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# AMBIENT TEMPERATURE AND NEST TEMPERATURE VARIATION IN ENCLOSED NESTS (SPANISH SPARROW) AND OPEN-CUP NESTS (IBERIAN AZURE-WINGED MAGPIE)

## ABSTRACT

Temperature plays a central role in the life of birds, especially during egg incubation and nestling thermal brooding. I investigated nest temperature variation relative to ambient temperature during incubation in an enclosed nest-builder species (Spanish sparrow *Passer hispaniolensis*) and an open-cup nest-builder species (Iberian azure-winged magpie *Cyanopica cooki*). The data for empty enclosed nests showed that the nest structure acted as a temperature buffer which reduced the impact of night-time temperature variation within the nest. The buffer effect was reduced as ambient temperature increased at dawn. The presence of an adult increased the difference between nest temperature and ambient temperature, and dissociated its variation from the ambient temperature variation. The enclosed nest also retained the body heat released by an adult in the nest. Both effects had a positive effect on the temperature balance in the nest. By contrast, open-cup nest temperature was more affected by the ambient temperature, although it did not affect the egg temperature directly. Thus the absence of an incubating parent would endanger the hatchability in open-cup nests more rapidly than in enclosed nests. The life histories of the investigated species correspond to these findings, i.e. a more pronounced presence of the female in the Iberian azure-winged magpie nests.

**Keywords:** nest temperature, Passerines, Mediterranean climate, adaptation, temperature buffer

## INTRODUCTION

Ambient temperature affects the presence and density of species, and plays an important role in species phenology, such as the timing of migration, breeding activities, and survival. Temperature is especially important during breeding because it affects the costs of incubation and nestling thermal brooding during the heterothermic stage (Martin et al. 2007, Martin 2008, Ardia et al. 2009).

Avian embryo development is known to be deeply influenced by temperature, which may be viewed as a temperature optimal envelope that depends on the temperature and the duration of temperature exposure. A moderate period of time of temperature between 0°C and the physiological zero temperature (PZT) suspends embryo development. Between the PZT (assumed to be approximately 26°C (Drent 1975, Conway and Martin 2000)) and Lower Limit of Optimal Development (LLOD, 36°C) development is reduced but not impaired, although prolonged exposure may lead to abnormalities (Webb 1987, Cooper et al. 2005). Optimal development occurs between the LLOD and the Upper Lethal Temperature (ULT, 40.5°C for chickens, but assumingly equal among species (Conway and Martin 2000)). Above the ULT, abnormalities and death are expected depending on the duration of exposure (Webb 1987). Even small variation in incubation temperature may influence the metabolism of hatchlings (Nord and Nilsson 2011, DuRant et al. 2012b) and in turn their growth, body condition or immunity (DuRant et al. 2012a, DuRant et al. 2012b), probably compromising their development and survival.

The geographic variation in temperature affects incubation patterns (Martin et al. 2007) and it is more favourable in the tropics. However, the ambient temperature in most regions world-wide is very different from the optimal development temperature, and parents must compensate for unfavourable ambient temperature by incubating their eggs (Cooper et al. 2005, Martin 2008). This task can be very demanding because incubation is energetically expensive and it can affect future reproduction and the survival of adults and their offspring (Bryan and Bryant 1999, Visser and Lessells 2001). Adults must balance the thermal needs of the developing embryos with their own energetic needs (Conway and Martin 2000). The amount of time and energy that can be allocated to different activities during reproduction must be balanced (Bryan and Bryant 1999) among incubation, nest defence, and feeding. Changes in the ambient temperature, such as those due to predicted climate change (temperature increase and greater daily temperature variability (IPCC 2001)), may disrupt the balance in the trade-off and affect the breeding success (Bryan and Bryant 1999, Both and Visser 2005).Therefore, studying the relationships between incubation, nest structure, and ambient temperatures is critical for understanding avian reproduction and processes such as the colonization of new areas and local extinction.

I investigated the nest insulation effect based on the nest temperature using two different types of nests: enclosed and open-cup nests. The initial question addressed was whether the enclosed structure had an insulation effect on the nest temperature. We studied the ambient temperature effect on the nest and the nest floor temperature in open-cup and enclosed nests. We aimed to determine the stage and the nest structure where the temperature variation was not correlated with ambient temperature oscillations. We compared temperatures by monitoring them outside and inside the nest.

