A temperature-based monitoring of nest attendance patterns and disturbance effects during incubation by ground-nesting sandgrouse

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ABSTRACT

Sandgrouse are birds of arid environments adapted to cope with extreme temperature variations. We used temperature data-loggers to remotely study incubation rhythms by pin-tailed and black-bellied sandgrouse in Spain. In both species, mates switched incubation roles twice a day, between 08:00 and 10:00 and between 19:30 and 21:30, when the nest and ambient temperature were most similar. During mate switches, sandgrouse preferred to risk a cooling rather than a warming of eggs. In the pin-tailed sandgrouse, the timing of morning switches was consistent within-pairs, while the timing of evening switches was more related to sunset time. Absences lasted longer following a disturbance than during a mate switch. During disturbances, changes in nest temperatures depended on the changes in outside temperature, and negatively correlated with absence duration. Absences following a disturbance were shorter when the outside temperature was higher. Nesting success was low (19%), with no noticeable effect of data-loggers. Our study highlights some of the constraints that birds breeding in arid environments, such as sandgrouse, face during incubation. It also stresses out the importance of evaluating the consequences of disturbances during incubation, in particular nest visits. Temperature data-loggers can provide an easy and effective way of monitoring nests, without the need of repeated nest visits.

1. Introduction

Knowledge of nest attendance patterns and incubation rhythms are key to our understanding of bird adaptations to extreme environments (Grant, 1982), the demands and energetic costs imposed on incubating parents (Reid et al., 2002; Thomson et al., 1998) and parental investment strategies and life-history trade-offs (Conway and Martín, 2000; Wiebe, 2001). It is also relevant to conservation and can inform about the timing and causes of breeding failures, and the potential effects of disturbance by humans (Ibañez-Alamo et al., 2012; Lloyd et al., 2000; Schneider and McWilliams, 2007).

A wide variety of nest monitoring methods have been used in avian field studies, depending on the characteristics of the target species and monitoring aims. Direct observations of nests are time-consuming and often not feasible or desirable, because the nest content sometimes cannot be observed from a distance, or because the presence of an observer may alter parental behaviour and be a source of disturbance and a cause of nest failure (Carey, 2011; Götmark, 1992; Ibanez-Alamo et al., 2012; Weidinger, 2006). When direct observations of nest activity are not feasible or desirable, researchers have used alternative means of monitoring nest activity, such as video camera recordings, electronic balances, lightsensitive and temperature data-loggers.

Temperature data-loggers have been successfully used to determine when a bird is on or off the nest (e.g. Arnold et al., 2006; Weathers and Sullivan, 1989; Weidinger, 2006) and may be particularly suited for studying incubation rhythms of birds in arid environments, where thermal conditions are critical. Technological advances have produced data-loggers that are smaller, more accurate and with greater battery and data storage capacities. During incubation, data-logger methods generate times series that can be used to determine the thermal conditions experienced by incubating birds, as well as the occurrence (timing, frequency) and duration of absences from the nest (hereafter off-bouts), by comparing the nest temperature with the outside temperature. Data-logger methods also allow studying the effects of disturbances, such as nest visits, as well as the breeding phenology and nest survival (Schneider and McWilliams, 2007; Weidinger, 2006).

In this study, we used for the first time temperature data-loggers to study the nest attendance patterns and the effects of...
nest visits during incubation by two birds typical of arid environments: the pin-tailed sandgrouse (*Pterocles alchata*, Linnaeus 1766) and the black-bellied sandgrouse (*Pterocles orientalis*, Linnaeus 1758) in Spain. Sandgrouse nest on the ground and have to cope with extreme temperature variations during incubation, which makes them of particular interest for studying incubation rhythms. Our specific aims were as follows: 1) to document the range of temperatures experienced by incubating birds and their clutch; 2) to determine the timing and duration of off-bouts; 3) to analyse within- and between-pair variation in the timing and duration of off-bouts (when mates normally switch incubation roles); 4) to relate the timings of mate switches to thermal conditions (differences between the nest and control temperatures); and 5) to evaluate the effects of nest visits and other disturbances (which may be by people other than researchers or predators) by determining how long a bird takes to resume incubation after a disturbance and the consequences of absences from the nest, in terms of exposure of the clutch to potentially harmful temperatures. We use the information to highlight the benefits and limitations of temperature data-loggers for monitoring nests during incubation, and to give recommendations for optimizing the breeding monitoring of sandgrouse and other birds living in similar arid environments.

