



Dual function of egg-covering in the Kentish plover *Charadrius alexandrinus*

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Abstract

Many bird species take recesses during incubation, and while the nests are unattended, the eggs may both be vulnerable to predation and reach suboptimal temperatures for embryo development. Perhaps to avoid these negative possibilities, some birds cover their eggs with materials when they depart from nests. We examined experimentally, using the ground-nesting Kentish plover as model species, whether egg-covering allows egg temperatures to remain within optimal limits for embryogenesis in unattended nests, thus reducing the requirements of contact incubation, and simultaneously maintain the eggs' camouflage. There was a negative relationship between nest attendance and ambient temperature, but only during mid-morning, the period of the day when egg-covering was most frequent. Indeed, during mid-morning egg-covering not only served to better camouflage the eggs, but also to maintain egg temperatures within optimal thermal thresholds for embryogenesis while the nests remained unattended. During other periods of the day, covered eggs in unattended nests overheated (e.g., afternoon) or did not reach the optimal temperature for embryogenesis (e.g., early morning). During periods in which eggs may be uncovered to alleviate overheating, unattended nests may be easier to locate by predators, because the eggs are less well camouflaged. Therefore, camouflage and appropriate thermal environment are inseparable functions of egg-covering in the ground-nesting Kentish plover.

Keywords

egg burial, egg crypsis, incubation, nest attendance, shorebirds, thermal environment.

1. Introduction

Incubation is the process by which eggs are kept at temperatures suitable for embryonic development, which in the case of birds are generally between 37 and 38°C, with most of the heat being provided by the incubating bird (Deeming, 2002). In birds, only the megapodes do not practice contact incubation to provide heat to their eggs, but instead bury the eggs in mounds of vegetation; these mounds receive considerable attention by males to maintain the appropriate incubation temperatures (Booth & Jones, 2002). Burrow nesting crab plovers *Dromas ardeola* rely to a great extent on solar assisted incubation (de Marchi et al., 2008). The needs of incubation may impose energetic costs on parents (Williams, 1996), and may also limit the time that they may spend away from nests in other activities necessary for self-maintenance, such as foraging (Reid et al., 2002b; Creswell et al., 2004; Weston & Elgar, 2005).

Many bird species take recesses during incubation, mainly to forage. However, leaving clutches unattended may have direct and immediate fitness costs through either suboptimal embryonic conditions and/or increased predation. Unattended nests may result in embryos diverging rapidly from developmental optima (Reid et al., 2002b). Because of this, off-bout duration is constrained by the optimal thermal needs of embryos, and particularly at both low and high ambient temperatures birds spend less time off the nest because at such temperatures embryo development is negatively affected (Conway & Martin, 2000; Weston & Elgar, 2005). As pointed out by Reid et al. (2002b), birds may reduce the requirements of incubation to some extent, for example by choosing nest materials based on their thermal quality (e.g., Hoi et al., 1994; Reid et al., 2002a; Mayer et al., 2009). Further, unattended eggs may be more vulnerable to predation, either because the incubating adults do not defend them, or because nests are easier to locate by predators (e.g., Remeš, 2005; Trnka et al., 2008; but see Brennan, 2010).

Some birds cover their eggs with materials when they depart from the nests. Egg-covering has also been recorded in both invertebrate and other vertebrate species (e.g., Keller, 1989; Shimoda et al., 1994; Villemart, 2001; Pérez-Santigosa et al., 2003; Opermanis, 2004; Kreisinger & Albrecht, 2008), and two non-mutually exclusive main functions have been attributed to this behaviour: camouflage of the nest and/or maintenance of egg temperature (Maclean, 1974; Haftorn & Slagsvold, 1995; for other functions of egg-covering see Sealy, 1995; Valera et al., 1997; Guigueno & Sealy,

2009). Therefore, under conditions of appropriate thermal environment and camouflage, egg-covering may be a mechanism with which birds reduce the requirements of contact incubation, allowing the incubating adults to spend more time in other activities, such as foraging (Howell, 1979; Davis et al., 1984). Consequently, there is likely to be selection for egg-covering if this allows the maintenance of an appropriate thermal environment for eggs in unattended nests, enabling adults to spend time away from nests in other activities necessary for self-maintenance.