## MATERIAL AND METHODS

### Study species and area

Temperature measurements were made during the 2008 breeding season in the nests of Spanish sparrows *Passer hispaniolensis* (enclosed nests) and Iberian azure-winged magpies *Cyanopica cooki* (open-cup nests) in the Castro Verde region of Southern Portugal during spring in olive groves. Temperatures were mild during daytime (16.3 to 35.6°C) and night-time (10.7 to 20.5°C). The Spanish sparrow is a passerine of approximately 30 g (Marques et al. 2004) that builds semi-spherical nests with a small entrance hole (± 20 cm), some of which have an access tunnel. Nests are composed of two layers (Marques et al. 2002), i.e. an exterior layer made from straw and an interior lining made of soft plant parts of about 20 cm. Iberian azure-winged magpies (approximately 70 g) build a cup-shaped nest (15±18 cm in external diameter) with two layers, of which the exterior is composed of small sticks and mud that holds the sticks together, and the inner layer composed of moss, lichen, and wool (personal observation) (Canário and Vicente 2000).

### Temperature monitoring

Enclosed nests. Empty nests were monitored during the night by measuring the ambient temperature (AT) and that inside the nest (INSIDE) (n = 3; three nests). Occupied nests were monitored the same way (n = 6; five nests). Occupied nests were also monitored during the night by measuring the INSIDE and the nest floor temperature (NFT) (n = 5; five nests).

Open-cup nests. Occupied nests were monitored by measuring the AT and the NFT during the night (n = 5; five nests) as well as during daytime (n = 6; four nests). Occupied nests were also monitored during the day by measuring the AT and the egg temperature (n = 4; two nests).

Night measurements started at approximately at 18:00 h and lasted for about 10 hrs, from dusk until dawn. Day measurements started from 10:00 h and lasted >10 hrs. The egg temperature was measured for between 1.8 and 2.9 hrs, avoiding the daily temperature peak period (between 13:30 and 15:00 h).

### Temperature measurement

The temperature was monitored using surface sensors (1.5 mm in size, Vernier software and technology, STS-BTA, Beaverton, OR) with an accuracy of ±0.2°C at 0°C (± 0.5°C at 100°C) and a response time in still air (time for 90% change in the reading) of 50 s. The sensors were connected to a Vernier Labpro device (Beaverton, OR). Temperature information was collected every 10 s. According to the specific setup, sensors were placed in different nest parts, i.e. on the nest floor (nest floor temperature), inside the nest (enclosed nests), outside at the nest edge (open-cup nests), outside the nest

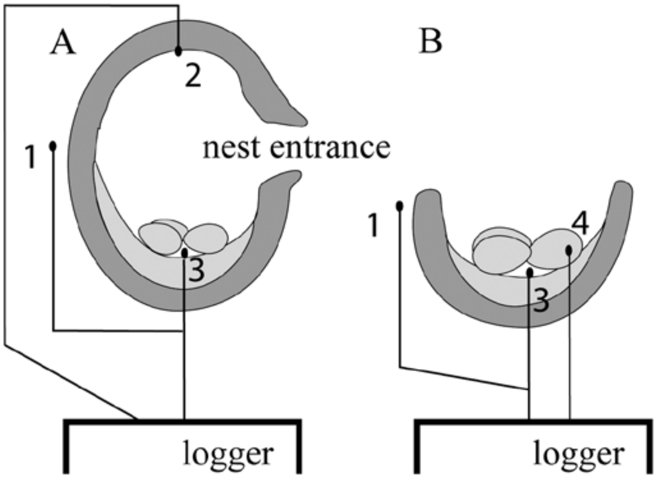


Fig. 1. Location of the temperature sensors in the different setups in enclosed (A) and open-cup nests (B). Sensors were placed outside the nest (1), inside de nest (2), on the nest floor (3), or on an egg (4)

(enclosed nests), or on an egg (Fig. 1). Surface temperature sensors were taped to eggs using cotton-tape bandage. Temperature sensors were placed on the floor and inside nests using a probe to minimize nest damage.

We used ANOVA to compare the temperature variation, correlation coefficients, and comparison of means against zero to test the mean correlation. Results were analysed conservatively due to repeated use of some nests. The results are expressed as mean ± SD.

The work conforms to the legal requirements of Portugal, including those relating to conservation and welfare (ICNB, Departamento de conservação e gestão da biodiversidade license nº 117/2008 for ringing adults and nestlings at the nest).

## RESULTS

### Enclosed nests

#### Empty nests during the night

During the night, the temperature inside the nest was higher than outside (17.3 ± 0.2°C and 16.4 ± 0.1°C, respectively; ANOVA: F = 67.04, df = 5, $p$ = 0.002). The two temperatures were highly correlated (average R= 0.89 ± 0.02; test of means vs zero: t = 89, $p$ = 0.001, df = 3). The difference reduced the impact of the ambient temperature in the nest by approximately 1°C (Fig. 2). The difference between the nest and the environmental temperature changed according to the rate of environmental temperature change during the night, and higher rates of temperature change corresponded to lower temperature differences between the nest interior and the environment (Fig. 3a).