2. Materials and methods

2.1. Study species

Sandgrouse (family *Pteroclidæ*) are medium-sized ground-nesting steppe-birds that are particularly difficult to observe because of their cryptic and well camouflaged plumage, discrete behaviour and sensitivity to human disturbance ([De Juana, 1997](#)). Sandgrouse are well adapted to cope with deserts and arid environments ([Hinsley, 1992; Johnsgard, 1991; Thomas, 1984; Thomas and Maclean, 1981](#)). These adaptations include a dense plumage and thick feet to increase isolation from extreme thermal conditions, heat regulation based on high evaporation rates and peculiar behaviour such as regular visits to waterholes for drinking and water transportation to chicks ([Hinsley, 1992; Johnsgard, 1991; Marder et al., 1986; Thomas, 1984; Thomas and Maclean, 1981; Thomas and Robin, 1977](#)).

The pin-tailed and black-bellied sandgrouse are typical of dry steppes and extensive agricultural habitats ([del Hoyo et al., 1997; Benítez-López et al., in press](#)). Both species have a “Least Concern” (LC) conservation status in Europe ([BirdLife International, 2004; De Juana, 1997](#)) and a “Vulnerable” status in Spain, due to recent population declines ([Suárez and Herranz, 2004a,b; Suárez et al., 2006](#)).

While some aspects of their general ecology have been studied, such as their distribution and habitat preferences ([Martin et al., 2010a,b; Seoane et al., 2010; Suárez et al., 1997](#)), other aspects, and in particular their breeding biology, are still poorly known ([De Borbón et al., 1999b; De Juana, 1997; Znari et al., 2006](#)). Pin-tailed and black-bellied sandgrouse are socially monogamous, and both sexes share reproductive duties, mainly to distribute the high demands associated with breeding in arid environments ([De Juana, 1997; Johnsgard, 1991](#)). Mates take turns to incubate the clutch and switch incubation roles in the morning and in the evening ([Johnsgard, 1991; Marchant, 1961](#)). The female typically attend the nest during the day, and the male attend it from dusk until mid-morning; during mate switches, the bird leaving the nest typically first visits a drinking place, and then feeds and rests before resuming its incubation duty ([De Borbón et al., 1999b; De Juana, 1997](#)). Young leave the nest soon after hatching ([De Juana, 1997](#)).

Breeding takes place from late spring to late summer, depending on the latitude, with clutches being usually laid in May–August and in June–September by pin-tailed and black-bellied sandgrouse, respectively ([De Borbón et al., 1999b; Znari et al., 2008](#)). Nests typically consist of a 10–15 cm wide shallow depression on the ground in an area with no or low vegetation cover, unlined or with a few pieces of dried grass (Fig. 1).

2.2. Study areas and field procedures

Fieldwork was conducted in May–August 2011 in Spain, in two study areas located in Campo de Calatrava, Castilla-La-Mancha, Ciudad Real province (Special Protection Area — SPA-157; 38°54′N, 3°55′W) and in the Bardenas Reales Biosphere Reserve and Natural Park, Navarra province (42°08′N, 1°26′W). These areas were characterized by agro-steppes (Ciudad Real), and by natural steppes and/or ploughed fields or barren areas with low vegetation cover (Bardenas Reales).

Sandgrouse nests were located by means of conventional radio-tracking of birds previously caught and fitted with radio-transmitters (see [Benítez-López et al., 2011; Martin et al., 2010a,b](#) for details on the capture method and tags), or by systematic search and field observations of unmarked individuals. When breeding was suspected (i.e. when a bird was repeatedly located within the same area and was observed without its partner indicating that its mate may have started incubation), we searched for the nest. To do so, we walked towards its putative location. When an observer approaches a nest, incubating sandgrouse typically walk away and take off from a short distance. We land marked the last location where the bird was seen and carefully searched around it to locate the nest. Each nest position was recorded using a GPS (Garmin eTrex) to the nearest 3–4 m in order to facilitate relocation.

2.3. Temperature recordings

We used DS1923 Hygrochron Temperature/Humidity Logger i-Buttons with a 8 kb data-log memory (Maxim/Dallas Semiconductor Corp; [Fig. 1](#)) for temperature recordings. These data-loggers record temperature ranging between –20 °C and +85 °C, with an accuracy ±0.5 °C in the range –10 °C to +65 °C.