Most studies on birds have interpreted egg-covering as an anti-predation tactic (Summers & Hockey, 1981; Keller, 1989; Kreisinger & Albrecht, 2008; Prokop & Trnka, 2011), and few studies have addressed the effects of egg-covering on egg temperature, or whether egg-covering may reduce the requirements of contact incubation (Howell, 1979; Grant, 1982).

In birds, egg-covering is particularly common among shorebirds (Charadrii) breeding in hot and arid environments (Maclean, 1974; Grant, 1982). Optimal egg temperature for embryo development in most Charadriiformes is 35–38°C (Drent, 1975; Grant, 1982; Rahn, 1991). Many shorebird species nest on small scrapes on the ground, in sites with little or no cover (Grant, 1982; Koivula & Rönkä, 1998; Brown & Downs, 2003; Amat & Masero, 2004a; AlRashidi et al., 2011), in which unattended nests may be easy to locate by visual searching predators and, thus, egg-covering may make the nests better camouflaged than if eggs remain uncovered (Summers & Hockey, 1981). On the other hand, if the function of egg-covering is to maintain an optimal thermal environment for embryos, then egg-covering should occur when it allows egg temperatures to be within those limits, i.e., 35–38°C, and should be avoided if it does not contribute to keep egg temperature within optimal limits for embryogenesis. These two main functions may not be mutually exclusive, however, as egg-covering may help to maintain nest camouflage and at the same time may serve to keep egg temperatures within more appropriate limits for embryogenesis than if eggs remain uncovered and unattended by adults. In addition, if egg-covering contributes to reduce the requirements of contact incubation, during periods in which eggs are covered there should be a negative relationship between ambient temperature and nest attendance by adults. We tested these predictions using the Kentish plover *Charadrius alexandrinus* as a model species, by analyzing the effects of egg-covering on egg temperatures, and quantifying the degree of egg camouflage in nests with both covered and uncovered eggs. We then used data on

average ambient temperatures at our study site to explain why egg-covering was more frequent during particular periods of the day.

2. Methods

2.1. Study species

Our study was conducted at Fuente de Piedra Lake in southern Spain, described in Amat et al. (1999). Kentish plovers are small-sized shorebirds that nest on the ground and partially cover their eggs with nest materials (George Kainady & Al-Dabbagh, 1976; Grant, 1982; Orr, 1999; Figure 1). Both sexes participate in incubation, with females practicing most diurnal incubation and males mainly incubating at night (Nazakawa, 1979; Fraga & Amat, 1996; Kosztolányi & Székely, 2002; Amat & Masero, 2004b; Al-Rashidi et al., 2011). The main visual searching nest predator at our study site is the gull-billed tern *Gelochelidon nilotica* (Fraga & Amat, 1996; Amat & Masero, 2004a).

2.2. Diurnal variations in egg-covering

To record variations in egg-covering according to time of day we visited nests, under clear-sky conditions, around early morning (5:30 h GMT), mid-morning (9:30 h), mid-afternoon (15:00 h), and late afternoon (18:30 h). When eggs were partially covered, we marked, using permanent pencil, the eggshell at the point at which the egg contacted with nest materials along the longest egg axis perpendicular to the ground (Figure 2). We then carefully

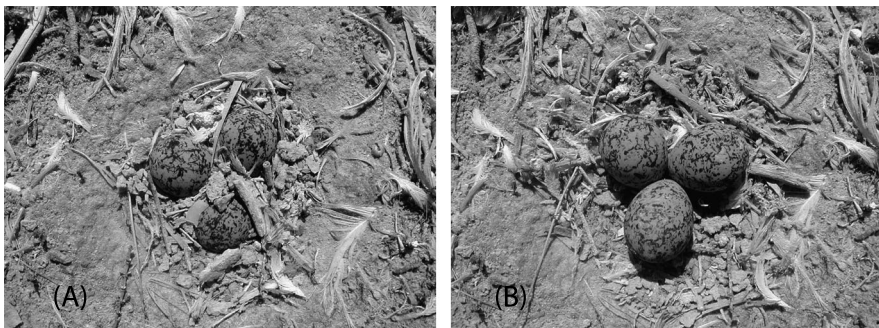


Figure 1. A Kentish plover nest with partially covered (A) and uncovered (B) eggs (photographs by José A. Masero).

