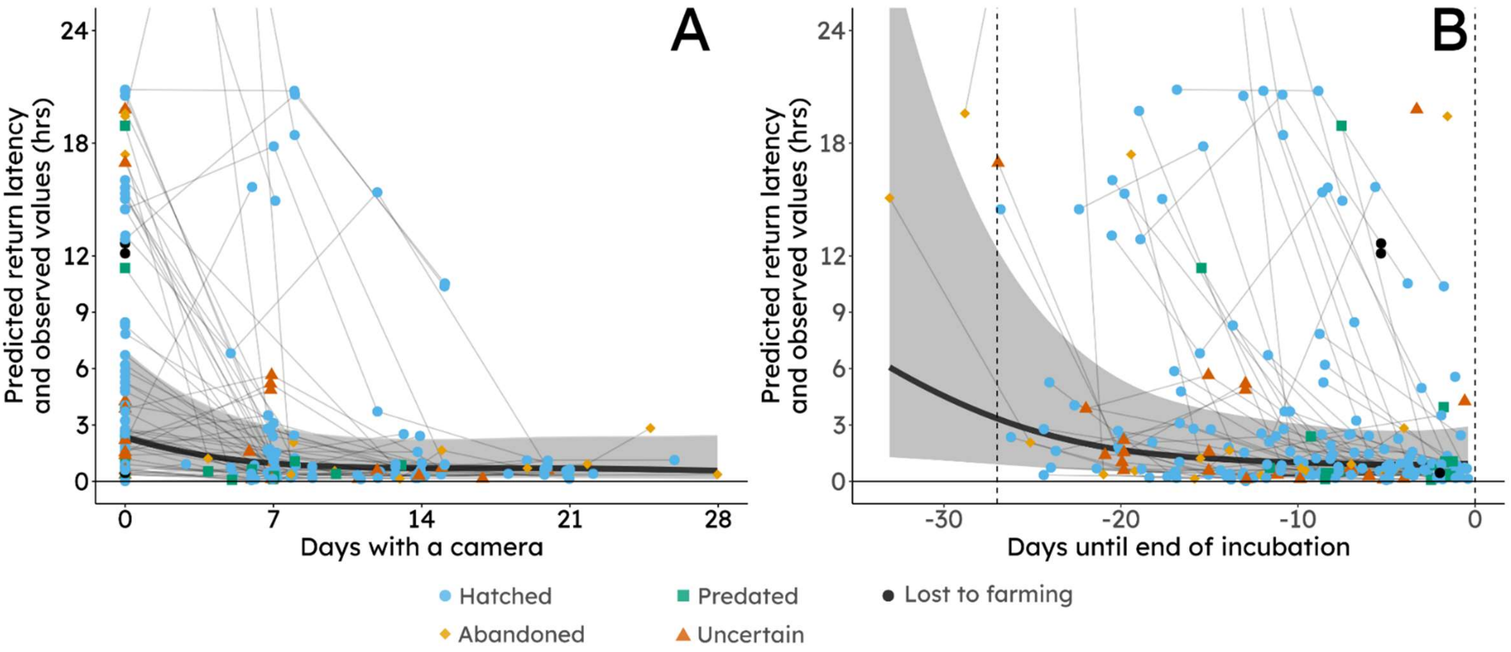

Figure 14: *The expected return latency curve (black line) as a function of: A) the number of days a nest has been followed by camera, B) the number of days remaining until the clutch will be assessed as having reached its outcome. The return latencies values are given on the response scale. Other variables are fixed at their respective medians. The shaded area indicates the 95% confidence interval. Points indicate observed return latencies. Point shapes and colours indicate the outcome of the clutch. Four extreme outliers returning after 24 hours are not shown. Dotted vertical lines on B) indicate the mean expected incubation duration of 27 days and the assessed end of incubation at 0 days. Grey lines connect measurement from the same nest*

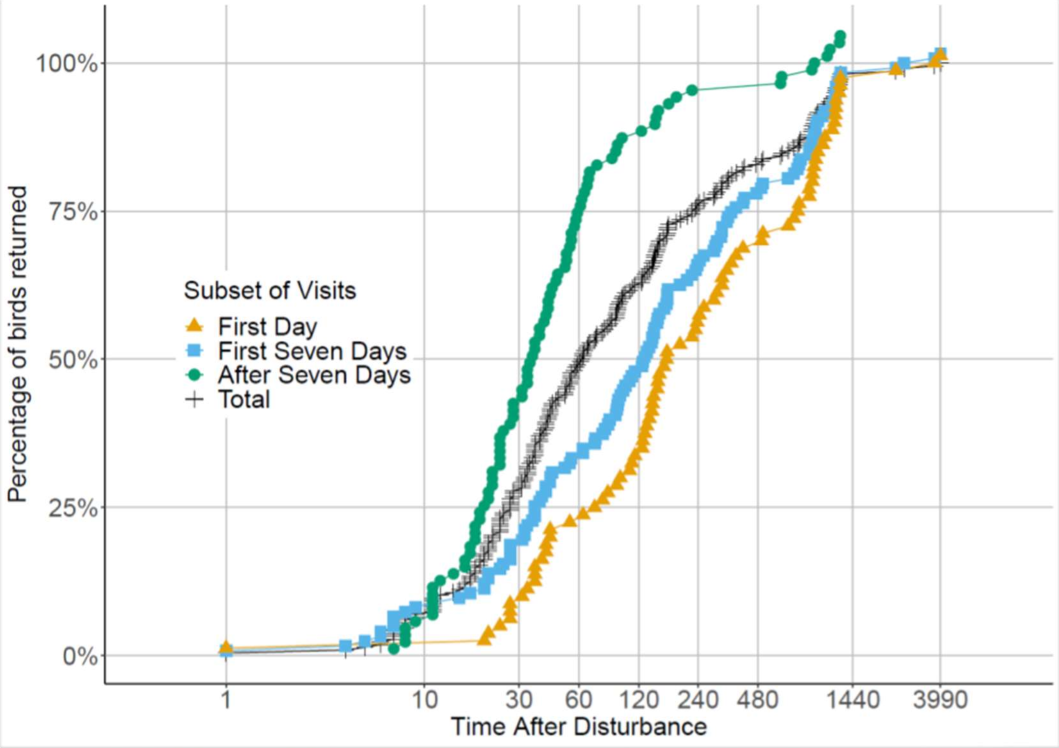

Figure 15: *Percentage of nests with a lapwing incubating as a function of the log-scale time that has passed since the end of the nest visit. On the first day, it takes more than 2 hours for half of all nests to be incubated again. For visits at least seven days after the first visit, it takes only slightly over 30 minutes for 50% of nests to be incubated.*

We found that the rate at which the camera was triggered based on detected motion predicted part of the measured return latency, with return latencies lower when rates of camera activity were higher (**Figure 16**). Moreover, high camera activation rates did not guarantee a fast return latency, nor did low camera activation rates prevent lapwings from being detected back on their nests rapidly, except at activation rates that would indicate a mean activation rate of 1 or 2 videos per hour. Camera activation rate and estimated wind speed were not correlated ($R^2 < 0.001$, $p = 0.7596$).

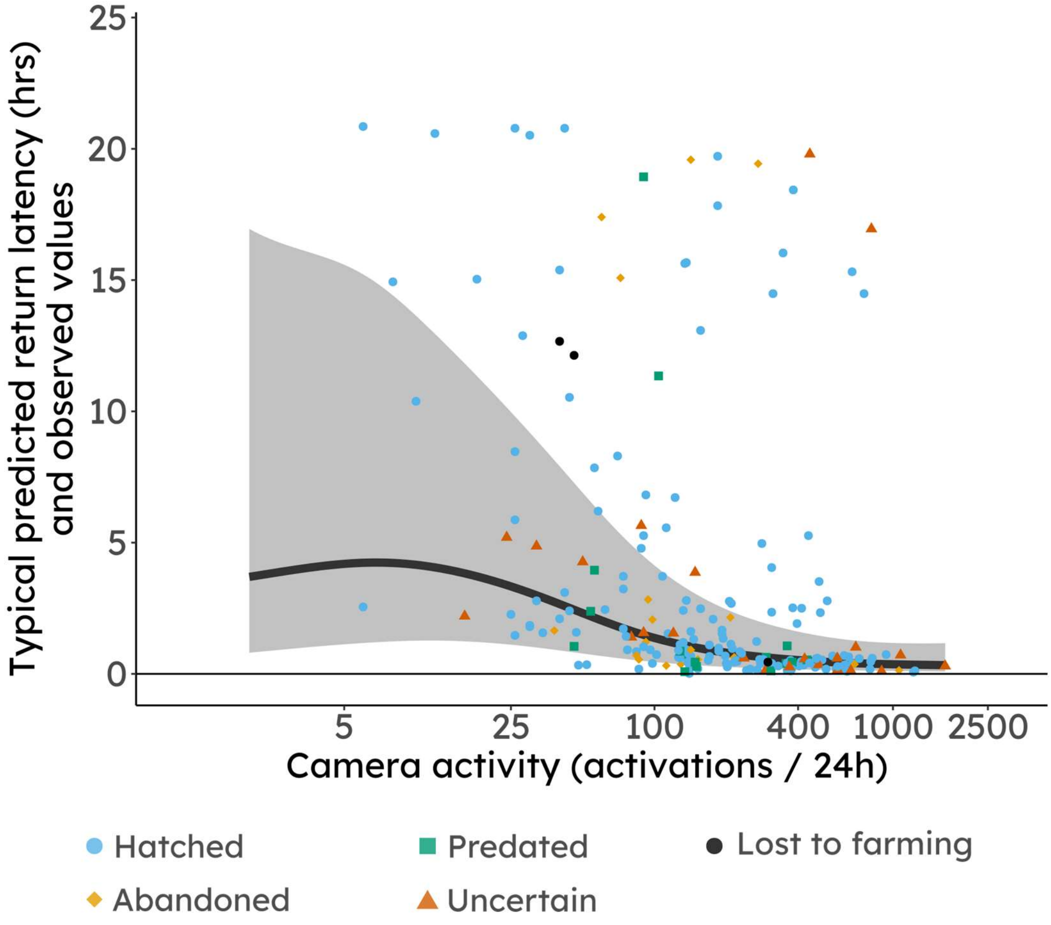

Figure 16: *The expected return latencies as a function of the activity rate of the camera in the 24 hours following a visit, with other variables fixed at their medians. The shaded area indicates the 95% confidence interval. Points indicate observed return latencies. Point shape and colour indicate the outcome of the clutch. Four outliers returning after more than 24 hours are not shown.*

4) Discussion

In this chapter we've presented lapwings' behavioural responses to human visits, conducted to facilitate monitoring by nest cameras. Our results revealed that our monitoring and visiting methods had a direct effect on lapwings' incubation behaviour. A human approach to a nest always resulted in the parent leaving its nest. We found that the time lapwings spent away from their nests after a disturbance was best explained by a combination of several factors. Lapwings returned faster the longer a camera had been at the nest and the closer the nest was to the end of incubation. Furthermore, the return latency was shorter in the mornings, when temperatures were higher, and wind speeds were lower. Finally, shorter return latencies were associated with higher camera activity rates over the 24 hours following a visit. The other parameters were not significant predictive variables when compared to the ones in the best-performing model.

Return latency could be partially explained by a complex relationship between three environmental variables at the time of the visit: soil surface temperature, wind speed, and the time of day relative to noon. We expected to find an optimum curve related to temperature, and faster returns in the morning as compared to the evening. We did not find our expected optimum curve relative to local temperature. This is most likely due to the lack of truly low temperatures in our dataset. Temperatures at our study sites only fell below freezing during the nights at the very start of the breeding season. Because avian eggs are resistant to periods of low temperatures, and shorebirds' especially so (Ahmad & Li, 2023), the clutches were not likely to be at risk of lethal undercooling. As there was little risk to the eggs, the adults could afford to be away from the nest at low temperatures.

At the high end of the observed temperature range, shorebird eggs are likely just as vulnerable as other birds' eggs to overheating and water loss (Webb, 1987). We have observed reduced return latencies at higher temperatures, as we would have expected based on the 'optimum curve' hypothesis. A replication of this study in a colder part of the breeding range might find the other end of the hypothetical optimum curve, where daytime temperatures might fall well below freezing. A similar temperature-related response was found for two wader species in Australia, with greater risk-taking behaviours shown at higher temperatures (Kostoglou *et al.* 2020), while Burrowing Owls (*Athene cunicularia*) showed the opposite pattern (Fisher *et al.* 2004). It's possible that the difference between the environmental risk to the offspring and the predator risk to the parent could explain these contrasting findings. Wader eggs in open nests may be at greater risk of overheating, which promotes riskier responses when temperatures are high. The sheltered burrow of the Burrowing Owls promotes less risky responses from its parent, as environmental risk to the offspring remains relatively stable (Nadeau *et al.* 2015).

We propose that our observed relationships between return latency and the three environmental variables can be primarily explained by the need to keep the clutch cool and prevent the eggs from drying out. At our sites the hottest time of day would be, on average, around solar noon. Temperature differences between the end of a visit and the return of a lapwing regularly exceeded 10°C. The switch between heating and cooling as the day progresses may explain why lapwings return more quickly in the mornings than in the afternoons at comparable temperatures. In the morning, it would be possible for their clutch to die of overheating if left unattended for several hours, but in the afternoon the clutch is likely to be safe from overheating if left unattended at non-lethal starting ambient temperatures.

Wind conditions have a direct impact on ambient temperatures. Air temperatures very close to the soil surface may differ from the general ambient air temperature by several degrees under low-wind conditions, and may be equalised with the surrounding air by stronger wind flow (Pfister *et al.* 2017). It follows that the clutch, which is located on the ground, may find itself differently impacted by higher wind speeds under different ambient environmental conditions. If the air close to the surface is cooler than the ambient air, the equalising effect of wind will tend to heat the clutch. Vice-versa, if the air close to the surface is warmer than the ambient air, greater wind speeds may be associated with greater cooling. Such differential effects of wind explain our observations where greater wind speeds reduced lapwing return latencies in the mornings but increased them in the afternoons. Under increasing ambient temperatures (mornings), extra wind will increase risk to the clutch, while under decreasing ambient temperatures (afternoons) extra wind will have the opposite effect. Whereas nearctic shorebirds breeding at high latitudes appear to modulate their nest absences to limit clutch exposure to low temperatures (Smith *et al.* 2012), lapwings in France appear to behave more similarly to their Australian counterparts (Kostoglou *et al.* 2020), or sandgrouse breeding in central Spain, which must prevent their clutches from overheating and will time their absences accordingly (Mougeot *et al.* 2014).

Rather than planning their absences to reduce danger to the clutch, the lapwings in our study were displaced from their nests by the arrival of a scientist. Our results suggest that lapwings habituated to our monitoring methods over time. The time it took lapwings to return to the nests decreased over each nest's monitoring period, with a greater drop for the first days. The observed pattern is consistent with habituation in a general sense (Rankin *et al.* 2009). Lapwings potentially could have habituated to the repeated visits by an experimenter, the presence of the camera, or both. The large difference in the return latency between the first and second visits (between 0 and 7 days, approximately) could be explained by a strong initial neophobic response to the camera itself. After the first visit the camera had become a permanent feature of the nest environment, with the lapwings having been continuously exposed to the setup for up to 168 hours. We would then explain any further decrease in return latency to habituation to the visits themselves. From our results, it appears that any habituation after 7 days was minimal, so most likely the lapwings did not further habituate to nest visits from the second visit onward.

A considerable proportion of lapwings were absent from their nests for more than 5 hours after the initial visit. This might mean that these lapwings experienced considerable stress as a consequence of the visit. If some lapwings were previously stressed by some unknown events or circumstances, this might partially explain why they reacted more strongly to the camera placement (Silverin 1998). Another part of the variation might be explained by intrinsic inter-individual differences in stress reactivity (Cockrem 2007). The combination of intrinsic propensity and pre-existing environmentally-related stress levels might explain the 7 pairs which seemed to abandon their nests directly after a camera was placed, having crossed a stress threshold sufficient for nest abandonment (Silverin 1998) after exposure to our monitoring protocol. It may also be worthwhile to investigate whether stronger initial responses might be followed by partial abandonment. It's possible that one of the two parents abandoned the incubation attempt in some cases. However, we would not have detected these abandonments because the other parent could have taken on full incubation duties. In these cases of partial abandonment, the clutch might hatch successfully, in which case we would score the nest as successful. Alternatively, if the incubation of the single remaining parent was not sufficient, this would show up in our results as a late abandonment. A closer examination of our footage may provide some preliminary indications for partial abandonment. However, we have no control measurements of the (highly naturally variable) distribution of nest attendance between the male and female (Sládeček *et al.* 2019), so we would not be able to differentiate between naturally uniparental nests and nests for which the male has abandoned the clutch.