For each study nest, we set-up two temperature data-loggers: one was placed inside the nest, underneath the nest lining material and the eggs, and covered by a thin layer of soil so that it could not be seen by the birds (hereafter nest data-logger), and the other one was placed at c.1 m away from the nest, also covered by a thin layer of soil (hereafter control data-logger). The location of the control data-logger was chosen to have similar vegetation, shading conditions and substrate as its corresponding nest data-logger. Data-loggers were programmed to record temperature every 5 min during a maximum period of 28 days (the data storage capacity of the i-Buttons). This programming ensured covering the whole incubation period, known to last 20–22 and 26 days in pin-tailed and black-bellied sandgrouse, respectively ([De Borbón et al., 1999b; del Hoyo et al., 1997](#)).

Nest monitoring included nest visits (during which we flushed the incubating bird to check the nest content) and triangulations (to check for the presence a radio-tagged bird at the nest from a distance of 50–100 m, without flushing the incubating bird; [Table 1](#)). Nests were visited in the morning between 06.40 and 11.00 or in the afternoon between 18.30 and 21.00, with one exception in mid-day (12.25). The repeated absence of a tagged bird from a nest during its normal period of nest attendance would indicate that the eggs had either hatched (chicks leave the nest with their parents after hatching) or that the nest had failed and the parents deserted it. For each nest visit and triangulation, we recorded the day and time of the visit, the presence of an incubating bird, as well as the nest content (for nest visits only). At the end of
the nest monitoring period, we retrieved both data-loggers and downloaded the temperature recordings using the Eclo Express-Thermo software 2007 (www.eclo.pt/expressthermo).

2.4. Analyses of temperature recordings

Off-bouts were identified by comparing the control and nest temperatures. Because nest temperature is much more stable than ambient temperatures during incubation (Fig. 2a), off-bouts are characterized by a sudden change in nest temperature relative to control data-loggers, which can be easily detected (Fig. 2b). During an off-bout, the nest temperature drops or increases when the control temperature is lower or higher than the nest temperature, respectively (Fig. 2b). For each identified off-bout, we recorded the following: 1) the nest (pair) identity, 2) the date, 3) the time of the off-bout onset (to the nearest 5-min), 4) the duration of the off-bout (in min), 5) the nest and the control temperature at the beginning of the off-bout; and 6) the nest and the control temperature at the end of the off-bout. We also calculated the changes (difference) in both the nest temperature and the control temperature between the start and the end of the off-bout (ΔNTemp and ΔCTemp for nest and control, respectively). Recordings around hatching were excluded because incubation behaviour becomes irregular after the first egg hatched (Fig. 2c).

We classified each off-bout a posteriori into the following three event categories: (1) a nest visit event, when its timing coincided with one of our visits to that particular nest (none of the 16 triangulations made to check for the presence of a tagged bird at a nest resulted in an off-bout); (2) a mate switch event, when the off-bout occurred at a time when mates normally switch incubation roles, i.e. between 0600 and 1200; when the male returns to replace the female; (De Borbón et al., 1999b); (3) a nest disturbance (other than a nest visit or a triangulation), when the off-bout occurred at a time when we did not visit a nest and when mates do not normally switch incubation roles (i.e. between 1200 and 1700). For some analyses, we only considered two classes of events, and regrouped the nest visit and other disturbance events into a “disturbance” event, as opposed to a “mate switch” event.

On some days, temperature recordings showed no visible off-bouts. In such cases, we assumed that a normal mate switch took place, but was too brief to be noticed by a change in nest temperature (it lasted less than 5 min). In such cases, we cannot determine the timing of the mate switch (or the temperature ranges associated with it), but we assigned these off-bouts a duration of 5 min (the maximum possible undetected absence), to avoid a possible bias in our estimation of nest absences during mate switches.

In order to investigate the associations between sunrise/sunset times and the timing of morning and evening mate switches, we obtained data on sunset/sunrise times for each day of monitoring in each study area from the Astronomical Applications Department, U.S. Naval Observatory (www.usno.navy.mil). Times are given as local times (GMT+1).

2.5. Sample sizes for analyses

We monitored with data-loggers a total of 14 pin-tailed sandgrouse nests (11 in Ciudad Real and 3 in Bardenas Reales) and one black-bellied sandgrouse nest (in Bardenas Reales). Out of 11 pinto-tailed sandgrouse nests monitored in Ciudad Real, only 7 gave useful temperature recording data for analyses (the others failed too soon after set-up). We thus had useful temperature recordings from 10 pin-tailed sandgrouse nests and one black-bellied...
sandgrouse nest, covering incubation periods that ranged between 1 and 15 days (Table 1). We only analysed statistically the data from pin-tailed sandgrouse nests, and report on the data obtained from the black-bellied sandgrouse nest for descriptive and comparative purposes.