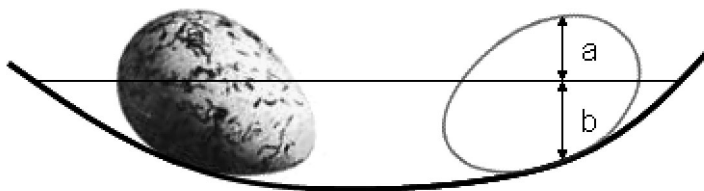


Figure 2. Schematic representation of the mode in that egg-covering was measured. The length of the part of the longest egg axis perpendicular to the ground that was uncovered with materials (a) was measured to the nearest 0.1 mm using digital calipers, as well as the length of that axis ($a + b$). The degree of egg-covering was expressed as $(a/(a + b)) \times 100$.

removed the egg from the nest while maintaining that longest axis perpendicular to the ground. Using digital callipers, one of us (always the same) measured to the nearest 0.1 mm the length of that axis, as well as the length of the part of the axis that was uncovered with materials. After this, we left the eggs in a state of covering similar to which we had found them. The procedure took 3–5 min. The degree of egg-covering was expressed as the length of the part of the axis that remained covered relative to total axis length (Figure 2), and this was expressed as percentage. Therefore, egg-covering may vary between 0 (egg completely uncovered) and 100 (egg completely covered). We took these measurements for every egg in 15 nests, and then averaged these values for each nest.

2.3. Egg-covering and nest camouflage

To evaluate whether egg-covering rendered the nests more cryptic, we photographed Kentish plover nests, using an Olympus C900Z camera. Photographs were taken approximately 30 cm above the nests, under clear-sky conditions, between 9:00 and 11:00 h (GMT). We chose this period because during previous studies we noticed that such period was when the eggs were more frequently covered with materials (see below). A photograph of each nest was taken with eggs partially covered, and immediately after this we removed the materials that partially covered eggs and took a second photograph with eggs uncovered.

In such photographs, we quantified the coloration of eggs and nest scrape with Adobe Photoshop CS4 (Adobe, San José, CA, USA). The eyedropper was set at 51×51 pixels, with a resolution of 72 pixels/inch, and values in the $L^*a^*b^*$ colour space were recorded (see Nguyen et al., 2007; Pereira & Amat, 2010), where L^* defines lightness, a^* denotes the red/green value

and b^* the yellow/blue value (X-Rite, 2000). We took readings at spaced points on the images, noting whether the readings were on eggs or nest scrape. Five metric values were obtained for each category (egg, nest scrape), which were averaged for each one of these categories for each photograph. Colour differences (ΔE^*) between eggs and nest scrape were defined by the equation (X-Rite, 2000)

$$\Delta E^* = (\Delta L^{*2} + \Delta a^{*2} + \Delta b^{*2})^{1/2}.$$

The larger ΔE^* , the lower the similarity in coloration between eggs and nest scrapes.

2.4. Nest attendance

We set up blinds 15–20 m from 13 nests to record nest attendance by adults. We made observations during 2-h periods in the early morning (04:30–06:30 h, GMT), mid-morning (08:00–10:00 h), mid-afternoon (14:00–16:00 h) and late afternoon (17:00–19:00 h). An observation started when adults returned to nests after we had entered the blinds. The birds resumed incubation 15.9 ± 11.14 min (average \pm SD; range = 2–49 min, $n = 32$ observations at 13 nests) after we entered the blinds. We considered nest attendance as the percentage of time that the nest was attended by an adult, either male or female, relative to total observation time, and related nest attendance to ambient temperature, which was recorded every 40 s as indicated below, and averaged for each of the observation periods.