For any individual nest, there was a direct relationship between the number of days the nest was followed by camera and the incubation stage of the nest. Nevertheless, nests were found in different stages of incubation — including on the last day of their incubation. This allowed us to disentangle the effects of the duration the nests were monitored and the incubation stage.

Lapwings were absent from the nest longer if they were at the earlier stages of incubation. The parents that were closer to the end of the incubation period, on the other hand, returned more quickly to their nests after a disturbance. This relationship falls within our expectations, given that bird embryos become more vulnerable to temperature anomalies in later stages of their development (Tazawa & Rahn 1986). Additionally, the required future effort to incubate the clutch to hatching is smaller when the clutch is closer to hatching, and this may lead the parents to be willing to take more risks. However, evidence for this hypothesis has been mixed in other bird species (Graham & Shutler, 2019).

Some notable factors that might influence trade-offs of this particular type were not accounted for in our study. We had no information on parental body condition, age, or previous breeding status. Furthermore, our random control variable operated on the scale of the breeding pair, not on the scale of the individual. A parent's body condition may influence how much it is willing to risk, with birds in particularly good condition able to incur greater energetic costs (Hegyi & Sasvari 1998), while birds that are in such bad condition that they might not survive until the next breeding season may initiate terminal investment in the current clutch (Sköld-Chiriac et al. 2019). Similarly, old birds may initiate terminal investment near the end of their life, while younger birds may prioritise their own future survival over the clutch's success (Velando et al. 2006).

One variable which might influence trade-offs of this type is clutch size, as lapwings show lower rates of nest attentiveness for smaller clutches when their clutches are artificially reduced (Larsen et al. 2003). However, the number of eggs in a clutch did not provide significant predictive value for our measured return latencies. It is possible that our sample of three-egg clutches may not have been large enough to produce a measurable effect in light of the other variables determining return latency. Alternatively, the nest manipulation as employed by Larsen and colleagues (2003) may be equivalent to a partial predation. Lapwings returning to a partially predated nest may adjust their reproductive investment as the expected gain from the reproduction attempt is reduced. Such an adjustment would not take place for nests where the number of eggs did not change.

In our study, part of the lapwings' return latency could be explained by the activity rate of the camera in the 24 hours following the nest visit. Higher rates of camera activation are expected when lapwings are moving more, when vegetation is set in motion by the wind, or when other species pass in front of the camera. Wind speed does not seem to provide a good indication of the camera activation rate, indicating that vegetation swaying in the wind is not a likely explanation for most camera activations.

Alternative explanations for the observed relationship between camera activation rate and return latency may be found in the differences in incubation schedules between pairs, and local differences in predator abundance. There are large variations in average incubation bout duration between lapwing pairs, as well as large differences in the participation of the male (Sládeček *et al.* 2019). In pairs with shorter incubation bouts, we expect more incubation exchanges, and so more movement in front of the nest cameras. The non-attending mate might have no information about the scientist's visit, and thus may return after its habitual off-bout duration. In this case, we expect pairs with shorter incubation bouts to show faster return latencies. We would then additionally find the returning lapwing to be the opposite sex of the lapwing incubating just before the visit, but we have not yet completed the labour-intensive process of individual recognition required to verify this.

At sites that are more frequently visited by potential predators, lapwings may be more active. Lapwings may rely on nest crypsis, distraction displays, and mobbing responses to ensure the survival of their nests, leaving the nest in 40% of cases where crows and Marsh Harriers (*Circus aeruginosus*) are sighted (Elliot 1985, Šálek & Cepáková 2006). Thus, in areas where there are more avian predators we expect movement in front of the cameras to be more frequent. Furthermore, we would expect the parents to return to the nest more quickly, as they should be present to prevent the depredation of their clutch by mobbing these predators (Kis *et al.* 2000).

We expected our lapwings to return more quickly later in the breeding season, as opportunities for laying replacement clutches would be reduced. When the current breeding attempt is likely to represent the only remaining opportunity to reproduce successfully, we can expect greater investment (Williams, 1966). However, in our study the day of the year did not explain variations in return latencies. There are several possible explanations for the lack of an effect of date. First, later clutches will consist of smaller eggs, from which smaller and weaker chicks will hatch (Hegyi 1996, Kubelka *et al.* 2020), representing a smaller reproductive benefit. Second, the parents themselves likely will have a reduced body condition later in the year (Hegyi & Sasvari 1998, Lislevand & Byrkjedal 2004), so they may have less energy remaining to invest in a rapid return. These factors, in addition to the increased temperatures later in the year, may obscure any effect that we can expect from the date.

5) Conclusion

In recent years the use of cameras has become a useful tool to monitor animal populations, including by observing the breeding success of ground-nesting birds. Any type of monitoring that involves repeated visits can impact animals directly or indirectly. The visits undertaken as part of protective measures can have measurable positive effects on nest survival (Kragten & De Snoo 2007, Zámečník *et al.* 2018). On the other hand, these visits may also entail inherent costs to the incubating birds such as increased risks of predation (Goedhart *et al.* 2010) or of adverse thermal conditions for the clutch.

Marking the nests of breeding lapwings with human objects, including cameras, can save their nests from destruction due to agricultural practices (**Chapter 1**), but it can also result in dozens of hours of absence from the nest or in rare cases even a nest abandonment. At our study sites, the majority of nests hatched successfully even with these long absences (**Chapter 1**). Throughout the study the birds habituated to the presence of the cameras. When controlling for activation rates of the cameras, lapwings showed return latencies that were consistent with behaviour that was sensitive to changes in the future weather conditions. The birds tended to return faster to their nests when the risks of overheating were increasing. Therefore, we suggest limiting the overall number of visits and taking into account the temperatures during monitoring visits especially for lapwings breeding in the warmer parts of their breeding range.

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Chapter III:

Thermoregulatory Behaviours of Northern Lapwings During Incubation in Warm Weather

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Abstract

Ground-nesting birds may show a range of thermoregulatory behaviours to cope with high temperatures at their nest sites. Over much of the breeding range of Northern Lapwings (*Vanellus vanellus*), a ground-nesting wader breeding in open habitat across the palearctic, a warming of several degrees Celsius over the next decades is expected during the habitual breeding period. In this study, we observed thermoregulatory behaviours of incubating lapwings in France, a part of their breeding range that already shows high temperatures at the end of the lapwing breeding season. We modelled lapwing thermoregulatory behavioural responses to environmental conditions. At the median observed wind speed of 0.55 m/s at 1 cm above the ground, the temperature threshold above which 50% of lapwings were expected to show some kind of thermoregulatory behaviour was 29.9°C measured by nest cameras 1 m above the ground. The threshold for finding a panting response in 50% of cases was 32.6°C, and the threshold to observe shading behaviour in 50% of cases was 34.5°C. Increased wind speeds affected both the probability to observe thermoregulatory behaviours and the proportion of time lapwings would be observed to spend on them. Shading and preening behaviours were increased under higher wind speeds, while the probability to observe panting was reduced. Our results suggest that lapwings may be under considerable heat stress during certain parts of their breeding cycle in France. If lapwings are unable to shift their breeding phenology, they will be experiencing higher temperatures at their breeding sites in the coming decades due to global warming. This may impact their breeding success or result in a breeding range contraction.

Keywords: thermoregulation, wader, climate change, self-directed behaviour, ethogram

1) Introduction

To successfully hatch their eggs, ground nesting birds should provide their clutch with the thermal conditions required for development, as well balance water loss so that the eggs do not contain too much or too little water (Rahn & Ar 1974, Davis *et al.* 1988). Over a range of species, this involves extensive contact between the clutch and an incubating parent's brood patch. The brood patch is maintained at a temperature between 35–42°C (Deeming, 2008), without allowing the clutch to exceed lethal temperatures of much more than approximately 41°C, depending on species (Webb, 1987). Though some embryos may exceptionally survive at temperatures of up to 47°C (Grant 1982). The thermoregulatory costs of incubation depend on weather conditions. When ambient conditions would result in the eggs cooling to below their optimal developmental temperature, birds should keep them warm. Conversely, when ambient conditions would heat the eggs above lethal temperatures, the incubating parent should cool its clutch. As spring and summer temperatures in western Europe are expected to increase over the coming decades (Rowell 2005, Guerreiro *et al.* 2018), local bird species may have to contend with higher temperatures during their breeding seasons.

To cope with high temperatures, birds may exhibit varying thermoregulatory behaviours. Panting, or hyperventilation, increases heat loss by evapotranspiration through the lungs (Bouverot *et al.* 1974, Amat & Masero 2004, Sharpe *et al.* 2021), and is observed for many bird species. Wing drooping — holding the wings outward from their usual resting position — increases the exposed surface area of birds compared to their wings' habitual resting position (Amat & Masero, 2004; Smit *et al.*, 2016). Ptiloerection, or raising the feathers, usually has the effect of increasing the insulative layer of air trapped by the feathers (Walsberg *et al.* 1978). When fully erect, the space between the feathers opens up, allowing air to pass between them more easily, at which point the behaviour serves a cooling function (Grant 1982, Battley *et al.* 2003, Amat & Masero 2004, Willmer *et al.* 2006). Standing above the nest, also described as 'shading', exposes more of a bird's body to the ambient air when compared to direct contact incubation (Purdue 1976, Brown & Downs 2003, Vincze *et al.* 2013), and exposes the highly vascularised brood patch (Bailey 1952). Finally, birds may soak their belly feathers in water, which results in evapotranspiration with minimal water loss for the bird involved, and provides water to the clutch if the bird resumes contact incubation while wet (Grant 1982, Amat & Masero 2004).

The thermoregulatory behaviours mentioned above have different costs. Panting results in increased water loss (Bouverot *et al.* 1974), as do behaviours that increase cutaneous evapotranspiration like wing drooping, shading, and ptiloerection, though perhaps to a lesser degree. Some behaviours additionally may not be equally available depending on environmental conditions. For example, wetting feathers can only occur when surface water is present, while under high relative humidity the potential for evapotranspiration is reduced (Gerson *et al.* 2014). There appears to be a trade-off between methods of heat loss. Panting is an effective heat loss method over a range of ambient humidity, while other methods of evapotranspiration may be more water efficient (Gerson *et al.* 2014). Therefore, we could expect different sets of thermoregulatory behaviours under different environmental conditions and different habitats.

The Northern Lapwing (*Vanellus vanellus*), a ground-nesting wader in the order *Charadriiformes*, can be found breeding in the palearctic from Morocco in the south to the Norwegian arctic circle in the north, and from the western edge of Europe to Mongolia in the

East (Cherkaoui & Hanane 2011, BirdLife International 2017). There has been evidence of dispersal on the order of thousands of kilometers for lapwings, indicating that there is likely considerable gene flow across the breeding range (Evans, 1968; Mead *et al.*, 1995). With such a wide breeding range, lapwings could be expected to show behaviourally plastic responses to a range of different environmental conditions. For example, by varying their nest structure according to the local environment (Kubelka *et al.*, 2019), by showing thermoregulatory behaviours, or by adapting their breeding phenology.

While the species has shown advances in laying dates (Musters *et al.*, 2010; Santangeli *et al.*, 2018), and individual lapwings show varied migration and reproductive schedules (Eichhorn *et al.*, 2017), there may be a limit to the plasticity of lapwings' breeding phenology. Should a limit be reached in the timing of the start of the breeding season, this may result in an increase in the average environmental temperatures during incubation and chick rearing (IPCC 2023).

Where the behavioural and physiological adaptations of the lapwings become unable to cope with local environmental conditions, we would expect them to be limited in their reproductive capacity. Prohibitive thermoregulatory costs, then, might be part of the mechanism underlying the limit of Northern Lapwings' southern distribution, and the temporal limit of their breeding season at their warmer breeding sites. Previous work has demonstrated the utility of comparing birds' responses to environmental conditions based on their behaviour, for example by defining a limit at which 50% of individuals may be expected to show thermoregulatory behaviours (Smit *et al.*, 2016). To help predict future breeding success of lapwings in the warm parts of their range and in a warmer future, an assessment of the apparent heat stress of lapwings may be insightful. Several thousand lapwings breed in France (Joyeux et al., 2022). As France is found on the warmer side of the lapwing breeding range, it likely provides an excellent place to observe lapwing thermoregulatory behaviour.

The objective of this study was to investigate the thermoregulatory and incubation behaviours of lapwing parents during the incubation phase of their reproductive cycle, and how these relate to environmental conditions at the nest site. We aimed to determine: 1) which of the commonly observed avian thermoregulatory behaviours lapwings show at their nests, 2) at which local environmental conditions, particularly in terms of temperature thresholds, they can be expected to show these behaviours at least 50% of the time, and 3) whether different thermoregulatory behaviours may be observed under different environmental conditions.

To investigate this, we analysed videos of Northern Lapwings at their nests. We modelled lapwings' behaviour according to local environmental conditions, how close their clutches were to hatching, the time of day, and the date.

2) Materials & Methods

2a) Nest monitoring

We scored videos of breeding lapwings from the 2021 and 2022 breeding seasons, monitored as part of a study of their hatching success (**Chapter 1**). The year 2022 was an exceptionally dry and warm year in France (Mittelberger et al., 2024). Monitored nests were spread between two regions in France: one coastal region and one inland region (**Figure 17**). This spread resulted in some variation in weather conditions throughout the season, while nests found within the regions showed closely related weather conditions on any particular day.

Videos from each nest were obtained with a motion sensitive trail camera (Victure HC300), including an onboard thermometer. Cameras were set to record 30-second videos, preceded by a photo, when movement was detected in front of them. Monitoring continued until the fate of the nest under observation could be determined. Cameras were deployed at 98 nests. To date, 55.05 hours of video from 58 nests have been scored.