In order to compare the fate of nests with and without data loggers, we also monitored the breeding of another 18 pin-tailed sandgrouse nests in Ciudad Real, in which we did not set-up data-loggers, during the same breeding season (May–August 2011).

2.6. Statistics

We analysed the data from the monitored pin-tailed sandgrouse nests using Generalized Linear Mixed Models (GLMM), which

<table>
<thead>
<tr>
<th>Species</th>
<th>Monitoring start</th>
<th>Monitoring end</th>
<th>Days incubated</th>
<th>Nest visits</th>
<th>Triang.</th>
<th>Fate</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. alchata</td>
<td>03/06 at 1830</td>
<td>16/06 at 1930</td>
<td>11</td>
<td>4</td>
<td>0</td>
<td>Failed 14/6/2011 at 0934. Eggs predated</td>
</tr>
<tr>
<td>P. alchata</td>
<td>13/07 at 2100</td>
<td>20/06 at 2100</td>
<td>7</td>
<td>3</td>
<td>0</td>
<td>Failed 20/06/2011 at 2100. Empty nest</td>
</tr>
<tr>
<td>P. alchata</td>
<td>13/07 at 2100</td>
<td>18/07 at 1330</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>Failed 17/7/2011 at 0929. Eggs predated</td>
</tr>
<tr>
<td>P. alchata</td>
<td>14/07 at 1815</td>
<td>19/07 at 1800</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>Hatched, after data-logger removal</td>
</tr>
<tr>
<td>P. alchata</td>
<td>05/07 at 1020</td>
<td>20/07 at 1220</td>
<td>15</td>
<td>3</td>
<td>6</td>
<td>Hatched 19/7/2011 — leave the nest at c.0900</td>
</tr>
<tr>
<td>P. alchata</td>
<td>13/07 at 2130</td>
<td>21/07 at 1910</td>
<td>5</td>
<td>1</td>
<td>3</td>
<td>Failed 19/7/2011 at 0923. Eggs predated</td>
</tr>
<tr>
<td>P. alchata</td>
<td>17/06 at 0934</td>
<td>21/06 at 1930</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>Hatched 18/06/2011 — leave nest at c.0800</td>
</tr>
<tr>
<td>P. alchata</td>
<td>25/7 at 1800</td>
<td>1/8 at 0800</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>Failed 27/7/2011 at 0800. Empty nest</td>
</tr>
<tr>
<td>P. alchata</td>
<td>15/7 at 0800</td>
<td>21/7 at 1200</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>Failed 17/7/2011 at 2244. Empty nest</td>
</tr>
<tr>
<td>P. orientalis</td>
<td>10/07 at 0900</td>
<td>01/08 at 1915</td>
<td>9</td>
<td>1</td>
<td>6</td>
<td>Failed 28/7/2011 at 0447. Empty nest</td>
</tr>
<tr>
<td>P. orientalis</td>
<td>18/07 at 0859</td>
<td>3/8 at 0900</td>
<td>14</td>
<td>1</td>
<td>1</td>
<td>Hatched 31/07/2011 — leave nest at c.1000</td>
</tr>
</tbody>
</table>

* Including the nest visit for data-logger set-up.

* During a triangulation, the nest is not visited but the presence of a radio-tagged bird at the nest is confirmed from a distance.

* The nest monitoring started when the female had just laid the last egg of a clutch of 3. The nest was not incubated at night (by the male) during the first night (laying being not complete) but the male incubated on the following nights; the female incubated all days.

* The nest monitoring started when the female was still laying eggs. The nest was not incubated at night (by the male) during the first 4 nights (the male most likely waited until laying was complete to start), but incubated on the following nights; the female incubated all days.

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Fig. 2. Times series of temperature recordings (in °C) of the control (dashed black line) and nest (solid red line) data-loggers obtained (a) during a 15-days monitoring pin-tailed sandgrouse nest; (b) for a particular day showing two off-bouts (absences from the nest, highlighted with vertical grey bars); and (c) for the last two days of nest-attendance, with hatching on the second day. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
included “nest identity” as a random variable (in order to take into account that data from the same nest were not independent). Dependent variables (time and duration of off-bouts, change in nest temperature during off-bouts) were fitted to models using a normal error distribution and an identity link function.