All nests were not in a similar stage of incubation when we conducted the observations. Nevertheless, our results were not likely affected by this, since nest attendance in plovers is not affected by clutch's age (Weston & Elgar, 2005; O. Vincze et al., unpubl.).

2.5. Eggs and ambient temperatures

To ascertain how egg-covering affected egg temperatures, we performed an experiment on sunny days. For this, we used Kentish plovers eggs previously collected from deserted nests. These eggs were emptied and filled with plaster of Paris, which has a thermal conductance almost identical to that of natural eggs (see Ward, 1990; Amat & Masero, 2007). We placed a model egg in each of 25 empty nests of plovers that were in sites exposed to direct solar radiation. We partially covered with materials one model egg, with a degree of coverage similar to that found in natural nests, and left it shaded

for 3 min, after which we removed the shade and left the egg exposed to direct solar radiation during 10 min. After this, we shaded the egg again during 3 min, and while the egg was shaded we removed the partial covering of nest materials. Finally, we removed the shade and left the egg exposed for another 10 min. We recorded the maximum temperature reached by model eggs during the 10-min periods. The order of treatment of model eggs (first covered, then uncovered, or vice versa) was arbitrary. We used eight model eggs.

Temperatures of model eggs (T_{egg}) were recorded with 36-gauge copper-constantan thermocouple probes (Omega Engineering, Stamford, CT, USA) inserted into the eggs. Ambient temperature (T_{a}) was measured at an exposed site about 1 m from nests, and 5 cm above ground level, using a 20-gauge copper-constantan thermocouple probe, with its tip covered with white reflective tape (Ward, 1990). All probes were connected to Omega OM-550 dataloggers, which were programmed to record temperatures every 40 s.

3. Results

3.1. Diurnal variations in egg-covering

The degree of egg-covering varied throughout the day, being greater during mid-morning (Figure 3, Friedman ANOVA, $\chi^2_3 = 15.6$, $N = 15$, $p = 0.001$). Although there was also some degree of covering at other times of day, it was very small and it seemed that this was due to the eggs being slightly depressed in the nest materials rather than to a true egg-covering.

3.2. Egg-covering and camouflage

The difference in coloration (ΔE^*) between eggs and nests was lower in nests with partially covered eggs (mean \pm SD 7.6 ± 4.04 , $N = 8$) than in the same nests with eggs uncovered (15.0 ± 6.57) (Student's paired t -test, $t = 3.20$, $DF = 7$, $p = 0.015$). Therefore, the eggs were better camouflaged when they were covered.

3.3. Nest attendance and temperatures

There was a negative relationship between the percent of time incubating and T_{a} during mid-morning (Figure 4, $r = -0.64$, $N = 12$, $p = 0.027$), but not during the rest of the day ($r = 0.06$, $N = 13$, $p = 0.836$).