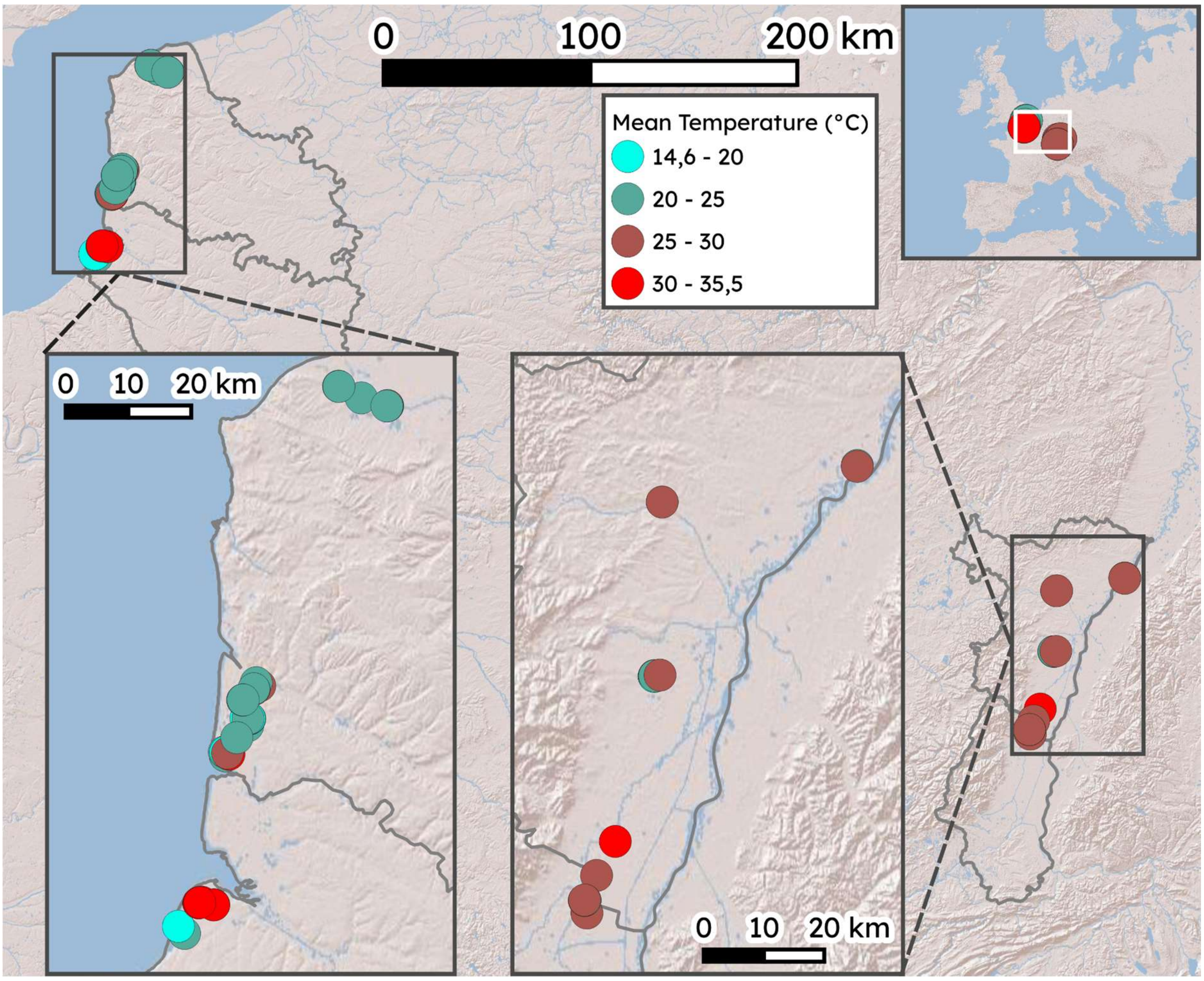

Figure 17: *Map of the nests for which videos were analysed. Point colours indicate the mean temperature measurements of the scored videos at that nest.*

2b) Video analyses and ethogram

We focused our observations on the warmest period of the day for our field sites, selecting all available videos for our nests between the hours of 11:00 and 14:00 CEST. We considered each nest-day as ‘an observation’, and observed all videos for one observation per nest before proceeding with a second observation. We concentrated our analyses on videos during the incubation phase, i.e. before hatching.

We defined and classified the following behaviours of interest: drinking, bathing, panting, wing drooping, preening, direct contact incubation, feather wetting, shading, absence, non-attending, at nest, and vigilance (see the ethogram in **Table 7**). We considered any behaviour that was observed to a greater degree in warmer conditions to be potentially related to thermoregulation or heat stress.

We scored all occurrences of behaviours of interest for each video for the focal animal using the program BORIS (Friard *et al.*, 2016). The focal animal was the Northern Lapwing located closest to the nest under observation. For state behaviours, we considered any bout as stopped when the behaviour was not observed for three consecutive seconds, or when the video ended. Because the interval between videos was unpredictable — with minutes passing between activations in some cases — we could not assume that behaviours observed at the end of one video and the start of the next occurred continuously in the interval between videos. A three-second delay between the end of observed behaviour and the end of scoring the state behaviour was applied to account for brief interruptions in behavioural patterns, for example during a preening bout: lapwings would often stop touching their bodies for up to two seconds before continuing.

Table 7*: Ethogram for focal all-occurrence behavioural observations of Northern Lapwings at their nests, in the context of heat stress. 'Description' contains the observable characteristics of a behaviour needed to describe it during an observation, type indicates whether it is scored as a point or state behaviour ("instantaneous counts" vs. "start and end points"), 'exclusion criteria' describe behaviours which are closely related or also covered by the content of 'description' but which are nonetheless not counted as that behaviour, and 'comments' contains other information relevant to replication.*

Behaviour	Description	Type	Exclusion criteria	Comments
Direct contact incubation	Sits on the nest cup, with its abdomen touching one or more eggs. May include momentary breaks during which the parent repositions itself or the eggs, or re-arranges nest lining.	State	Apart from momentary breaks, the abdomen should touch the surface of the nest and eggs.	
Shading	Stands above one or more eggs or chicks with less than one body length's lateral displacement.	State		Can be confused with an initial hesitation before starting direct contact incubation.
Panting	Holds its beak open for at least 3 seconds, usually varying the angle between the top and bottom halves of the beak slightly over time. Periodic apparent swallowing motion.	State		
Preening	Touches its own body where it is covered with feathers with its beak or feet, often rhythmically.	State	Does not include 'resting posture' (head curled onto its back, moving very little).	Not to be confused with nest maintenance behaviour during direct contact incubation.
Not visible	Parent, or its drop shadow, is not in view of the camera.	State	Drop shadows in flight are not counted for this behaviour.	
Non-attending	Parent is absent from the nest cup and its immediate area (1 body length radius around the cup).	State		
At nest	Parent around the nest (within 1 body length) but not incubating or shading.	State		
Vigilance	Parent rotates head so one eye is facing the sky.	Point		
		Behaviours of interest not observed in this study		
Drinking	Dips beak in water, scooping water up, then swallows.	Point		
Bathing	Submerges part of its body which is covered in feathers in water, ceases lateral locomotion.	State		
Wing drooping	Wings held below the resting position, extended away from the flanks.	State		
Feather wetting	Direct contact incubation with wet feathers in an otherwise dry environment.	State	During rain, birds are not considered to be wetting.	

2c) Weather variables

We measured and estimated weather variables at the nest sites with three different methods: 1) direct measurements by the nest camera, 2) measurements by 29 iButton loggers (iButton DS1925) placed 50 cm from the nest, or 3) values derived from microclimate modelling using the R packages *NichemapR* and *microclima* (Kearney & Porter, 2017; Maclean *et al.*, 2019) based on the ERA-5 dataset of the Copernicus institute (Hersbach *et al.*, 2020; Klinges *et al.*, 2022). For our model-derived weather variables, we scaled our hourly weather variables to a per-video scale by linear interpolation between hourly values to the videos' start times.

Microclimate modelling derived variables were available on an hourly basis, while iButton measurements were made every 20 minutes. Temperature data from the cameras is available for every second of video footage recorded, but was evaluated at two timescales: first by OCR (Optical Character Recognition) software for every 30 s video using the R packages *tesseract* and *magick* (Ooms, 2023b, 2023a), then averaged for all videos comprising a greater timescale unit for analysis of time budgets.

Air temperatures at 2m height from the microclimate model were strongly correlated with temperatures reported by the cameras (r^2=0.819, pearson's correlation, t=166.95, n=6153). Temperatures reported by the camera were moderately correlated with temperatures reported by the iButtons (r^2= 0.279, pearson's correlation, t=32.78, n=2773). The weaker correlation with the iButtons is likely related to the difference between the general air temperature and temperatures very close to the surface, which are more variable over time (Sigmund *et al.* 2017), whereas satellite-based estimates of air temperature track the temperatures of the cameras more closely.

2d) Data analysis

To more accurately represent changing weather conditions over time, we subdivided each observation between 11:00 and 14:00 into four time bins: 11:00 – 11:30, 11:30 – 12:30, 12:30 – 13:30, and 13:30 – 14:00.

We calculated mean values for each bin by taking the mean value of temperature measurements by the camera for each video in the bin, and means of the interpolated weather variables from the microclimate model. We summed the observed values of "Not visible" and "Non-attending" from the ethogram to a more general category of "Absence".

For each behavioural category observed, we constructed two different models: a model predicting the proportion of time spent on the behaviour during the hourly bins described above, and a model predicting the probability of observing the behaviour during any particular video. For model building, we considered two variables too strongly correlated for including in the same model if their correlation coefficient exceeded |0.65| (Dormann *et al.*, 2013).

To address the question of at which environmental conditions lapwings may be expected to perform thermoregulatory behaviours at least 50% of the time, we constructed probability models. These were logistic regression models, constructed using the *lme4* R package (Bates *et al.*, 2015). Model selection for probability models was performed using an exhaustive model selection procedure based on Akaike's Information Criterion (AIC, Akaike, 1998; Sugiura, 1978), using the *MuMIn* R package (Bartoń, 2023). The top-level models supplying their variables to the exhaustive selection procedure were defined as:

Behaviour (Binomial) ~ Camera Temperature * Wind Speed +
Time difference from noon + (1 | Nest identity)

In these models, camera temperature, wind speed, and time difference from noon were considered fixed variables. To account for repeated sampling from each breeding pair, nest identity was considered a random variable. We verified a lack of multicollinearity between the fixed variables using the R package *performance* (Lüdecke *et al.*, 2021) with a fully additive version of the top level model (because interaction terms are naturally multicollinear). Relative to the model showing the lowest AICc, more complicated models were not considered supported by the data if they showed an increase in parsimony of less than 2 units of AICc for every added degree of freedom (Arnold, 2010). Out of 6606 scored videos, logistic regression proceeded for the 6153 videos at 58 nests for which temperature values could be read from the videos (mean 106.1 videos per nest, sd = 75.8 videos, n=58). Following Smit *et al.* (2016), we estimated the temperature values at which we would expect 50% of cases (videos for our study) to feature a particular behaviour. We defined these for a range of observed wind speed values to account for models' dependence on multiple environmental parameters, based on observed 5%, 25%, 75%, and 95% quantiles of wind speed. We name these estimates the "50%-prevalence points", or "behaviour50" where behaviour is an abbreviation of the relevant behavioural category, e.g. "pant50" for panting behaviour.

The probability models would provide an estimate of environmental conditions at which lapwings would be expected to perform a behaviour at least once in 50% of all 30-second intervals. However, we were also interested in when lapwings would be expected to perform a behaviour for 50% of their available time. To investigate this, we constructed the proportion models. These were beta regressions with a logit link, constructed using the *glmmTMB* R package (Brooks *et al.*, 2017). Model selection for proportion models was performed using a backward stepwise process. The models included variables to estimate dispersion and zero-inflation as a function of environmental variables. The top-level model for each behaviour was defined as:

Behaviour (Proportion of time) ~ Camera Temperature * Wind Speed +
Days until end of incubation * Day of the year + (1 | Nest identity)
Dispersion ~ Camera Temperature * Wind Speed
Zero-inflation ~ Camera Temperature * Wind Speed

For the proportion models, we considered camera temperature, wind speed, the interaction effect between temperature and wind speed, the days left until the end of incubation, the day of the year (days since 1 January), and the interaction effect between the days until the end of incubation and the day of the year, as fixed variables that might explain the proportion of time spent on a behaviour. To account for repeated measurements from breeding pairs, we considered nest identity as a random variable. Beta regressions allow for a dispersion parameter which varies over some parameters, for which we considered camera temperature, wind speed, and their interaction effect to be likely candidates. We included a zero-inflation parameter, accounting for the probability that a particular behaviour would be expressed exactly 0% of the time. We considered that camera temperature, wind speed, and the interaction between temperature and wind speed might be likely variables explaining whether lapwings would spend no time at all on certain behaviours.

The models for every behaviour category were based on the same top-level model structure, except direct contact incubation, for which the number of measured zeroes (3) did not warrant the inclusion of a zero-inflation factor. In this case, we transformed the three zero values to an arbitrarily small value instead. The top-level model was otherwise identical. We verified a lack of multicollinearity in a fully additive version of the top-level model. Parameters were removed based on the highest p-value estimate for the individual variables' effects in the model, until all model variables were assessed as significantly predictive ($p<0.05$). Selection started with the zero-inflation part of the model, then proceeded to the dispersion part, until finally selecting down the variables in the part of the model predicting behaviour. Out of 55.05 hours of observed video footage from 58 nests, 54.39 hours from all 58 nests were used for the proportion models / time budget analysis (mean 56.3 minutes per nest, sd=37.5 minutes, n=58). We removed two hour bins for which a temperature measurement could not be established.

3) Results

3a) Population-level time budgets

Out of the behaviours listed in the ethogram (**Table 7**), we did not observe the following: drinking, bathing, feather wetting, and wing drooping.

Videos featured the following behaviours: 4254 videos direct contact incubation (69.1%), 1183 videos shading (19.2%), 1342 videos panting (21.8%), 1013 videos preening (16.5%), 252 videos 'at nest' (4.1%), and 1278 videos 'absence' (20.8%, of which 1088 not visible and 336 non-attendance, 146 videos with both).

Over the 54.39 hours of analysed video footage, lapwings spent a total of 34.59 hours in direct contact incubation (63.6%), 8.56 hours shading the nest (15.7%), 10.62 hours panting (19.5%), 5.17 hours preening (9.5%), 0.82 hours 'at nest' (1.5%), and 10.39 hours in 'absence' (19.1%, of which 2.8%-point visible on camera and 16.3%-point not visible). 4860 instances of vigilance were observed, for an average rate of 1.49 per minute over all nests.

3b) Weather conditions at the nests

Temperature values from close to the ground were higher than those from above the ground. This was true for microclimate model derived values at 2m above the ground as compared to those at ground level (wilcox test, p<0.001, n=6153), as well as measurements from the cameras as compared to those from the iButton loggers at the same nests (wilcox test, p<0.001, n=2773). The combination of high wind speed and temperature was rare. Similarly, the combination of low temperature and low wind speed was also rare (**Figure 18**).

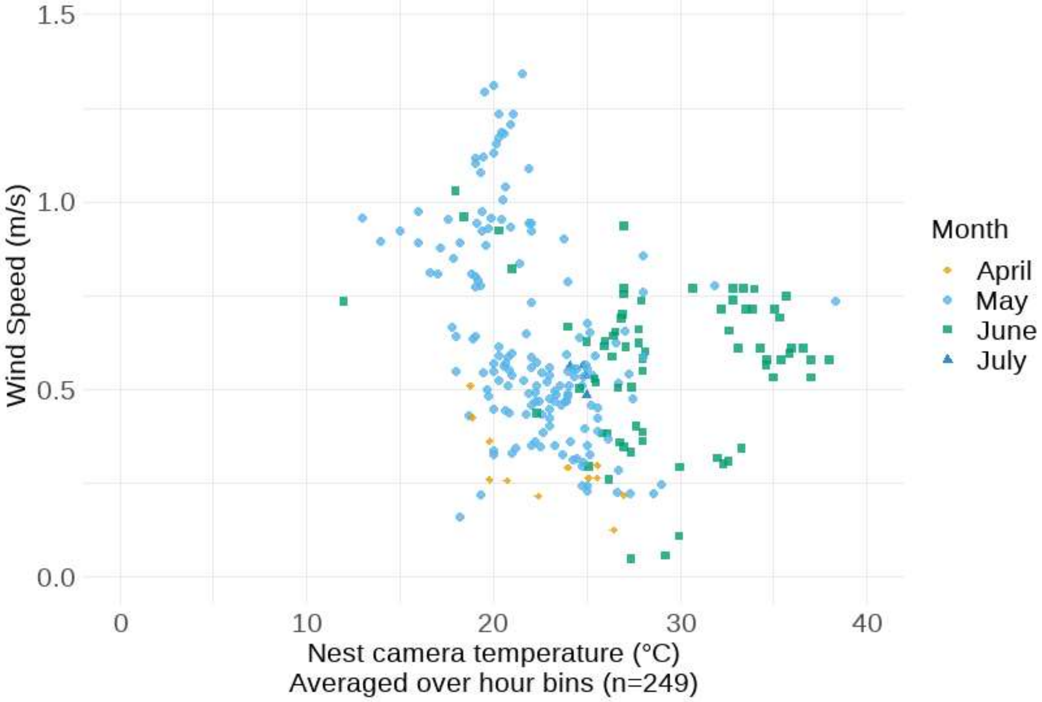

Figure 18: *Temperatures and wind speeds for scored videos. Temperatures were automatically extracted using Optical Character Recognition (OCR). Shown are the averages for each hour bin. Point colours and shapes indicate the month from which the video originates.*

3c) Probability of observing a particular behaviour

Our analysis of the individual observed state behaviours showed that **direct contact incubation** was less likely to be observed with increasing temperatures at low wind speeds, but with increasing wind speeds, direct contact incubation was likely to be seen even at high temperatures. In addition, direct contact incubation became more likely later in the day (**Figure 19, Table 8**). The probability of observing a bird performing **shading** behaviour increased with increasing temperatures and later in the day, but was unaffected by wind speed (**Figure 19, Table 8**). **Panting** behaviour was more frequently observed at higher temperatures, but was seen less with increasing wind speeds, especially when temperatures were high (**Figure 19, Table 8**). **Preening** behaviour was seen less at higher temperatures when wind was almost absent, but was seen more at higher temperatures when there was some degree of wind, with greater wind speeds resulting in a higher chance to observe preening behaviour at the same temperature (**Figure 19, Table 8**). Finally, **Absences** were less frequently observed at higher temperatures, higher wind speeds, and later in the day (**Figure 19, Table 8**).