We first tested whether the duration of an off-bout differed between daytime periods (morning vs evening) and between event types (nest visit vs disturbance vs mate switch) using GLMMs that included these variables and their interaction as explanatory variables.

We estimated the repeatability of the timing and duration of the off-bouts associated with mate switches by comparing within- and between-pair variation. Repeatability indicates how strong the individual consistency in a trait is in the population (the proportion of behaviour variation explained by the variation among individuals). We calculated both “repeatability” and “adjusted repeatability” (i.e. repeatability after accounting for other variables such as sunset or sunrise time), as the ratio “between-individual variance/residual (within-individual) variance” from the null models or the models with covariates, respectively (see Nakagawa and Schielzeth, 2010).

To investigate factors influencing the changes in nest temperature during an off-bout (∆NTemp), we used GLMMs that included the type of event (disturbance vs mate switch), duration of the off-bout, and the change in the control temperature during the off-bout.
(\(\Delta C_{\text{Temp}}\)), as well as the interactions between these factors. Initial models also included the factor daytime period, but this variable was highly related to \(\Delta C_{\text{Temp}}\) and not retained in final models. Finally, we analysed factors modulating off-bout duration using GLMMs that included the control temperature at the onset of the off-bout, the type of event, and their interaction.

Data are expressed as means ± SD and tests are two-tailed. We used SAS 9.2 (SAS, 2012) for all analyses.

3. Results

3.1. Off-bouts characterization and duration

Control temperatures greatly fluctuated daily while nest temperatures showed dampened fluctuations when a nest was normally incubated (Fig. 2a,b). When a nest was deserted (either because it hatched or failed), nest and control temperature became similar, so the monitoring allowed to determine precisely the timing of hatching or failure (Fig. 2c; Table 1).

For the pin-tailed sandgrouse \((n = 10\) nests), we identified a total of 97 off-bouts, which lasted on average 30.3 ± 25.3 min (range 10–165). Most off-bouts were associated with putative mate switches \((n = 71)\), followed by nest visits \((n = 17)\) and other putative disturbances \((n = 9)\).

Off-bouts caused by nest visits lasted on average 46.6 ± 34.1 min (range 10–140), and those caused by other disturbances lasted 50.6 ± 46.9 min (range 10–165). Off-bouts associated with mate switches lasted on average 23.8 ± 14.2 min (range 10–85, \(n = 71\)). However, if we include mate switches that were too short to result in an off-bout detectable by a change in nest temperature over a 5 min period (25% of all switches), off-bouts lasted 19.0 ± 14.8 min (range 5–85; \(n = 95\)).

Overall, off-bouts associated with disturbance events (nest visits and other disturbances combined) were significantly longer than those associated with mate switches (Mixed model: \(F_{1,85} = 20.84; P < 0.001\)). In addition, off-bout duration depended on the period of day (morning versus evening) in interaction with the type of event (Time period × Event: \(F_{1,84} = 4.38; P = 0.040\)). In the morning, off-bouts related to mate switches lasted 26.4 ± 4.2 min (\(n = 48\)), and those related to disturbances 59.9 ± 6.2 min (\(n = 14\)). Event effect: \(F_{1,39} = 13.99; P < 0.001\). In the evening, off-bouts related to mate switches lasted 22.5 ± 4.1 min (\(n = 47\)) and those related to disturbances 34.2 ± 7.0 min (\(n = 12\)); Event effect: \(F_{1,39} = 5.48; P = 0.024\).

For the black-bellied sandgrouse \((n = 1\) nest), we identified 18 off-bouts, which lasted on average 31.9 ± 16.8 min (range 10–60). All off-bouts were associated with putative mate switches (the nest was not visited after data-logger set-up until after the young hatched, and we had no evidence of disturbances during incubation). If we also consider those mate switches that were too short to result in a detectable off-bout, absences during mate switches were estimated to last 23.0 ± 18.8 min (range 5–60; \(n = 27\)). Absences lasted 26.5 ± 23.12 min (\(n = 13\)) and 19.6 ± 13.7 min (\(n = 14\)) during the morning and evening mate switches, respectively.

3.2. Timing of off-bouts associated with mate switches

In the pin-tailed sandgrouse, detected mate changes took place between 08:00 and 10:00 and between 19:30 and 21:30 (Fig. 3a). Interestingly, mate switches occurred at a time in the morning when the control temperature was lower than or nearing the nest temperature, and in the evening at a time when the control temperature was similar to or cooler than that of the nest temperature (Fig. 3a).