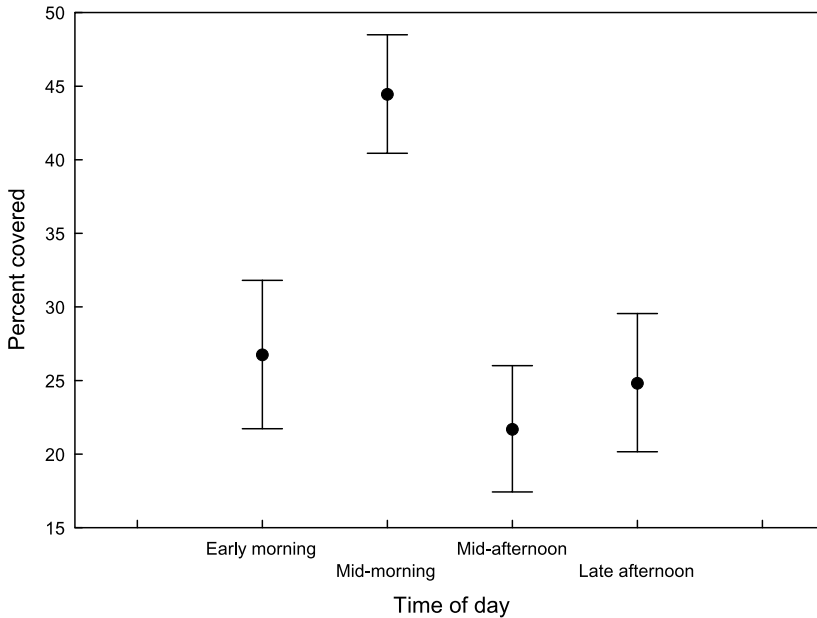


Figure 3. Diurnal variations in the mean degree of egg-covering (\pm SE) in 15 Kentish plover nests.

3.4. Egg-covering and temperatures

Ambient temperatures explained a large proportion of the variance in T_{egg} , both in uncovered ($r^2 = 0.85$, $N = 25$, $p < 0.001$) and covered model eggs ($r^2 = 0.89$, $N = 25$, $p < 0.001$). However, the slope of the relationship between both variables was steeper in covered than in uncovered model eggs (Figure 5; $F_{1,46} = 8.4$, $p = 0.006$), meaning that at high temperatures covered eggs gained temperature at higher rate than uncovered nests ($F_{1,46} = 5.7$, $p = 0.022$).

To reveal why egg-covering is more frequent during mid-morning than during other periods of the day, we used data on diurnal average T_a at our study site (Amat & Masero, 2004b), together with the equations relating T_a and T_{egg} in nests with covered and uncovered eggs (Figure 5). According to these equations, for unattended uncovered eggs, T_{egg} would be optimal for embryogenesis ($35\text{--}38^\circ\text{C}$) at T_a $28.7\text{--}32.3^\circ\text{C}$. On the other hand, for unattended covered eggs, T_{egg} would be optimal for embryogenesis at T_a $28.0\text{--}30.5^\circ\text{C}$. This range of T_a ($28.0\text{--}32.3^\circ\text{C}$) is usually found during mid-morning (Figure 1 in Amat & Masero, 2004b), which is the period in which

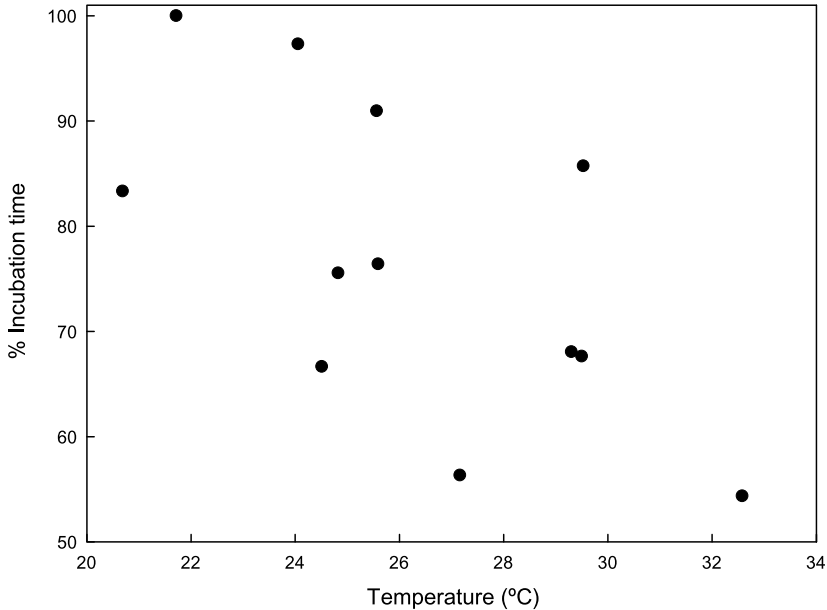


Figure 4. Percent time spent incubating by Kentish plovers in relation to ambient temperature during mid-morning (08:00–10:00 h).

the eggs remain more frequently covered (Figure 3). During average conditions in the morning at Fuente de Piedra, it takes 74 min for T_a to rise from 28.7 to 32.3°C (after Figure 1 in Amat & Masero, 2004b). It takes 51 min for T_a to rise from 28.0 to 30.5°C in the morning, i.e., the period in which unattended eggs encounter optimal thermal conditions for embryogenesis during the morning may be extended for 23 min when eggs are uncovered relative to when eggs are covered.