Based on our behaviour scoring of individual videos, our models estimated the 50%-prevalence points of each behaviour along the observed temperature range according to wind speed conditions (**Table 9**). Direct contact incubation occurs in 50% of cases (Contact50) at 28.7°C at low wind speeds, and increases beyond our observed temperature range for high wind speeds. Shade50 (Shading) occurs at 34.6°C and is unaffected by wind speed. Pant50 (Panting) occurs at 31.4°C for low wind speeds and increases to 36.2°C at high wind speeds. Preen50 (Preening) does not occur at low wind speeds and becomes 31.5°C at high wind speeds. Nest50 (At nest) is not predicted to occur at any part of our temperature range at any observed wind speed. Absence50 (Absence) is also not expected in any part of our observed temperature and wind speed ranges, but is more common than ‘at nest’ (**Table 9**).

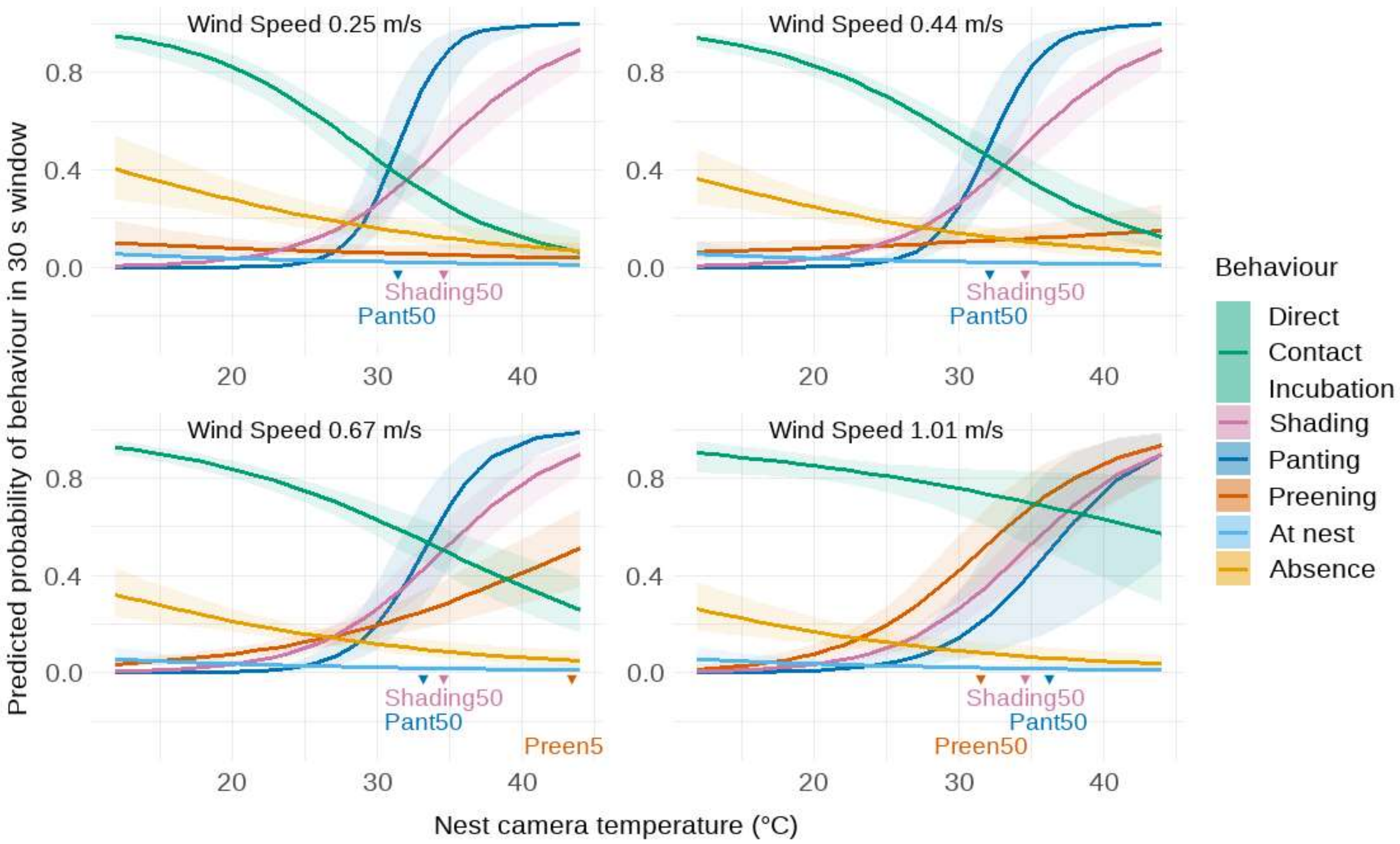

Figure 19: *Estimated probabilities to observe behaviours as a function of camera temperature and wind speed, according to the best-fit models for each behaviour category. Lines indicate model estimates while shaded areas indicate 95% confidence intervals.*

Table 8*: Slope estimates of the best-fit logistic regression models. Variables not occurring in the model are indicated with '—'. Bolded variables are assessed as significant model terms, at the level of p<0.05 (*), p<0.01 (**), and p<0.001 (***). df: degrees of freedom of the model. weight: model weight out of 16 possible models.*

Behaviour	**Intercept**	**Camera Temperature**	**Wind**	**Temperature : Wind**	**Time from noon**	**df**	**weight**
Direct contact incubation	**5.957*****	**-0.214*****	-2.759	**0.152***	**0.195*****	6	0.902
Shading	**-7.812*****	**0.230*****	—	—	**0.112***	4	0.528
Panting	**-22.166*****	**0.719*****	**11.732*****	**-0.430*****	—	5	0.273
Preening	-0.208	**-0.112****	**-6.533*****	**0.325*****	—	5	0.727
At nest	**-2.223****	-0.052	—	—	—	3	0.148
Absence	0.467	**-0.070*****	**-0.844***	—	**-0.187*****	5	0.613

Table 9: *Predicted 50% prevalence points of behaviours from the logistic regression models, assessed over the observed temperature range (12°C – 44°C) at different wind speeds, while time from noon is kept constant at its median value of -1.05 hours. Arrows indicate when a behaviour is expected to be observed more (↑) or less (↓) than in 50% of cases for the entire temperature range, in which case the closest prevalence to 50% is provided.*

Behaviour	**Wind speed 5% quantile 0.25 m/s**	**Wind speed 25% quantile 0.44 m/s**	**Wind speed 75% quantile 0.67 m/s**	**Wind speed 95% quantile 1.01 m/s**
Direct contact incubation	28.7°C	30.8°C	34.7°C	↑ (57% at 44°C)
Shading	34.6°C	34.6°C	34.6°C	34.6°C
Panting	31.4°C	32.1°C	33.2°C	36.2°C
Preening	↓ (10% at 12°C)	↓ (15% at 44°C)	43.4°C	31.5°C
At nest	↓ (5% at 12°C)	↓ (5% at 12°C)	↓ (5% at 12°C)	↓ (5% at 12°C)
Absence	↓ (40% at 12°C)	↓ (36% at 12°C)	↓ (32% at 12°C)	↓ (26% at 12°C)

3d) Proportion of time engaged in a particular behaviour

Beta regressions on the proportion of time spent on behaviours converged mostly around effects of temperature and wind speed. Of these, the models for direct contact incubation and shading indicated that they were primarily explained by local temperatures, while the model predicting the proportion of time spent preening also relied on local wind speeds (**Table 10**). The proportion of time spent in 'absence' or panting was explained by the most complicated models, incorporating not only local weather variables but also the development of the clutch and the day of the year (for panting only).

Table 10: *Effect slopes for the proportion models on the logit scale. p-values are indicated at p<0.05 (*), p<0.01 (**), and p<0.001 (***). Variables selected out of the model are indicated by '—' while 'NA' indicates that the variable was never estimated. The dispersion parameter for panting was selected down to a constant without calculated p-value (indicated by x). The model predicting direct contact incubation did not include a zero-inflation parameter.*

Behaviour	**Aspect**	**Intercept**	**Camera temperature**	**Wind speed**	**Temperature : Wind Speed**	**Day of the year**	**Days until end of incubation**	**Day of the year : Days until end of incubation**
Direct contact incubation	Mean	3.426***	-0.112***	—	—	—	—	—
	Dispersion	-0.049	0.057**	—	—	NA	NA	NA
Shading	Mean	-10.543***	0.338***	4.334*	-0.169*	—	—	—
	Dispersion	5.672***	-0.06*	-2.377***	—	NA	NA	NA
	Zero-Inflation	-0.259	—	6.845***	-0.328***	NA	NA	NA
Panting	Mean	-23.791***	0.450***	10.657**	-0.410**	0.072***	-0.981***	0.007***
	Dispersion	6.66^{X}	—	—	—	NA	NA	NA
	Zero-Inflation	13.204***	-0.510***	—	—	NA	NA	NA
Preening	Mean	-2.930***	—	-2.416**	0.134***	—	—	—
	Dispersion	3.464***	—	—	-0.045*	NA	NA	NA
	Zero-Inflation	5.687***	–0.286***	—	—	NA	NA	NA
Absence	Mean	6.381***	-0.320***	-10.169***	0.445***	—	-0.022*	—
	Dispersion	-7.769***	0.407***	13.651***	-0.626***	NA	NA	NA
	Zero-Inflation	-5.264***	0.109***	1.885**	—	NA	NA	NA

The proportion of time spent on direct contact incubation decreased with increasing temperature. The dispersion of direct contact incubation behaviour was related to temperature, with a greater predicted variation in direct contact incubation at higher temperatures (**Figure 20A**).

The proportion of time predicted to be spent on shading behaviour increased with temperature and wind speed, but decreased with the interaction between the two (**Figure 20B**). The dispersion of time spent shading was negatively affected by wind speed and temperature, predicting a tighter distribution at higher temperatures, higher wind speeds, or both. The zero-inflation factor for shading was affected positively by wind speed but negatively by wind speed's interaction with temperature, predicting more zeroes at higher wind speeds (and consequently less shading), except at high temperatures, where the probability of seeing no shading behaviour at high wind speeds approaches zero. This resulted in a pattern in lapwings' responses, such that they would be predicted to show shading behaviour at high temperatures and wind speeds, and a greater proportion of time would be predicted to be spent on shading behaviour when wind speeds were lower.

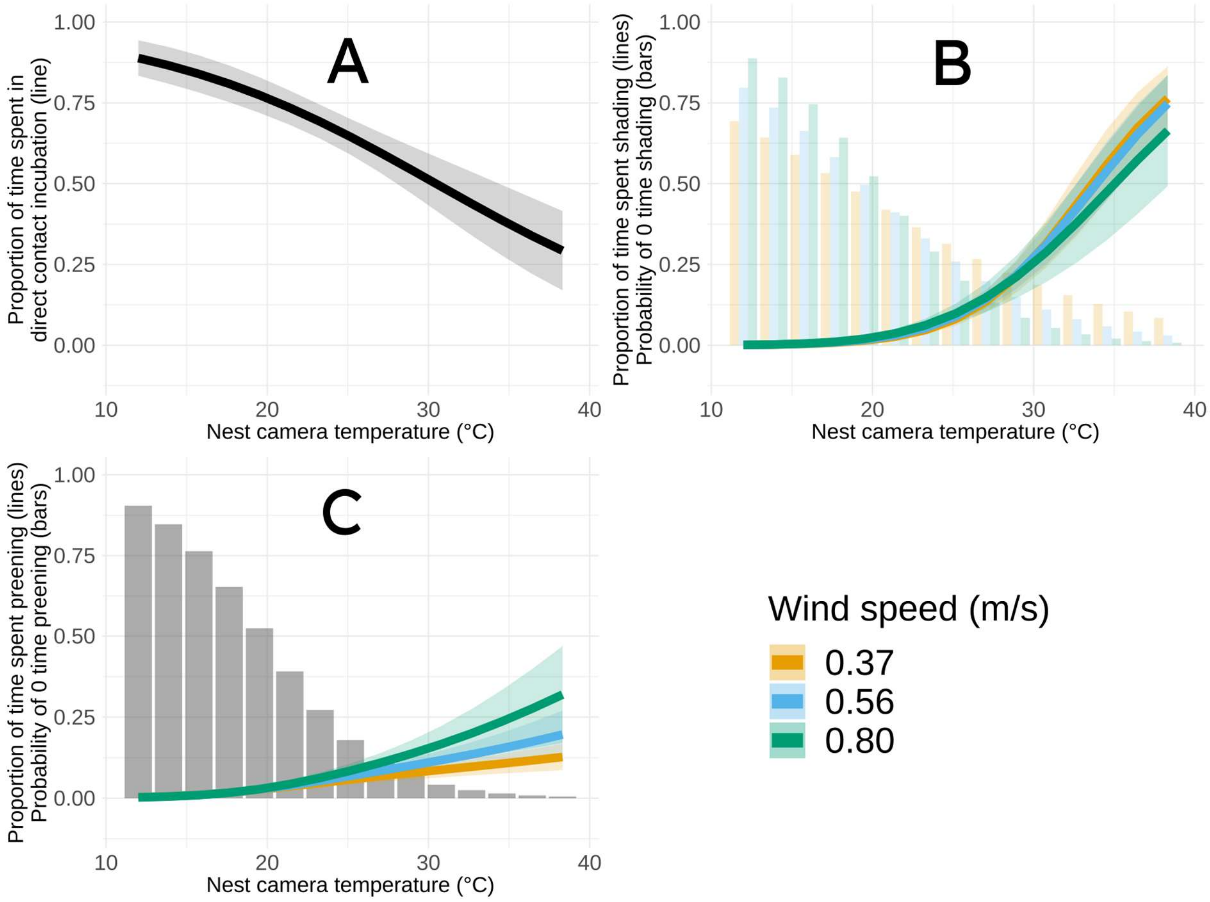

***Figure 20**: Predicted proportions of direct contact incubation (A), shading (B) and preening (C) as a function of temperature and wind speed. Shaded areas indicate 95% confidence intervals. The model describing direct contact incubation included no zero-inflation factor. In the graphs for the other behavioural categories, this factor is indicated by bars. Colours indicate different wind speeds.*

The proportion of time spent preening was best explained by wind speed and the interaction between wind speed and temperature (**Table 10**). The dispersion of preening behaviour was best predicted with an interaction effect of wind speed and temperature, with less variation at the combination of high wind speed and temperature. The complete absence of preening behaviour was related to temperature, with fewer cases of zero preening at higher temperatures. For our observed temperatures and wind speeds, this resulted in preening being predicted when temperatures were high, and more preening being predicted when wind speeds were also high (**Figure 20C**).

The proportion of time spent panting was predicted to be higher at higher temperatures, and higher wind speeds, but lower as a function of their interaction effect. Furthermore, less panting was expected when the end of incubation was close, but more was expected later in the year, and as a function of the interaction between the approaching end of incubation and the progressing year. The dispersion of panting behaviour was best modelled as a constant, but zero-inflation of panting was predicted as a function of temperature (**Figure 21**): at higher temperatures, we expected to find fewer cases without panting as well as the aforementioned greater mean proportion of time spent panting. We expected lapwings at high temperatures to spend less time panting if wind speeds were higher. At fixed temperatures and wind speed, we would expect more time spent on panting later in the year when the end of incubation is closer, and less time spent on panting early in the year when the end of incubation is closer.