In the black-bellied sandgrouse, detected mate changes took place between 08:00 and 10:00 and between 20:00 and 21:00 (Fig. 3b). As for the pin-tailed sandgrouse, the timing of mate changes occurred at times when the control and nest temperatures were similar (Fig. 3b).

3.3. Consistency in the timing and duration of mate switches

In the pin-tailed sandgrouse, the timing of morning switches was unrelated to sunrise time \((F_{1,37} = 0.27; P = 0.608)\), while the timing of evening switches positively correlated with sunset time \((F_{1,36} = 4.99; P = 0.032)\). In June–July, morning mate switches occurred on average 3 h after sunrise, and evening switches 7 min before sunset. The time at which mate switches occurred in the morning was less variable within-pairs than between pairs and had a high repeatability value \((R = 0.61)\). A similarly high repeatability value was obtained when including sunrise time as a covariate \((R = 0.63)\). The time of evening mate switches was also repeatable \((R = 0.45)\), but less than that of morning switches. Controlling for sunset time gave a similar repeatability value \((R = 0.44)\). In contrast, the duration of off-bouts was not repeatable \((R\)-values of 0.06 and 0.24 for morning and evening off-bouts, respectively).

3.4. Off-bouts and changes in nest temperature

In the pin-tailed sandgrouse, changes in nest temperature during off-bouts depended on the duration of the absence \((F_{1,85} = 5.58; P = 0.020)\) and the change in control temperature \((\Delta C_{\text{Temp}})\) in interaction with type of event \((\Delta C_{\text{Temp}}: F_{1,85} = 32.94; P < 0.001); \text{Event: } F_{1,85} = 5.58; P = 0.020; \Delta C_{\text{Temp}} \times \text{Event: } F_{1,85} = 5.46; P = 0.022)\). The shorter the absence from the nest, the less the nest temperature changed during the off-bout (duration effect: slope ± se: +0.023 ± 0.009). In addition, changes in nest temperature were positively correlated with change in control temperatures, with a steeper slope during disturbance events (slope ± se: +0.426 ± 0.099) as compared with mate switch events (slope ± se: +0.201 ± 0.056; Fig. 4).

3.5. Modulation of off-bout duration

In the pin-tailed sandgrouse, off-bout duration depended on the type of event, the control temperature at the start of the off-bout \((\Delta C_{\text{Temp}})\), and their interaction \((\Delta C_{\text{Temp}}: F_{1,86} = 21.87; P < 0.001); \text{Event: } F_{1,86} = 23.70; P < 0.001; \Delta C_{\text{Temp}} \times \text{Event: } F_{1,86} = 13.20; P < 0.001; \text{Fig. 5})\). During mate switch events, off-bout duration was unrelated to control temperature \((F_{1,85} = 1.39; P = 0.242); \text{slope ± se: −0.279 ± 0.236})\). In contrast, during disturbances, off-bout duration decreased with increasing control temperature \((F_{1,15} = 7.95; P = 0.013); \text{slope ± se: −2.333 ± 0.828})\). When a sandgrouse was disturbed during high-temperature hours, it returned more rapidly to its nest to incubate.

3.6. Nest fates

The only monitored black-bellied sandgrouse nest successfully hatched. Out of the 14 pin-tailed sandgrouse nests with temperature data-loggers (see Methods and Table 1), 3 (21%) successfully hatched and 11 failed. Out of the 18 pin-tailed sandgrouse nests without temperature data-loggers, 3 (17%) successfully hatched and 15 failed. We therefore had no evidence that nest success rate differed between nests with or without data-loggers.
metabolic demands for clutch formation and egg-water loss (Thomas, 1984). Sandgrouse eggs are also relatively smaller than those of similar-sized species (e.g. Charadriiformes), allowing them to complete their clutch with a low investment of resources (minerals, nutrients and water), which is an advantage in arid and desert environments (Thomas, 1984).