At average T_a at Fuente de Piedra (Figure 1 in Amat & Masero, 2004b) during other periods of the day, T_{egg} in covered unattended nests was not optimal for embryogenesis, according to equation in Figure 5 for covered eggs, either in the early morning ($T_{egg} < 28.0^\circ\text{C}$) or in the mid-afternoon ($T_{egg} > 43.8^\circ\text{C}$). However, in the late afternoon, T_{egg} in unattended covered nests would be 37.5°C, which is within the optimal range for embryogenesis. Therefore, these results explain why eggs are not covered in the early morning or mid-afternoon, because during such periods eggs in unattended covered nests do not achieve appropriate conditions for embryogenesis. But these results do not explain why eggs are not covered in the late afternoon,

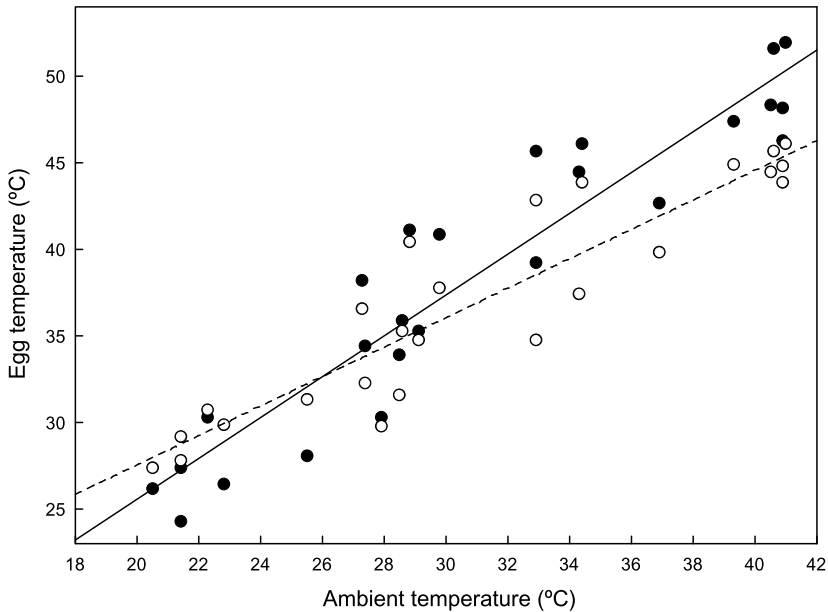


Figure 5. Linear relationships between egg and ambient temperatures in covered (filled circles, solid line) and uncovered Kentish plover nests (open circles, dashed line). Regression line for uncovered eggs: Egg temperature ($^{\circ}\text{C}$) = $10.5469 + 0.8504 \times$ Ambient temperature ($^{\circ}\text{C}$). Regression line for covered eggs: Egg temperature ($^{\circ}\text{C}$) = $1.9840 + 1.1793 \times$ Ambient temperature ($^{\circ}\text{C}$).

since in this period unattended covered eggs would result in optimal thermal conditions for embryogenesis.