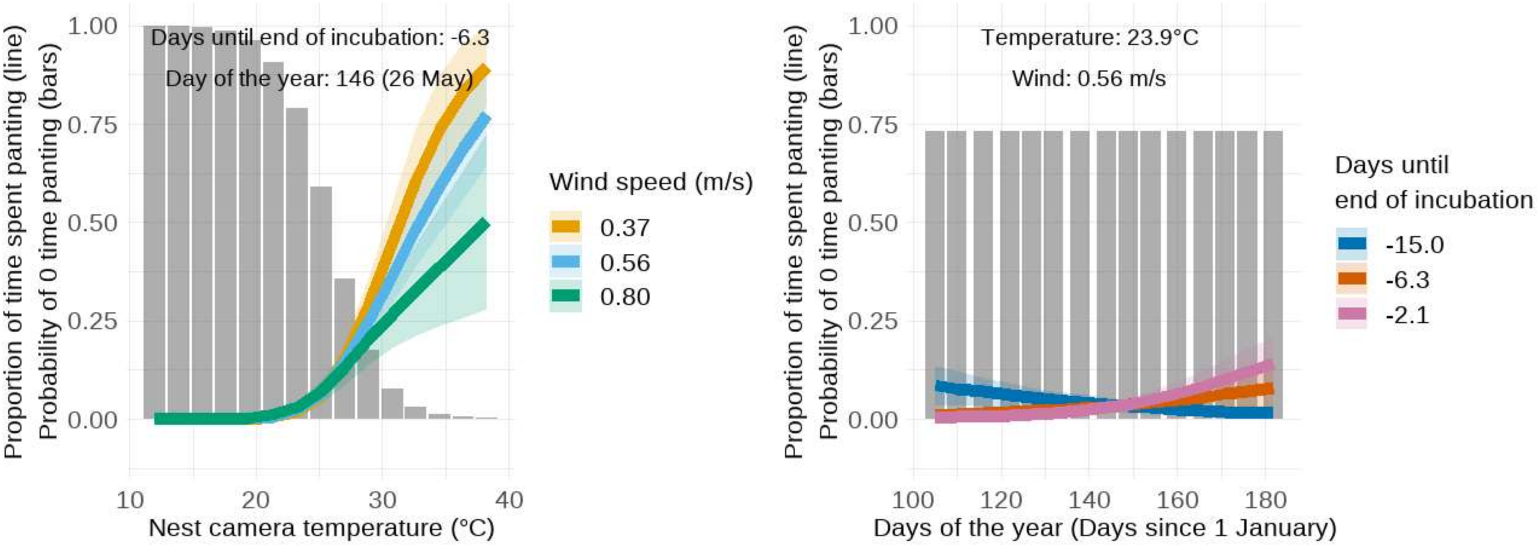

***Figure 21**: Predicted proportion of panting (lines) and probability of observing 0 panting (bars) as a function of temperature and wind speed (Left), or days until the end of incubation and days of the year (Right). Shaded area indicates the 95% confidence interval. Colours indicate different wind speeds (Left) or days until the end of incubation (Right). The variables not varying in either graph are kept constant at their median values.*

The proportion of time a lapwing was predicted to be ‘absent’ was explained by a combination of temperature, wind speed, their interaction effect, and the days left until the end of incubation (**Table 10**). The dispersion of ‘absence’ was best explained by the combination of temperature, wind speed, and their interaction effect, predicting greater variability at high wind or temperature, but with the combination of both not resulting in an additive increase of variability. A complete lack of absence was best predicted by temperature and wind speed.

For our observed temperatures and wind speeds, these relationships resulted in a saddle-shaped response: little 'absence' where extremes of wind speed or temperature are not accompanied by an equivalent of the other variable, greater 'absence' at the combination of low temperatures and low wind speeds, and intermediate 'absence' at intermediate combinations of temperature and wind speed as well as the combination of high temperature and wind speed (**Figure 22**). However, neither the combination of low wind speed and temperature nor the combination of high wind speed and temperature were frequently observed (**Figure 18**). Independent of environmental conditions, lapwings were 'absent' less when the end of incubation approached.

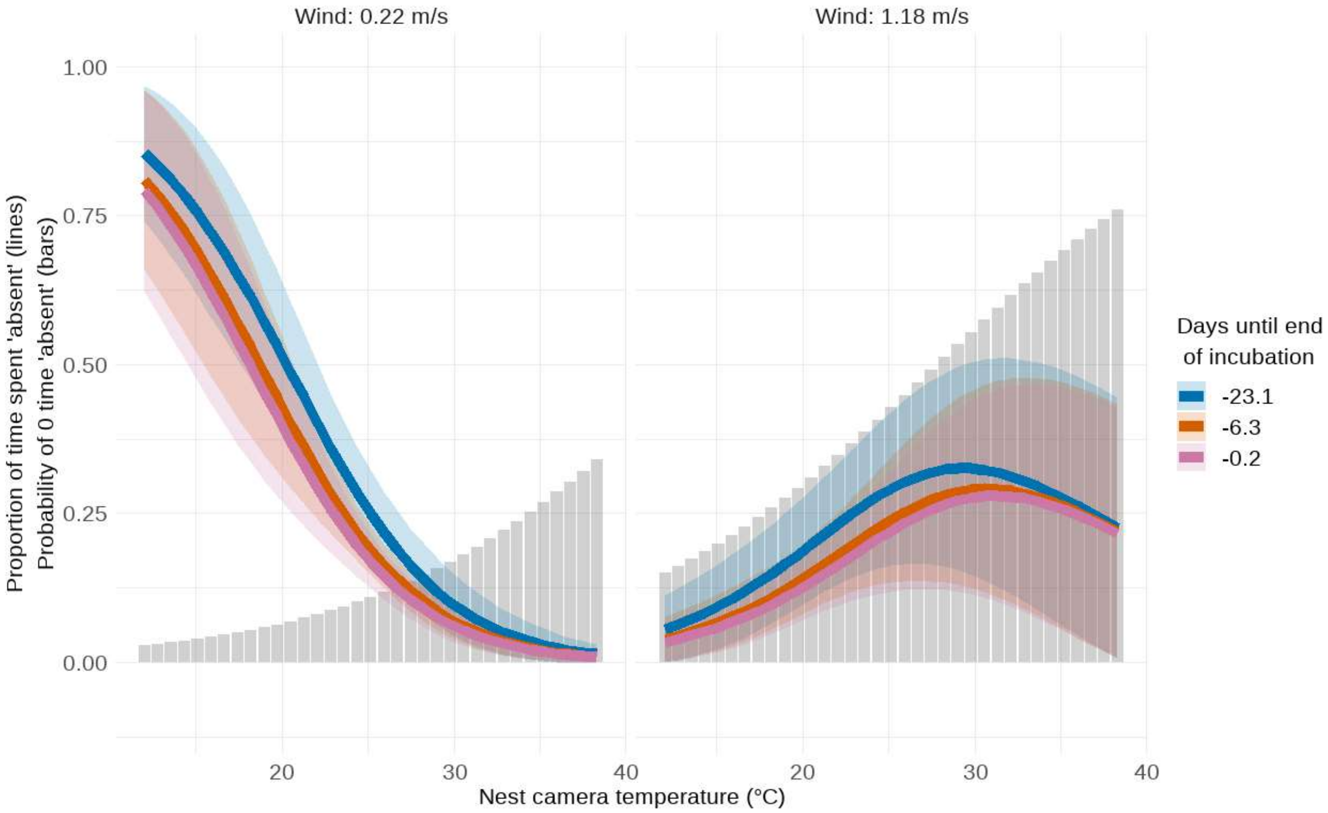

Figure 22: *Predicted proportion of 'absence' and the probability of observing 0 'absence', as a function of temperature (x axis), wind speed (panel columns), and days until the end of incubation (colours). Colored shaded areas indicate the 95% confidence intervals. Wind speeds are presented at the limits of the 95% quantile. Days until the end of incubation are presented at the limits of the 95% quantile and the median.*

As for the logistic regression 50%-prevalence points presented above (**Table 9**), we estimated 50%-occurrence frontiers for our time budgets based on beta regressions (**Figure 23**). Over our observed environmental conditions, the models predicted a range of conditions above 27-28°C and below approximately 30.5°C where lapwings should spend about 50% of their time in direct contact incubation while also showing a considerable amount of thermoregulatory behaviour. In accordance with the results for the logistic regressions and the more general time budget, the models predicted panting to be prevalent at a lower temperature limit than shading, and for preening to be most prevalent at high wind speeds. The models also predicted lapwings to be absent from the nest when the environment was cool with relatively slow winds, where they predicted very little thermoregulatory activity. The conditions under which the model predicted to see a large proportion of time spent 'absent' became more restricted as the end of incubation approached.

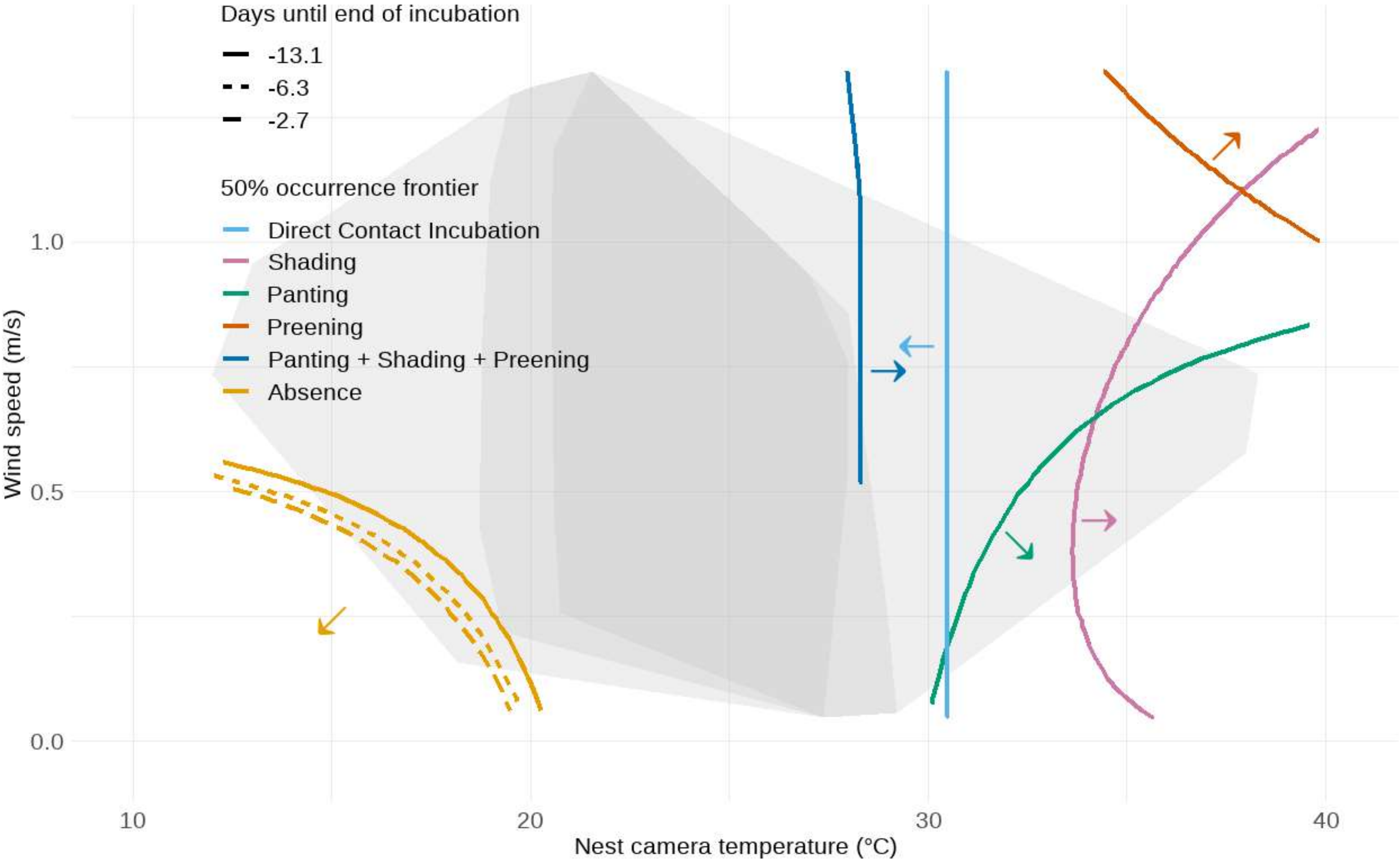

Figure 23: *50%-occurrence frontiers for some of the behaviours shown by lapwings at their nest sites. Grey polygons indicate the 100%, 80%, and 60% minimum convex polygons of observed temperature and wind speed values. Lines indicate the weather conditions under which proportion models expect lapwings to engage in a behaviour 50% of the time within the ranges of observed temperatures and wind speeds, with other variables kept at their median values. Absence from the nest was assessed at the 25%, 50%, and 75% percentiles of observed values of days until the end of incubation. Arrows indicate the side of the space in which lapwings are predicted to show a particular behaviour more than 50% of the time.*

4) Discussion

In this study, we showed that Northern Lapwings in their current breeding range exhibited a range of thermoregulatory responses during the incubation phase of the reproductive cycle. This included at least three distinct thermoregulatory behaviours: panting, shading their eggs, and preening. Preening was more prevalent at higher wind speeds, presumably because its theorized method of action — promoting convective heat transfer and evapotranspiration — is expected to be more effective at higher wind speeds. Conversely, panting behaviour was observed less at higher wind speeds, potentially due to added heat loss from the other thermoregulatory behaviours. Thermoregulatory behaviours became more common at higher temperatures.

Three of our behavioural categories could only be scored in a mutually exclusive way, and so we should discuss their results together: direct contact incubation, shading, and ‘absence’. At the high end of the temperature range, direct contact incubation and ‘absence’ were less likely to be observed and comprised a smaller proportion of the total time budget, while the reverse was true of shading behaviour. The patterns of these three mutually exclusive behaviours likely reflect the behavioural limitations of the lapwings imposed by the thermoregulatory needs of their clutch.

Contact with the brood patch maintains eggs at favorable temperatures for development (Lea & Klandorf, 2002). At the higher end of our observed ambient temperature range (up to 40°C at camera height and 50°C on the ground), the parent would have needed to cool itself and its clutch to sub-lethal temperatures. For some set of environmental conditions, this might be achieved while maintaining full-time contact incubation. However, in many cases a parent may have been required to stop direct contact incubation to facilitate heat loss. By exposing a larger part of their bodies – including the brood patch – to ambient air, they allow for cutaneous evapotranspiration (Marder & Ben-Asher, 1983), and thus greater heat loss. Shifting from the direct contact incubation posture to a shading posture necessarily exposes the clutch to the ambient air. When the ambient air temperature is greater than the incubation temperature, the clutch would warm up when the parent is shading it instead of incubating (Brown & Downs, 2003). In addition, eggs could lose water when the hydrologic balance of the nest is disturbed by the intrusion of ambient air (Deeming, 2011). The parent should try to limit the time the eggs would be exposed to the ambient air.

When the parent is absent from the nest during the day, the clutch will also be exposed to direct insolation. Lapwing nests are often built in short vegetation (Shrubb 2007, Bertholdt *et al.* 2017, Madsen *et al.* 2019), where very little shade is available. We would then expect to see nest absences occur mostly when ambient conditions are favorable for the clutch, or at the very least expect them to be limited when ambient conditions would force egg temperatures beyond lethal limits. This is reflected in our findings, where we find absences becoming rarer at higher temperatures, and our models predict that absences should be most common when temperatures are relatively low and wind speeds are low (so there is less infiltration of ambient air into the nest environment). If temperatures are low and wind speeds are high, we would expect the greater amount of wind chill to be a limiting factor for nest absences (Heenan & Seymour 2012). Temperatures at our breeding sites were not particularly low, which may explain why our models do not predict such a limitation. In cooler habitats, where temperatures become low enough that prolonged absences risk cooling the clutch below temperatures that allow for development (Lislevand, 2001), we would expect this limitation to become apparent.

As we did not observe the lapwings outside of the nest context, we do not know what they were doing during their absences from the nest. A study involving GPS and accelerometer data from breeding lapwings might discover whether these off-bouts are used for foraging trips, scouting for future chick rearing sites, or other behaviour. Such studies have already been performed on Eurasian Curlew (*Numenius arquata*), a threatened ground-nesting wader species, revealing much about their habitat use during the breeding season (Ewing *et al.* 2018, Bocher *et al.* 2024).

Lapwings showed more panting behaviour at higher temperatures. Lapwings will pant less when wind speeds are higher for the same level of temperature, an effect which is stronger at higher temperatures. They are predicted to pant more when closer to the end of incubation later in the year, but also more when far from the end of incubation early in the year. This first set of effects is very similar to the pattern found for shading behaviour, and we propose to explain it the same way. At higher temperatures, lapwings will pant more to get rid of more heat. Where wind speed allows for a greater heat loss through convection and cutaneous evapotranspiration, there will be less need to induce evapotranspiration by panting, and so the amount of observed panting would decrease.