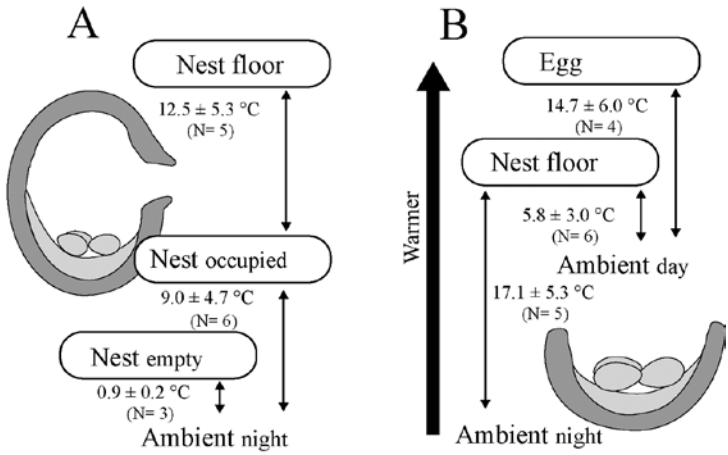


Fig. 2. Difference in temperature measured under the different temperature monitoring setups in enclosed (A) and open-cup nests (B)

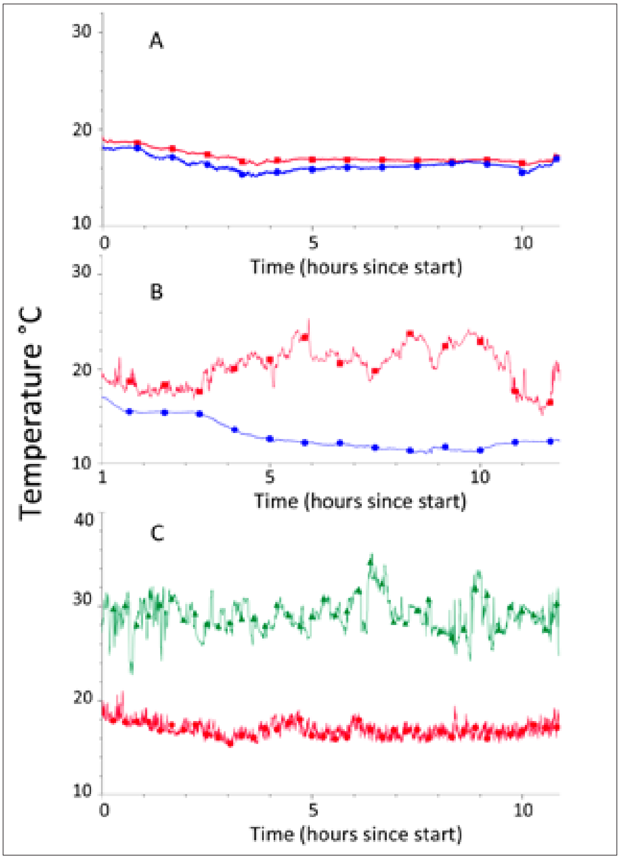


Fig. 3. Examples of temperature variation in enclosed nests under different temperature monitoring setups. A – Empty nest during the night with inside nest temperature (red squares and line) and ambient temperature (blue dots and line). B – As A but occupied nest. C – Occupied nest during the night with inside nest temperature (red dots and line) and nest floor temperature (green triangles and line)

### Occupied nests during the night

The temperature of nests occupied by adults was higher than the ambient temperature (23.0 ± 5.6°C and 14.1 ± 1.2°C, respectively; ANOVA: F = 14.47, df = 11, $p$ = 0.003) and it was maintained at an average of ±9 °C as the mean difference in temperature (Fig. 2). The temperature pattern resulted in the absence of a correlation between the nest and ambient temperature, and the trend variation did not differ from zero (average correlation R = 0.03 ± 0.33; test of means against zero: t = 0.25, $p$ = 0.815, df = 5). The nest temperature oscillated during the sampling period (Fig. 3b).

### Night-time nest floor temperature and nest temperature

The temperature of the nest floor was higher than that inside the nest (30.6 ± 4.0°C and 16.8 ± 2.7°C; ANOVA: F = 14.47, df = 11, $p$ = 0.003). The average difference was 12°C (Fig. 2). No relationship was found between the variation in temperature inside the nest and the nest floor temperature during the night (average correlation R = 0.07 ± 0.18; test of means vs zero: t = 0.92, $p$ = 0.41, df = 4). The nest floor temperature showed large variation, although it was always above the ambient temperature (Fig. 3c).