This study is the first, to our knowledge, to use data loggers for studying incubation rhythms by birds in arid environments. In terms of incubation, breeding in arid climates implies that eggs, although protected by parents most of the time, are exposed to large temperature variations, and, in particular, occasionally exposed to very high temperatures. For instance, during the incubation of monitored pin-tailed sandgrouse nests, the temperatures recorded at the control data-logger greatly fluctuated, with daily oscillations between a minimum average of c.19 °C (between 06:00 and 08:00) and a maximum average of c.55 °C (between 14:00 and 17:00; Fig. 3a). In contrast, the temperatures recorded at the nest showed dampened oscillations between average temperatures of 30 and 39 °C (Fig. 3a). Note that these are not directly equivalent to ambient and egg temperatures, respectively, but indicate an average amplitude variation of c.36 °C outside the nest, but of only c.9 °C at the nest. Incubation by both sexes (by the female during the day and by the male at night) therefore prevented exposure of eggs to critically high temperatures during daytime, or to an excessive cooling of eggs at night, respectively. Since the eggs are on the ground, soil-surface temperatures are critical for sandgrouse nesting success. For example, when temperatures are particularly high, incubating namaqua sandgrouse (Pterocles namaqua) raise their body, and face the wind to allow a convective cooling of eggs (McLean, 1995). If soil temperatures are too high (>55 °C), incubating birds are unable to regulate effectively nest temperature and the embryos do not survive (McLean, 1995; Webb, 1987). Deviations from the normal nest incubation temperatures, if prolonged in time, may provoke egg desiccation and threaten the embryo’s viability (McLean, 1995). During some absences from the nest associated with disturbances, we recorded changes in nest temperatures of up to 10 °C above the normal nest temperatures (Fig. 4). Absences from the nest during incubation, irrespective of their cause, may therefore be critical for nesting success of these species.

The combination of a nest and control temperature data-logger allowed us to accurately characterize off-bouts in terms of their timing, duration and temperature context (Fig. 2). A limitation, however, is that their cause was not always known (except when we visited nests). Knowing the biology and incubation routines of these sandgrouse species, we could reasonably well characterize off-bouts that were related to mate switches and incubation reliefs. Both the pin-tailed and the black-bellied sandgrouse exhibited similar incubation rhythms and mate switch times (Fig. 3; De Borbón et al., 1999a,b), which normally occurs during cooler hours after dawn and before dusk, as described in other sandgrouse species (De Borbón et al., 1999b; De Juana, 1997). In the pin-tailed sandgrouse, the timing of morning mate switches was not tightly related to sunrise time (at least in June–July, during the course of the study) but was repeatable, indicating that each pair had its routine for morning incubation reliefs. In the evening, mate switches correlated with sunset time and appeared more synchronous between pairs, possibly because the window of optimal thermal conditions for a mate switch is more constrained than in the morning. A similar relief pattern was documented in the namaqua sandgrouse, with variation in evening switch times related to sunset throughout the breeding season (Lloyd et al., 2001). Longer absences associated with mate switches may thus correspond to cases in which male or female leave the nest before the return of its mate, as reported to occur sometimes in the pin-
tailed sandgrouse species (De Borbón et al., 1999a; Benítez-López, personal obs.).

Interestingly, we found that in both studied species the timing of mate switches occurred when the differences between the nest and control temperatures were typically minimal (Fig. 3). On the one hand, this may reduce our ability to detect such off-bouts using the temperature data-loggers (when nest and control temperatures are similar, off-bouts are less noticeable). Indeed, c.25% of mate switches that must have occurred, given the normal incubation routine of sandgrouse, were not detected, either because they were too short (<5 min), or because they happened precisely at a time when nest and control temperature were identical. On the other hand, this indicates that the timing of these mate switches is adaptive, in order to maintain the clutch within an optimal temperature range. The changes in nest temperature recorded during the off-bout associated with mate switches were mostly temperature decreases (range 0 to –5 °C) and very rarely temperature increases (see Fig. 4). This indicates that during a mate switch, sandgrouse are more willing to risk a cooling rather than a warming of their clutch. While a cooling of eggs may slow down the embryo’s development, and have consequences in terms of duration of incubation, an overheating might be more critical for the embryo’s viability (Grant, 1982; McLean, 1995; Webb, 1987).

Sandgrouse are characterized by highly synchronized early morning and late afternoon arrivals to drinking points during breeding season, a behaviour that has been mainly interpreted as a strategy to reduce predation risk or to reduce evaporative water loss and save energy (Ward, 1972; Yosef and Zdunak, 2011). Our data indicate that the timing of incubation reliefs, and therefore for travelling to drinking points is constrained by thermal conditions (in order to maximize eggs and small chick survival). We suggest that the limited window of optimal thermal conditions for leaving the nest in order to maximize nesting success should also be considered when explaining the high synchrony in sandgrouse drinking behaviour.