The effects of the combination between the number of days until the end of incubation, and the day of the year, on lapwing panting behaviour require a more complex explanation. First, as the season progresses there will be fewer lapwings starting their incubation. Therefore, we should expect only the nests closest to incubation to still be active later in the season. Under our model results, this would mean a greater amount of panting behaviour. Second, the date range between 30 April and 9 June, which covers the majority of our dataset, also shows the most restricted range of difference (**Figure 21**). The combination between the effects of progress in incubation and date may be driven by an increasing effort of thermoregulation later in incubation, which is confounded by the tendency for a greater proportion of nests to be far advanced in incubation later in the year. A follow-up analysis with a broader coverage of data may clarify this potential explanation.

We observed that lapwings would preen more at higher temperatures, and when wind speeds were higher. This preening behaviour may be shown as a maintenance behaviour (taking care of the feathers), as a stress-related displacement behaviour (reducing heat-related stress), or as a true thermoregulatory behaviour that would reduce their body temperature.

Self-directed behaviours, such as self-preening or self-grooming, are often associated with stress in both mammals and birds (Castles & Whiten 1998, Beerda *et al.* 1999, Massen *et al.* 2014). It is possible that the increase in preening behaviour at higher temperatures reflected the birds' (heat-related) stress levels, and did not reduce the birds' body temperatures (the hypothetical proximate result having been a reduction in stress hormones, not a reduction in body temperature). We found that preening behaviour was more often observed at higher wind speeds. This response to higher wind speeds might be explained by an increased need to neaten the plumage if it is disturbed by gusts of wind, but this explanation alone does not hold for our data: we found that preening occurred more at higher wind speeds only when temperatures were high, but for the "neatening the plumage" theory to hold we should also have found this behaviour at low temperatures and high wind speeds.

It's possible that higher wind speeds result in an increased stress in lapwings related to predators: Faster winds can cause mammalian predators to be harder to detect, and cause prey animals to show greater vigilance (Bowyer *et al.* 2001, Studd *et al.* 2022). Hypothetically, if the combination of high temperatures (causing heat stress) and high wind speeds (causing anti-predatory stress) resulted in a greater total stress response, this may have exceeded some unknown threshold level and caused preening behaviour. If this were the case, it may explain why we found higher rates of preening at the combination of higher wind speed and temperature, but not at high levels of either separately: the individual causes of stress may not have exceeded the theorised threshold by themselves.

Alternatively, lapwings' frequent preening at higher temperatures and wind speeds may have occurred for reasons of thermoregulation. A potential mechanism explaining why preening would reduce birds' body temperatures may be that it disrupts the insulating properties of the plumage and allows ambient air to reach the skin. This would explain the observed interaction effects between wind speed and temperature on the expression of this behaviour, as such a mechanism would be more effective at higher wind speeds. Herring Gulls (*Larus argentatus*), will exhibit a "ruffled" plumage at high temperatures, and will preen more at higher temperatures as well (Drent *et al.* 1970).

One weakness of the current analysis is the mutually exclusive nature of three of the behavioural responses: Absence from the nest, direct contact incubation, and shading are mutually exclusive behaviours. Thus, they are most accurately modelled together such that they must sum to 1 (for "100% of the time"). The current analysis does not provide for this, and results in the situation at low wind speeds and temperatures where lapwings are simultaneously expected to be contact incubating and absent for more than 50% of the time. A future analysis using Dirichlet regression may resolve these problems.

Behavioural measures of heat stress, such as the thermal limit at which 50% of birds show panting behaviour (Smit *et al.*, 2016), can provide indications for the thermal tolerances of species at a distance, with minimal added stress for the animals. Detailed knowledge of thermal tolerances may help predict the impact of future climate forcing and extreme weather on habitat use. Northern Lapwings, which nest on relatively open ground across the palearctic (reviewed in Shrubb, 2007), may be adapted to a wide variety of environmental conditions at the breeding grounds, including increasing temperatures as the breeding season progresses from its inception in February / March to its conclusion in July (Musters *et al.*, 2010, Chapter 1).

We found a range of temperature values at which we expect different thermoregulatory behaviours to be observed in 50% of cases. Our estimates were based on the temperatures reported by our nest cameras, but temperature values are often sourced from weather stations which measure air temperatures at 2m height. When we scale our temperature values to air temperatures 2m above the ground, we expect pant50 to occur between 25.7°C and 30.2°C depending on wind speed. Compared to birds living in the savannas of South Africa, which show pant50 thresholds between 31°C and 46°C over 30-second windows (Smit *et al.*, 2016). French lapwings start panting at lower temperature ranges. A finding that should not be surprising given the differences between the breeding ranges of Northern Lapwings and the set of species (e.g. Crowned Lapwings (*Vanellus coronatus*)) featured in the article from South Africa (Smit *et al.*, 2016). It would be interesting to compare the thermoregulatory behaviour of Northern Lapwings over their full breeding range, which may be acclimated to different conditions. Similarly, it may be interesting to compare individuals of different species of the genus *Vanellus*, found breeding all over the world. The South African Crowned Lapwings showed a pant50 threshold of approximately 39°C (Smit *et al.*, 2016). We might expect lapwing species on the southern edge of the Northern Lapwing's breeding range, such as the Spur-winged Lapwing (*Vanellus spinosus*, bordering Northern Lapwing breeding range in Turkey, Özkan, 2023) and the Sociable Lapwing (*Vanellus gregarius,* bordering Northern Lapwing breeding range in the East-European and Central-Asian steppes, Watson *et al.*, 2006) to be better adapted to higher temperatures than their West-European cousins.

Previous work on this group of Northern Lapwings has shown that their nest survival rates are positively impacted by higher wind speeds (**Chapter 1**). Moreover, lapwings' nest absences as a consequence of human disturbance are shorter at high temperatures, close to the end of incubation (**Chapter 2**). In this study, we find similar patterns for nest absence that do not follow human disturbance (and are thus presumed voluntary in most cases). We found that there should be fewer nest absences closer to the end of incubation, and that they should be shorter at high temperatures with low wind speeds.

This study further corroborates the previous findings that lapwings' nest survival rates are positively impacted by high wind speeds (**Chapter 1**). We found that lapwings should be expected to perform slightly fewer thermoregulatory behaviours, and show thermoregulatory behaviours that may be more water-efficient, when wind speeds are higher. On the scale of the breeding season, a small reduction in daily energy and water expenditure may translate to better nest survival. In the context of global climate change, differences in cost of incubation may lead to reduced reproductive output when the breeding season becomes hotter. At the median observed camera temperature of 23.9°C and the median wind speed of 0.55 m/s, we predict that lapwings should spend 5.8% of their time preening, 3.3% of their time panting, and 6.3% of their time shading (for a total of 15.5%-point). At a simplified temperature increase of 2°C, we predict 7.5% preening, 9.2% panting, and 10.7% shading (27.4%-point total), and at an increase of 4°C we expect 9.2% preening, 19.0% panting, and 17.4% shading (45.5%-point total). Such increases would represent an added expense of time and energy with potential consequences for breeding activities and success.

Based on previous studies on birds in arid habitats (Amat & Masero, 2004, Smit *et al.*, 2016, Diehl *et al.*, 2023), we expected to find some clear cases of wing drooping. However, we were unable to find any clear cases where we could identify this behaviour. Feather wetting, which should be a comparatively rare behaviour (Amat & Masero, 2004), was also never clearly observed in our data.

A future analysis may investigate whether observed thermoregulatory behaviour can be correlated with subsequent nest fate, or whether the difference between the expected and observed levels of thermoregulatory behaviour can be correlated to similar effect. In the former case, we theorize that persistent high investment in thermoregulatory behaviour would be associated with unsuccessful nests. In the latter case, we might consider lapwings that "under-invest" in thermoregulatory behaviour relative to environmental conditions to be showing signs of lower individual quality.

5) Conclusion

We found that lapwings will incubate less at higher temperatures. The thermoregulatory behaviours they show to deal with these temperatures will vary depending on the combination between temperature and wind speed, favouring shading and preening behaviours at higher wind speeds, and relying more on panting behaviour at lower wind speeds. We also found that nest absences should be expected to be observed more often in cool and windstill conditions.

Based on these behaviours, we expect that high temperatures result in added costs for lapwings during the incubation phase of their reproductive cycle. Higher wind speeds can mitigate some of these costs, by allowing the use of different thermoregulation strategies. As Europe's summer climate is expected to become warmer over the next decades, we might expect that the cost of incubation for lapwings will increase in the warm part of their breeding range. This may result in the breeding season becoming shorter, as thermoregulatory costs of incubation become unbearable sooner in the year than before. A shorter breeding season may result in reduced reproductive success, especially in regions where many first nests are destroyed due to agricultural processes: a delay of several weeks may not leave much time to fledge chicks. Additionally, we may see a range contraction away from the southern border of the breeding range, as it becomes increasingly costly to breed in these habitats.

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Chapter IV: Synthesis

Animals' reproductive strategies have been selected, in their evolutionary past, according to the conditions at the locations they inhabited. Presently, we are witnessing rapid changes to ecosystems across the world. These changes may outpace animals' ability to adapt to new conditions (Gienapp *et al.* 2013, Santangeli *et al.* 2018). One of the major ecosystem changes over the last decades has been large-scale land use change, resulting in habitat loss for many species due to agricultural intensification (Tiainen *et al.* 2020). This is especially true for species previously breeding in wetlands and pastures, such as lapwings (Davidson 2014, Lislevand *et al.* 2021). In their remaining breeding habitat, birds might build their nests in meadows that would be mowed (Baines 1990, Kruk *et al.* 1996) or on crop fields that would be worked by agricultural machines (**Chapter 1**). Moreover, the impacts of climate change are becoming more pronounced in recent years (IPCC 2023). Unpredictable flooding, droughts, and heat waves can lead to reproductive failure or increased adult mortality, shifting selective pressures (Moreno & Møller 2011).

The goal of this thesis was to investigate the breeding ecology of lapwings in France (**Figure 24**). Would they reproduce at sustainable rates? Which local factors would be limiting to reproduction? What would be the influence of the local weather conditions on lapwing breeding? In **Chapter 1**, we focused on the hatching success of French lapwings, by investigating the different causes of nest failure, the nest survival rates, and how they related to environmental conditions. We found that nest failures were most often caused by agricultural processes, depredation, and abandonment. We noted that in our warm breeding habitat, nest survival rates would be lower at low wind speeds. Nest survival rates turned out to be different between regions, and were higher for nests monitored with cameras. Based on our findings, we hypothesized that the effect of wind speed may be related to thermoregulatory needs. In **Chapter 2**, we observed that lapwings habituated to our monitoring methods, and reduced the time they were absent from the nest following a disturbance as a factor of the development of their clutch and weather conditions. Temperatures that could lead to the overheating of the clutch resulted in significantly shorter absences. In **Chapter 3**, we confirmed that in the current French climate, lapwings may spend considerable time thermoregulating at their nests. Conditions that could cause the clutch to overheat also resulted in reduced absences when there was no prior disruption at the nest site, as they had done after disturbances in **Chapter 2**. Finally, we discovered that wind speed differences would result in different thermoregulatory behaviour, and might reduce thermoregulatory needs of the adults at their nest sites.

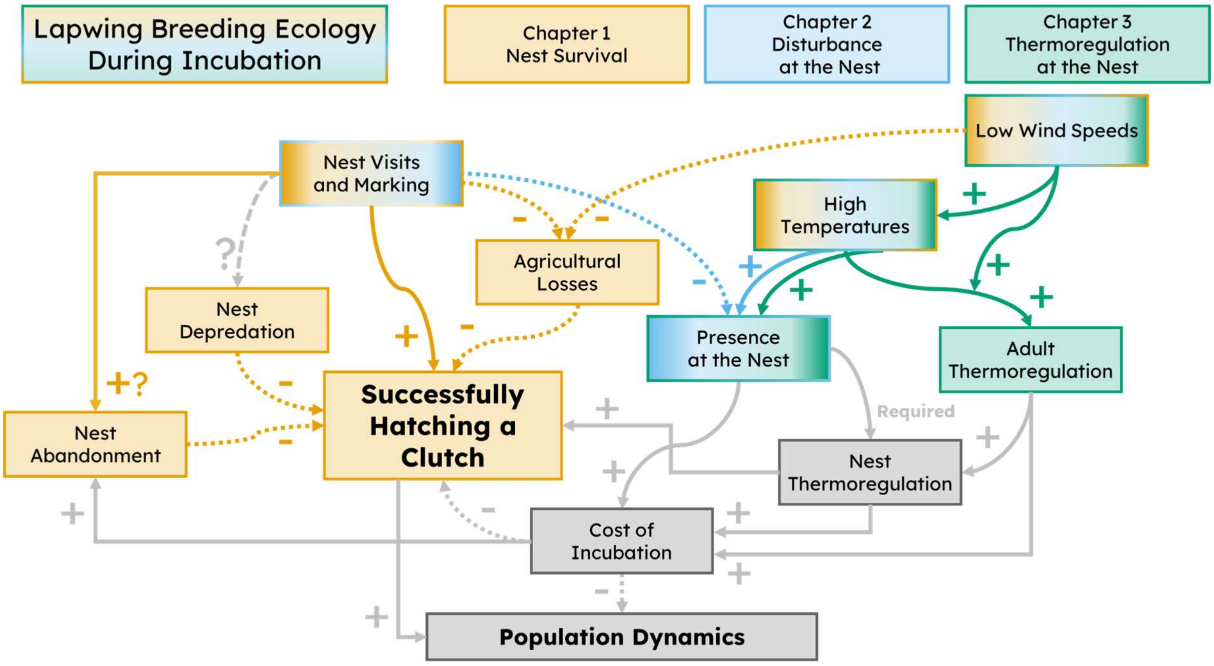

Figure 24: *Summary of the thesis results and their interrelations. Box colours indicate to which chapters the concepts relate. Solid lines indicate positive relationships between concepts, dotted lines indicate negative relationships, and dashed lines indicate unclear relationships. Grey boxes and lines indicate concepts and relationships that are inferred from literature, but not directly measured in this thesis. The observed negative effect of low wind speeds on hatching success is likely to be expressed through effects on thermoregulation. The net positive effect of nest visiting and marking in this thesis is likely the result of the combination of its effects on nest failure causes.*

In **Chapter 1**, we've seen that Northern Lapwing nest survival rates can differ greatly between regions. In the eastern region of Alsace, we observed very low nest survival rates, while in the western region of Hauts-de-France we noted very high nest survival rates. The observed differences are in part due to losses to agricultural procedures. In Alsace over half of all unmarked nests were destroyed by machinery. These losses occurred in the early parts of the season, when crop fields are prepared for sowing.

Farmers' activities on crop fields reduce the overall time window for successful lapwing breeding in Alsace. Any birds nesting on crop fields can only be successful if they lay their eggs after sowing. By contrast, in Hauts-de-France even clutches laid early in the season could be successful (**Figure 25**). Moreover, without a first round of early losses to agricultural procedures, any natural clutch losses may be more easily compensated by replacement clutches

The first chicks observed in the fields of Alsace were seen 10 May 2021 and 11 May 2022, which means the first successful clutches were likely completed around 13 April. The first chicks in Hauts-de-France were seen on 26 April 2021 and 16 April 2022, these clutches should have been completed around mid to late March.

The last chicks hatched in Alsace were observed 10 June 2021 and 1 June 2022, indicating favourable clutch completion windows of only 31 days in 2021 and 21 days in 2022. By comparison, the last chicks in Hauts-de-France were hatched on 27 June 2021 and 15 June 2022, which would mean lapwings in Hauts-de-France had favourable clutch completion windows of 62 days in 2021 and 60 days in 2022.