4. Discussion

Our results show that egg-covering in the Kentish plover mainly serves to make the eggs more cryptic, while also aiding to maintain egg temperature within optimal thresholds while the nests remain unattended. Consequently, the function of egg-covering in the Kentish plover is dual. But these two functions (camouflage and appropriate thermal environment) have to act simultaneously to be effective. For such reason, the time window during which egg-covering is functional is rather narrow. Indeed, our findings suggest that the time that adults could spend off the nests is constrained by the critical thermal conditions that covered eggs experience when $T_a > 30.5^{\circ}\text{C}$, which would be alleviated by uncovering eggs until T_a reaches 32.3°C , but then the eggs in unattended nests would be more vulnerable to predators, as they

are less cryptic. This is the reason for which both functions would have to act simultaneously to be effective, thus precluding the use of egg-covering during some periods of the day. This may be so during the early morning because T_{egg} in unattended covered nests is below the range for optimal embryo development, or during the mid-afternoon, when unattended covered eggs overheat. Nevertheless, eggs in unattended covered nests would find optimal conditions for embryogenesis during the late afternoon, yet the eggs are not usually covered during this period. A reason for this may be that at such time male and female Kentish plovers shift incubation (Fraga & Amat, 1996), and there would be no need to cover the eggs for a better camouflage because the nest would not remain unattended. Similarly, in other studies it was found that eggs were only covered in the morning (Liversidge, 1965; George Kainady & Al-Dabbagh, 1976; Howell, 1979; but see Clark, 1982).

Previous studies on invertebrates and vertebrates have concluded that facultative egg-covering renders the clutches better camouflaged (Summers & Hockey, 1981; Keller, 1989; Shimoda et al., 1994; Opermanis, 2004; Kreisinger & Albrecht, 2008). Prokop & Trnka (2011) also found that, in the laboratory, cooling rates were higher in grebe nests with uncovered eggs than in nests with covered eggs. However, few studies examined how the interaction between egg-covering and thermal environment may affect egg temperatures suitable for embryogenesis (Howell, 1979; Grant, 1982).

Clark (1982) and Szentirmai & Székely (2004) concluded that, in plover nests with covered eggs, nest material could shade the eggs during parental absences from the nests, thus preventing the eggs from overheating. However, Grant (1982) showed experimentally that during the hottest part of the day even shaded eggs buried partially or totally at shallow depths in dry sand would be fatally overheated. Because neither Clark (1982) nor Szentirmai & Székely (2004) presented data on egg temperatures, their conclusions are difficult to assess. In fact, Howell (1979) noted that in the Egyptian plover *Pluvianus aegyptius* temperatures of covered eggs remained within safe limits as solar heat was moderate during periods when nests were unattended, and that adult birds returned to nests when heat became intense (see also Weston & Elgar, 2005).

As predicted by Conway & Martin (2000) for birds attending nests, off-bout duration was longer during periods in which the thermal needs of embryos were more favourable. This may facilitate that, during such periods, birds are released from contact incubation and, therefore, may spend more time foraging (Weston & Elgar, 2005). Indeed, we found that when T_a was

27–32°C the adults spent 12–55% off the nests (Figure 4). At such T_a , T_{egg} in unattended covered nests would vary between 33.8 and 39.7°C, a range that encompasses the optimal temperatures for embryo development. Such ambient temperatures are usually found during mid-morning (Figure 1 in Amat & Masero, 2004b), the period in which the eggs remain more frequently covered. During the thermal conditions of mid-morning the eggs may be left unattended for longer periods when uncovered than when covered. However, during these periods in which the eggs may be uncovered to alleviate overheating, unattended nests may be easier to locate by predators (Keller, 1989; Opermanis, 2004; Prokop & Trnka, 2011), because the eggs are less well camouflaged. As shorebirds suffer high nest predation rates (e.g., Fraga & Amat, 1996; Neuman et al., 2004; Saalfeld et al., 2011), better egg camouflage may be adaptive because this may improve nesting success (Solís & de Lope, 1995; Lee et al., 2010; Colwell et al., 2011).

Previous work on the adaptive value of egg-covering has been mainly aimed at studying the effects of egg concealment on egg survival, and to a lesser extent on egg temperatures. However, as egg-covering also allows birds to reduce the requirements of contact incubation, to fully understand the adaptive value of this behaviour, future studies should also consider its direct effects on the incubating adults (e.g., by analyzing changes in their body condition).

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