4.2. Sandgrouse nest monitoring: usefulness and limitations of temperature data-loggers

By setting up data-loggers upon a unique nest visit, researchers can monitor the nest fate and obtain information on breeding phenology without the need of revisiting it again until after hatching. Successful hatching can be detected from temperature recordings (e.g. Fig. 2c; low amplitude nest temperature oscillations occur during hatching), and distinguished from breeding failures (abrupt change in nest temperature that quickly equals the control temperature). This may be particularly useful in precocial species because nests are sometimes left empty (without egg shell remains) after successful hatching (De Borbón et al., 1999a,b). If laying was not complete upon data-logger set-up, this can also be detected. Sandgrouse attend their nest as soon as the first egg is laid (Johnsgard, 1991), but incubation fully starts only after the last egg is laid (De Juana, 1997). The male does not incubate until laying is complete, but the female does, and stays at the nest during the day, protecting the egg from the heat and intense solar radiation (Herranz and Suárez, 1999; Hinsley and Hockey, 1989; Lloyd et al., 2001). For two study nests (see Table 1), the temperature recordings clearly showed that the nest was not being incubated at night (by the male) initially, but was attended (by the female) during the day, and our nest monitoring (visits) confirmed that in both cases, the data-loggers were set-up before laying was complete.

Temperature data-loggers allow determining precisely when a nest fails (Table 1). A limitation, however, is that distinguishing between causes of failure (abandonment, predation, or a predation after abandonment) may not be always possible without checking the nest content after failure. If a failed nest contains un-hatched (cold) eggs, abandonment is likely. Broken eggshells may indicate predation, their inspection may precise avian versus mammal predation, and the timing of nest failure indicate if it was by a diurnal or nocturnal predator. If a nest is found empty, however, the cause of failure could be predation or abandonment followed by predation (De Borbón et al., 1999a,b; De Juana, 1997).

Nesting success was overall low in the pin-tailed sandgrouse, with no evidence that setting up data-loggers at nests affected success during incubation (21% and 17% of nests with and without temperature data-loggers successfully hatched, respectively), as in other studies (e.g. Cervenl et al., 2011). Similar low nesting success has been previously reported for pin-tailed and black-bellied sandgrouse (10% and 25%, respectively; De Borbón et al., 1999a,b), for namaqua sandgrouse (7–15%; Lloyd et al., 2000) and for yellow-throated sandgrouse Pterocles gutturalis (25%; Tarboton et al., 1999).

Low productivities likely contribute to the vulnerable conservation status and population declines observed in some sandgrouse species. Predation is considered a main cause of failure (De Borbón et al., 1999a; Lloyd, 2004; Lloyd et al., 2000; Tarboton et al., 1999). However, nest abandonment or predation following disturbances could also be a significant cause of nesting failure.

Sandgrouse may be particularly sensitive to human disturbances during incubation. Indeed, we found that the duration of off-bouts was significantly greater when the cause was a nest visit or disturbance as compared with a mate switch. Sandgrouse also avoid leaving the nest unattended during the hottest hours of the day (De Juana, 1997), when the nest temperature can increase dramatically, even during a short absence. During a disturbance, we found that the incubating bird returned faster to its nests when the outside temperature was higher (Fig. 5), most likely to prevent an overheating of the clutch. Also, when incubating parents are disturbed and leave the nest, the eggs can be exposed to “abnormal” variations in temperature that may reduce egg viability or influence the duration of the incubation period. Prolonged incubation periods imply higher predation risk for both eggs and adults, and greater energetic costs associated with incubation (Thomson et al., 1998). Therefore, the need for a nest monitoring in species of arid climates should be carefully evaluated, and if it is considered necessary, carefully planned and timed.

5. Conclusions

This study highlighted some of the constraints that birds breeding in arid environments, such as sandgrouse, face when incubating their clutch. It also highlighted the importance of monitoring the potential impacts of nests visits. For monitoring purposes, the timing of nests visits should be carefully planned, taking into account the temperature context and the birds’ incubation rhythms, preferentially using the same time windows that the birds prefer for mate switches. The use of temperature data-loggers for monitoring sandgrouse nests has provided novel and useful information in that respect. We suggest that data-logger methods could allow an effective monitoring of other birds breeding in similar arid environmental conditions, without risking an exposure of the clutch to potentially harmful temperatures.

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