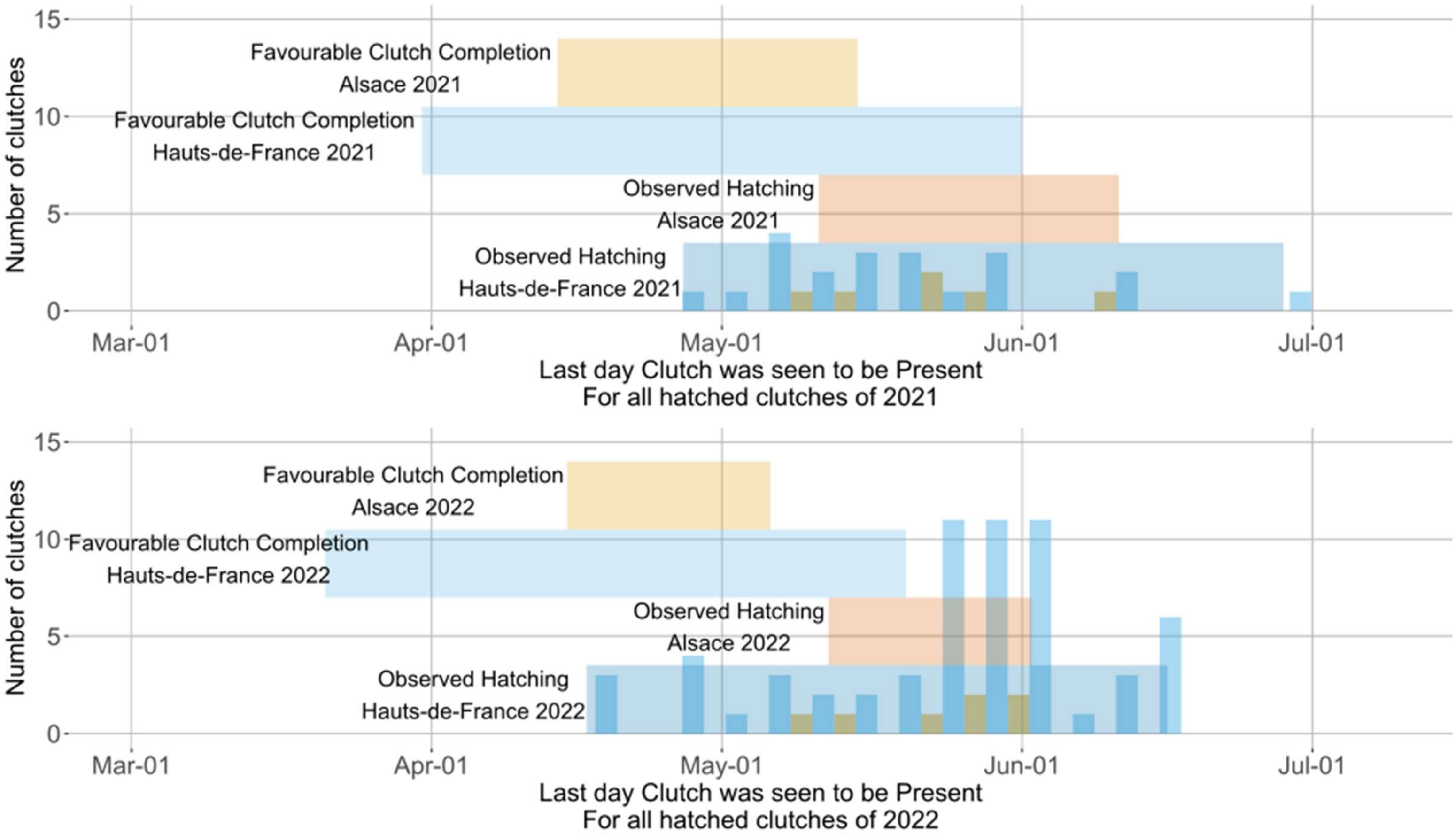

Figure 25: *Observed hatching dates of lapwings in Alsace (dark orange bars) and Hauts-de-France (dark blue bars), and the associated favourable window during which clutch completion may result in hatching for Alsace (light orange horizontal bars) and Hauts-de-France (light blue horizontal bars).*

Under current circumstances, lapwings in Hauts-de-France might be able to cope better with early nest failures, as there is a longer time to lay a replacement clutch if necessary. Conversely, lapwings in Alsace have a very limited time window to lay their replacement clutch, and no opportunity for a second replacement clutch.

Thus, it is important to reduce early clutch losses from human activity, specifically in Alsace.

Action to this effect has already been undertaken in countries such as: Czechia, Germany, The Netherlands, Switzerland, and The United Kingdom (Schifferli *et al.* 2006, Roodbergen & Teunissen 2014, Franks *et al.* 2018, Zámečník *et al.* 2018, Buschmann *et al.* 2023a). A reduction of clutch losses might be achieved through nest marking (Zámečník et al. 2018), by setting aside particular parts of crop fields for lapwing use ("lapwing plots"), or both (Buschmann et al. 2023a). Conservation measures of this kind can take many shapes. For example, an agri-environment scheme might compensate farmers for creating lapwing plots in their fields. The prospective participants will in such a case expect different levels of compensation depending on the exact details of the program, such as whether they would be committing for multiple years (Buschmann et al. 2023b). Ideally, these programs will be locally directed to prioritise traditional lapwing breeding sites, and include surface water features (Schmidt et al. 2017).

If the timing of agricultural procedures determines the beginning of the favorable incubation window for some birds, the end of this time window might depend on weather conditions and increasing thermoregulatory costs. In **Chapter 1,** we found that low wind speeds negatively affect daily nest survival rates, and suggested that thermoregulation at the nest might be helped by higher wind speeds. Then in **Chapter 2,** we saw that lapwings will return more quickly to their nests after a disturbance if it occurs under conditions that warm up their clutches more quickly (warm temperatures and low wind speeds). Returns are also faster later in the incubation phase, when the acceptable thermal range of embryos becomes increasingly strict (Tazawa & Rahn 1986). Finally, in **Chapter 3**, we noted that lapwings can be predicted to spend some considerable portion of their time on thermoregulation above 28°C. This explanation fits well with the known climates of our two regions. Hauts-de-France's milder oceanic climate would allow later breeding (as we observed), while Alsace's more continental climate would show higher temperatures that might limit successful breeding.

While overall milder temperatures may extend the favourable environmental window in Hauts-de-France as compared to Alsace, it might be extended even further by conditions that promote efficient thermoregulation when temperatures increase. The lapwings in Hauts-de-France experienced much greater wind speeds, which would have allowed for more efficient thermoregulation through convection and skin evapotranspiration (**Chapter 3**). The nests in Alsace experienced much lower wind speeds, resulting in higher thermoregulatory costs. While lapwings possess several effective behaviours to deal with high temperatures (**Chapter 3**), increasingly hot summers may increase the water and energy requirements for successful incubation. This can result in shorter breeding seasons in the future, or a reduction in suitable breeding habitat.

Consequently, these findings indicate that future climate should be taken into account when planning conservation measures for ground-nesting birds.

For example, when planning an agri-environment scheme to be implemented in Alsace, care should be taken that lapwing plots are implemented in places that will not become too hot in the foreseeable future. Lapwing post-fledging dispersal distances are often short (Lislevand *et al.* 2009). The lapwings hatched in a location may continue breeding in the same area for 20 years, if they successfully survive (Catchpole *et al.* 1999). Thus, it's best to ensure that conservation measures are put in place that can guarantee favourable breeding conditions several decades into the future. The lapwings breeding in Morocco have demonstrated that with sufficient nearby water, habitats which are warmer than those found in France may support breeding lapwings (Cherkaoui & Hanane 2011). Providing access to fresh water might provide a way for lapwings to cope with higher temperatures in the future. With appropriate management of the water levels and surrounding vegetation (no dense and tall grasses, no woody plants), new water sources at existing lapwing breeding sites should provide benefits not only to the thermoregulation of incubating lapwings, but also to the foraging of their chicks (Eglington *et al.* 2008). Naturally, other species present in the area may benefit from the water source as well.

According to climate projections, we are in the process of experiencing changes on a continental scale (IPCC 2023). The weather during the lapwing breeding season is expected to become warmer and less predictable. Lapwings may provide interesting opportunities to study the impacts of climate change, as the combination of long-distance gene flow (Evans 1968, Mead *et al.* 1995) and a wide breeding range should expose a relatively homogeneous species to a range of climate consequences.

One interesting question to ask is whether future lapwings may become more risk-averse, or prone to abandoning breeding attempts. Climate instability may cause unpredictable differences in the length of the favourable environmental window for reproduction, which may provide a selective advantage for lapwings that prioritise their own survival to a greater degree than generations in the recent past. For example, in a year with a particularly wet spring, agricultural activities may be delayed until machinery can be driven on the land (Baines 1990). If this pushes the dates of major agricultural procedures far enough into the lapwing breeding period, a large amount of lapwings' nests may be lost. Should the lapwings lay replacement nests when this happens? Under historical conditions, the answer must surely have often been 'yes', as lapwings have the ability to lay several replacement clutches (Shrubb 2007). After destruction of the nest, the favourable environmental window for incubation will have to be open for another 32-42 days (5–15 days of clutch replacement followed by 27 days of incubation, Berg *et al.* 1992).

As wet springs may delay the starting dates of potentially successful clutches, heat waves may curtail the end of the breeding season. It has been predicted that heat waves will increase in frequency in the coming years (Beniston *et al.* 2007, Guerreiro *et al.* 2018). If thermoregulation costs are too high at the nests, lapwings might be forced to abandon their incubation attempts. A short time window with favorable weather conditions might not provide sufficient time for any replacement clutches. In this case, should lapwings maximize adult survival in the future?

We have shown that relatively small increases in ambient temperature may result in large changes in expected thermoregulatory responses (**Chapter 3**). Under climate warming, it might become more costly to breed later in the breeding season. As a result, the propensity to attempt a replacement clutch may be selected against. Currently, not all first clutches are replaced if they are lost (Parish *et al.* 1997, reviewed in Shrubb 2007). The variability in behaviour is already present for selection to act upon, but conditions have likely not yet progressed to the point that there has been serious selection against replacement clutches. During our field study, we observed several cases of suspected clutch replacement. Furthermore, lapwings were observed to hatch clutches in June or July, when air temperatures periodically reached well above 30°C. For the majority of European lapwings breeding in the cooler climates further north, it may then be some time before thermoregulatory costs become prohibitively high. Lapwings in Eastern Europe, faced with habitat loss due to agricultural abandonment and the consequent ecological succession (Chasov *et al.* 2019), may also have to face the combination of droughts and heatwaves more often in the future (Schubert *et al.* 2014).

Besides pressures from agricultural activities and a changing climate, increasing human activities on the breeding grounds (including conservation activities) may also impact breeding attempts. There has been some debate on whether nest visitation could be deleterious to nest survival (Galbraith 1987, Fletcher *et al.* 2005, Goedhart *et al.* 2010). In our field study, we assessed that up to 7 out of 98 nests (7%) monitored by nest cameras were abandoned directly after camera placement. We were unable to determine the exact causes for this abandonment. The birds who abandoned their nests could have been more anxious than other individuals, could have previously experienced stressful situations, or might have been inexperienced breeders. In two cases, the camera was placed at a nest with fewer than four eggs. Lapwings may more easily abandon incomplete clutches, as they will lose a smaller clutch by doing so (Ackerman *et al.* 2003). Thus, placing nest cameras at incomplete nests should generally be avoided. Without a clear explanation for the other 5 cases, we will tentatively conclude that a risk of abandonment will exist for any monitoring method similar to ours. Nest abandonment will likely remain an important field of study, as rates of nest abandonment have been reported over wide ranges (e.g. 1.3% - 8.1% in Norwegian grasslands, but 12.6% - 46% on Swiss crop fields, Isaksson *et al.* 2007, Korner *et al.* 2024).

In order to prevent the needless abandonment or endangerment of nests, scientists and conservationists should follow the principle of caution. **Approaching ground-nesting bird nests when the parent's absence could be dangerous for the clutch should be avoided**. The potential negative effects of nest visits have been studied before (Galbraith 1987, Fletcher *et al.* 2005, Goedhart *et al.* 2010). In these studies, the focus has been on the risks of increased depredation. However, this thesis also demonstrates the importance of hazardous abiotic conditions.

Starting in early summer, when local conditions may lead to rapid temperature increases for unattended clutches, extra care should be taken when approaching the nests of ground-nesting birds. Temperatures in lapwing nests may become lethally warm at deceptively low ambient air temperatures. This is due to their proximity to the warm soil surface and the potential for a layer of warm air to form in the first centimetres above the ground (Pfister *et al.* 2017, Sigmund *et al.* 2017). In late summer, temperatures of unshaded objects on the ground may even reach up to 60°C, as was demonstrated by our iButton loggers.

The time of the day has a direct influence on the duration of time lapwings could be absent from the nest (**Chapter 2**). These findings should be taken into account when planning visits to the nests. Visits before noon could result in shorter absences of a parent, but increase dangers of clutch overheating. On the other hand, visits in the afternoon reduce risk of overheating, but result in longer unattended periods. This exposes the clutch to other dangers, such as predation.

Scientists who plan to visit lapwing nests and want to minimize the parents' absences might then make use of weather forecasts to gain an information advantage over the lapwings. The scientists know it will not be hot enough for the eggs to be in danger, but the lapwing can't be sure. As a result, the lapwing might return to the nest more quickly than if the scientists had postponed their visit to late in the afternoon, but without the actual risk of the clutch overheating if the bird stays away too long. Any application of such a practice should rest on very firm knowledge of the local microclimate, as an underestimation of nest temperatures could lead to the actual loss of the clutch.

To find an optimal visiting time it should be investigated whether it is more stressful for the adult to be away from the nest a short time under warm conditions or for a longer time under conditions that allow it to be absent longer without harm to the clutch. Higher stress hormone levels may induce a stronger response to disturbance (Silverin 1998). For some species, high stress levels may even result in nest abandonment (*ibid.*). Thus, if a method to minimize nest absences results in a higher stress level for the parent, it may have the counterproductive result of promoting nest abandonment. Furthermore, as visiting one nest in a colony will disturb the entire colony, these effects will be felt by multiple breeding pairs at once. Because lapwings may breed together with other wader species in the same habitat, the negative effects of nest visitation may even cross species boundaries and affect non-focal species.

The results of this thesis could be applicable to other ground-nesting birds that breed in habitats similar to lapwings'. These other species are likely to experience the same set of pressures as lapwings: predation, agriculture, and climate change. In some cases the pressures may be identical. For example, several wader species use lapwing breeding grounds for their own reproduction in Hauts-de-France. I have personally observed lapwings breeding on the very same crop fields as Pied Avocets (*Recurvirostra avosetta*), Black-winged Stilts, Eurasian Oystercatchers (*Haematopus ostralegus*), and Little Ringed Plovers (*Charadrius dubius*). Lapwings are also closely associated with Black-headed Gulls (*Chroicocephalus ridibundus*) and duck species (e.g. Northern Shoveler *Spatula clypeata*) in wetland sites. On shared breeding grounds, lapwings are often the first wader species to arrive and begin nest construction (pers. obs., Norway: Barrett 2002, Denmark: Meltofte *et al.* 2018). As lapwings are highly aggressive toward potential predators (but usually less so to other waders), other species may breed close to them in a 'protective nesting association' (Dyrcz *et al.* 1981, Quinn & Ueta 2008). Thus, ensuring that suitable habitat is available for breeding lapwings may also provide benefits to other ground-nesting birds.

Lapwings' wide breeding range and ability to breed in a diverse set of climates may be what secures their future for the coming decades. However, they might not breed under the same conditions as before, and they might require some human help to remain one of the most iconic farmland birds far into the next century. The combination of loss of habitats, intensive agricultural practices, and climate change puts the population in Europe at risk. Effective conservation measures should be explored and put into practice to protect under-protected breeding populations. The results of this thesis can be applied to help with the conservation of local populations in France as well as other countries in Europe.

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Apart from covid, the project faced a number of challenges, not the least of which being the fact that the collaborators were roped into the project against their will. Despite this, Arne and Brett graciously agreed to remain part of the project, and have provided their priceless advice throughout. Jean-Patrice joined them as the third leg of the thesis committee, an expert not only in biology but also navigating the French research system. By Jean-Patrice's hand the project could continue after the company closed, under a funding agreement that managed to unite FNC funds under the CNRS.

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During my fieldwork, I was joined by several people who supported and helped me, including Loris, Augustine, and Ellyn, as well as Thomas who I mentioned above. And Caroline, who was not only very helpful during both field seasons, but also became a very important part of my life, and I can't imagine my life without her anymore. I hope she feels the same.

During the field seasons, I received local knowledge and benefitted from the networks established by the local hunter federations and their local conservation partners, and particular thanks go to Nicolas Dilly, Jacques Houart, and Alain Brunet in the Somme department, as well as Benjamin Bigot, Michel Defosse, and Rémy Wambergue in the Pas-de-Calais department. The national hunters' federation of France provided the funding for the project under the continued encouragement of Pascal Lapébie and Carole Bodin.

After the fieldwork of 2021 I was moved to the DEPE, on the same campus where I was previously hosted by the social and cognitive ethology team. It was there I met Céline, my second supervisor, who supported me in my work while I was at the DEPE. It was a very sudden transition after an intense fieldwork season, so I was glad to meet people there who treated me kindly. Many thanks to Julie, Nico, Anouch, Benjamin, Timothee, Laura, Clem, Lilia, Téo, and all the others who made me feel part of the team.

Many thanks go to the landowners and farmers who allowed me to work on their fields, and agreed to the placement of all those many cameras that generated the data in this thesis. It's not every day some weird guy from the Netherlands comes to meet you asking about the birds on your fields, when you're a French farmer, and I was very pleasantly greeted by many of them. It's very encouraging to meet so many people out in the field who feel warmly about the species you're studying.

Finally, I want to thank the members of the jury, Sylvie, Jean-Yves, and Arnaud, for their time and attention dedicated to reviewing this thesis, and for their trip all the way across France for the defense. I hope to meet them again in the future, as we all work for the continued presence of these birds in France.

Résumé de la thèse

Le vanneau huppé (*Vanellus vanellus*), limicole nichant dans des habitats ouverts en Eurasie tempérée – y compris la France métropolitaine – et dans une moindre mesure en Afrique du Nord, est une espèce dont les populations déclinent depuis plusieurs décennies. Ce déclin est expliqué par une reproduction insuffisante (Joyeux et al., 2022, Plard *et al.*, 2020; Roodbergen *et al.*, 2012), due à la prédation, à la modification de l'habitat, et à la perte d'habitat (Bellebaum & Bock, 2009, Donald *et al.*, 2006, Eglington *et al.*, 2009, Leyrer *et al.*, 2018). A l'échelle des populations, le taux de réussite de reproduction varie selon les années et les régions. Cette variabilité est probablement liée aux variations locales des facteurs environnementaux dans les sites de reproduction.

Dans cette thèse, l'objectif principal du chapitre 1 était de quantifier les taux d'éclosion dans deux régions de France, caractérisés par des conditions climatiques différentes, et de déterminer les causes principales d'échec de reproduction en phase d'incubation, pour mieux orienter les actions de conservation. Nous avons prédit des taux de survie des nids différents entre les régions.

Une grande partie des vanneaux se reproduisent dans des champs où l'agriculture intensive est pratiquée. Une méthode répandue pour protéger les nids est alors de les marquer (Schifferli *et al.*, 2006; Zámečník *et al.*, 2018). Dans un contexte de conservation de l'espèce, nous nous sommes ainsi intéressés à l'impact de notre méthode de marquage des nids et de dérangement lors de nos visites sur le comportements de vanneaux issus de populations non encore habituées à ce type de perturbation (Chapitre 2). Une telle étude sera utile pour prédire les réponses comportementales des vanneaux à de futurs programmes de marquage. Nous avons prédit une réponse d'accoutumance des vanneaux aux visites répétées des nids, et une plasticité comportementale aux conditions environnementales : un retour au nid plus rapide quand les conditions sont défavorables à la survie des oeufs, et un retour plus lent voire une légère négligence lorsque les conditions ambiantes sont favorables au développement des oeufs sans la surveillance du parent.

Enfin (Chapitre 3), dans un contexte de changement climatique produisant des événements météorologiques extrêmes plus fréquents, nous avons cherché à déterminer quels sont les comportements compensatoires développés par les vanneaux lors de ce type d'événements. Nous avons également cherché à déterminer à partir de quel seuil ils apparaissent. Avec ces résultats, nous pourrons prédire, au moins en partie, la période durant laquelle la reproduction restera possible en fonction des capacités de thermorégulation des vanneaux. Nous avons l'hypothèse que les vanneaux auraient des comportements compensatoires pour des températures ambiantes supérieures à 35°C, comme déjà observé chez le pluvier neigeux (*Charadrius nivosus*, Purdue 1976), mais probablement aussi à des températures plus basses, étant donné que l'aire de reproduction des vanneaux s'étend plus au nord que celle des pluviers neigeux.

Pour répondre à ces questions, nous avons suivi des populations de vanneaux pendant leur période d'incubation en utilisant des pièges-photos placés au niveau des nids. Nous avons ainsi pu déterminer le devenir des nids, réussite ou échec, et les causes d'échec, et caractériser les comportements parentaux sur et autour du nid. Nous avons également comparé des nids avec et sans piège-photo afin de prédire l'effet de potentiels futurs programmes de marquage.

Méthodes et Résultats

Nous avons suivi les vanneaux durant leur période de reproduction durant les années 2021 et 2022, en visitant régulièrement 92 sites de reproduction, sur lesquels nous avons suivi 184 nids, dont 92 équipés de pièges-photo. Les sites de reproduction étudiés étaient situés en zone littorale dans les Hauts-de-France et le long de la vallée du Rhin en Alsace.

Chapitre 1

Nous avons pu analyser les taux de survie de 145 des nids suivis, à l'aide du *package 'Rmark'*, en considérant la période durant laquelle les nids sont exposés à un risque d'échec. Nous avons pris en compte à la fois des effets spécifiques aux nids comme le nombre d'œufs et la région où se trouve le nid, ainsi que des effets environnementaux comme la pluviosité, la température au niveau du sol, et la vitesse de vent.

Nos résultats montrent que le taux de survie est plus élevé dans la zone littorale des Hauts-de-France que dans la vallée du Rhin en Alsace. Le taux de survie est également plus élevé pour les nids équipés d'un piège-photo, et lorsque le vent est plus fort. Les effets des pièges-photo et du vent sont des facteurs dépendant de la région. L'ensemble de ces résultats conduit à un taux de succès à l'éclosion globalement plus faible en Alsace, avec une population reproductrice risquant de disparaître dans cette région si les taux de survie restent aussi faibles (**Figure 1**).

Figure 1 : Estimation du taux de survie journalier des nids selon la région, la présence de piège-photo, et la vitesse journalière moyenne du vent. Les courbes moyennes sont indiquées en couleurs foncées et les zones claires correspondent à l'intervalle de confiance de 95%. Les lignes verticales en tiret indiquent la médiane de la vitesse du vent pour chaque région. Les boîtes à moustaches indiquent la distribution de la vitesse journalière moyenne du vent pour chaque région. Pour les Hauts-de-France, les valeurs obtenues avec ou sans piège-photo se chevauchent très clairement.

Chapitre 2

Nous avons analysé la réponse des parents de 86 nids à nos visites répétées. Nous avons relié le temps passé entre la fin des visites et le retour des parents au nid avec des variables environnementales et spécifiques aux nids (vitesse du vent, température, stade de développement des œufs, nombre de jours passés depuis l'installation du piège-photo).

Nous avons observé un retour au nid plus rapide des vanneaux lorsque le piège-photo était posé depuis plusieurs jours (**Figure 2**), quand la couvée était plus proche de l'éclosion, et lorsque que les températures étaient plus élevées. Les vanneaux revenaient d'autant plus tardivement que la vitesse du vent était élevée et que nous intervenions à des heures plus tardives. Nous interprétons ces effets environnementaux comme des réponses limitant l'impact de la température ambiante, partiellement modulé par la vitesse du vent et l'heure de la journée.

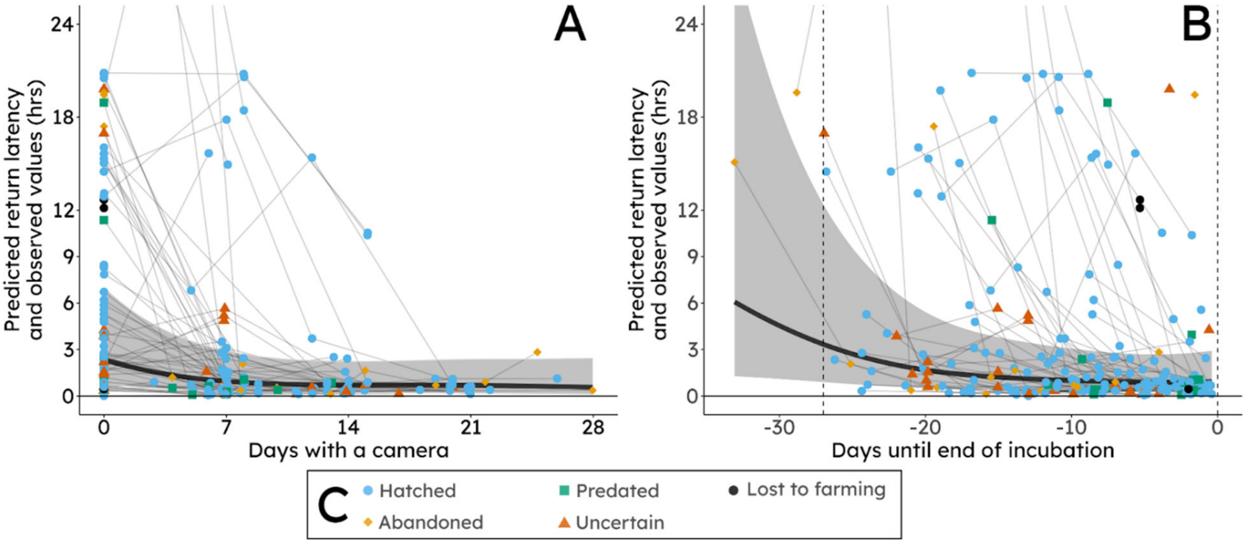

Figure 2 : Prédiction du temps de latence avant le retour du vanneau selon le nombre de jours passés depuis la pose du piège-photo (A) ou selon durée restante d'incubation (B), calculée avec d'autres variables fixées à leurs valeurs médianes et rétro-transformée à l'échelle de réponse. La zone grisée indique l'intervalle de

confiance à 95%. Les points indiquent les valeurs réelles observées. Les lignes grises fines relient les points qui proviennent d'un même nid. Le devenir des œufs des différents nids est indiqué par des symboles et couleurs différents (voir cartouche C). Quatre points extrêmes ne sont pas montrés sur cette figure.

Chapitre 3

Nous avons analysé le budget-temps des vanneaux autour du nid durant la période la plus chaude de la journée. Nous avons quantifié le temps consacré aux comportements compensatoires liés aux températures élevées : halètement-hyperventilation, faire de l'ombre à la couvée en restant debout au-dessus du nid, activité de toilettage. Nos résultats préliminaires indiquent qu'aux températures les plus élevées, les vanneaux ont des durées d'absence au nid réduites, et consacrent davantage de temps à des comportements compensatoires (faire de l'ombre, halètement, toilettage. **Figure 3** - haut). A environ 50-60°C, une température critique semble être atteinte. Les vanneaux souffrent d'un stress thermique considérable, comme le montre le fait que tous les vanneaux observés consacrent au moins 25% de leur temps à haleter (**Figure 3** - bas).

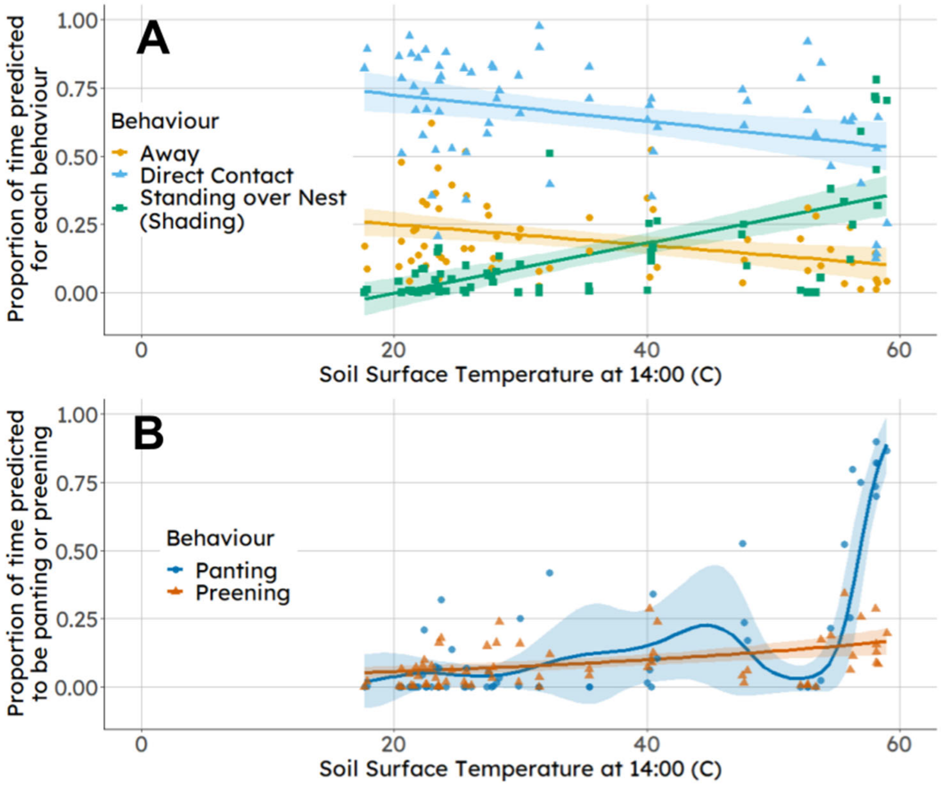

Figure 3 : La variation du budget-temps selon un gradient de température, avec la vitesse de vent fixée à sa valeur médiane (0.58 m/s) a été prédite à l'aide d'un modèle additif généralisé (GAM). Les lignes en gras indiquent les estimations du modèle, les zones claires représentent l'intervalle de confiance à 95%, et les points indiquent les observations faites entre 11:00h et 14:00h. **A**: Modèle combiné de prédiction des trois comportements liés à l'incubation qui s'excluent mutuellement (absence, incubation directe, et être au-dessus du nid). **B:** Modèles de prédiction des comportements (halètement et toilettage) qui coexistent avec les comportements indiqués partie A.

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The Breeding Ecology of the Northern Lapwing (Vanellus vanellus) in France

Investigating the Decline of a Widely-distributed Wader

École Doctorale des Sciences de la Vie et de la Santé
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Résumé

Le vanneau huppé (Vanellus vanellus), limicole nichant dans des habitats ouverts en Eurasie tempérée – y compris la France métropolitaine – est une espèce dont les populations déclinent depuis plusieurs décennies.

Dans cette thèse, l'objectif principal était de quantifier les taux d'éclosion dans deux régions de France, où nous avons observé des taux plus élevés en Hauts-de-France par rapport à ceux en Alsace.

Dans un contexte de conservation de l'espèce, nous nous sommes ainsi intéressés à l'impact du dérangement lors de nos visites sur les comportements des vanneaux. Nous avons observé un retour au nid plus rapide des vanneaux quand la couvée était plus proche de l'éclosion, et lorsque que les températures étaient plus élevées.

Enfin, dans un contexte de changement climatique produisant des événements météorologiques extrêmes plus fréquents, nous avons cherché à déterminer quels sont les comportements compensatoires développés par les vanneaux lors de ce type d'événements.

Vanellus vanellus ; Succès à éclosion ; Suivi par piège-caméra ; Thermorégulation ; Comportement

Résumé en anglais

The Northern Lapwing (Vanellus vanellus), a wader breeding in open habitat across temperate Eurasia – including mainland France – is a species undergoing a decades-long population decline.

In this thesis, the primary objective was to quantify the rates of hatching success in two regions of France, where we found higher success rates in the region of Hauts-de-France as compared to Alsace.

In a species conservation context, we were interested in the impact of disturbances during our nest visits might have on lapwings' behaviour. We observed lapwings return to their nests more quickly when the clutch was closer to hatching, and when temperatures were higher.

Finally, in the context of climatic change, which will lead to more frequent extreme climate events, we investigated which compensatory behaviours would be shown by lapwings in warm weather.

Vanellus vanellus ; Hatching Success ; Camera monitoring ; Thermoregulation ; Behaviour