## Open-cup nests

### Night-time ambient temperature and nest floor temperature

The night-time ambient temperature was much lower than the nest floor temperature (ANOVA: F = 76.15, df = 9, $p$ = 0.001; 14.1 ± 2.2°C and 31.2 ± 3.8°C, respectively). The average temperature difference was 17 °C (Fig. 2). The oscillations in the ambient temperature reflected the nest floor temperature with low correlation coefficients (average correlation R= 0.33 ± 0.23; test of means vs zero: t = 3.14, $p$ = 0.03, df = 4). Nest floor temperatures had some oscillations (Fig. 4a).

### Day-time ambient temperature and the nest floor temperature

Throughout the day, the average ambient temperature was significantly lower than the temperature of the nest floor (ANOVA: F = 7.38, df = 11, $p$ = 0.021; 29.3 ± 3.7°C and 35.1 ± 3.6°C, respectively). The temperature difference was ± 5°C, and the oscillations in the ambient temperature reflected the nest floor temperature (average correlation R= 0.57 ± 0.23; test of means vs zero: t = 6.13, $p$ = 0.001, df = 5). During the day, the nest floor temperature had some oscillations (Fig. 4b).

### Day-time ambient temperature and egg temperature

The average egg temperature was 34.1 ± 3.0°C, ranging from 30.4°C to 36.9°C, and was significantly higher than the ambient temperature of 19.4 ± 3.6°C (ANOVA: F = 39.06, df = 7, $p$ = 0.001). The temperature difference was about 15°C. The ambient temperature oscillations did not affect the egg temperature (average correlation R = 0.09 ± 0.39; test

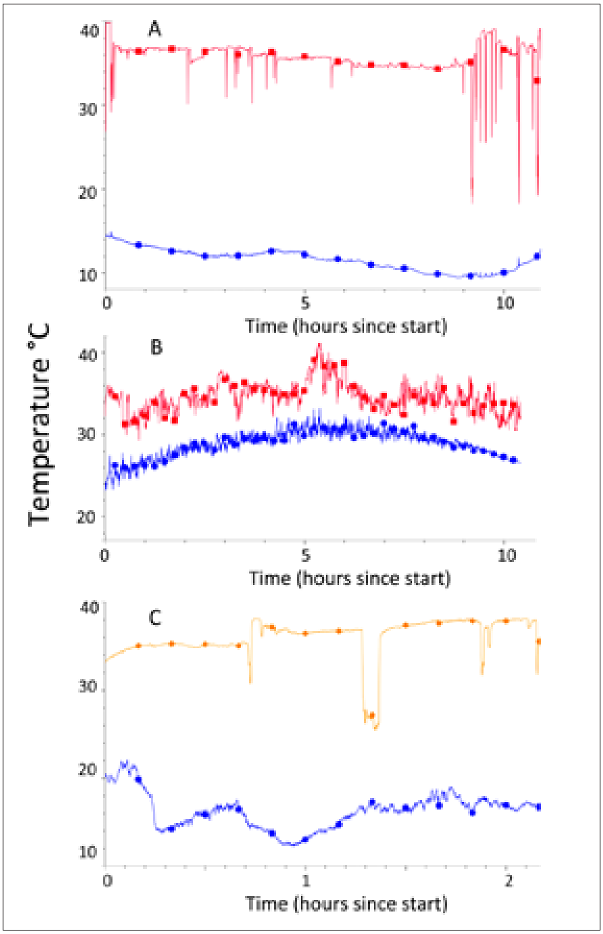


Fig. 4. Examples of temperature variation in open-cup nests under different temperature monitoring setups. A – Occupied nest during the night with nest floor temperature (red squares and line) and ambient temperature (blue dots and line). B – As A but during the day. C – Occupied nest during the day with ambient temperature and egg temperature (orange diamonds and line)

of means vs zero: t = 0.471, $p = 0.67$, df = 3). Egg temperature had occasional variations that fall below the PZT (Fig. 4c).

## DISCUSSION

### Enclosed nests

We found that the empty enclosed Spanish sparrow nests had a buffering effect. During the night, the average nest temperature was 1°C above the ambient temperature, mainly due to a reduction of the wind cooling effect. The wind cooling effect is expected to affect the choice of the nesting place and the structure of the nest (Tulp et al. 2012) 2012. Our results were obtained in mild ambient temperatures that were below the PZT (between 14 and 20°C). This small difference may be of critical importance during colder periods when the survival of the clutch and the adult might be at stake (Haftorn 1988, Tulp et al. 2012)2012, such as during cold nights. Adults must maintain the eggs above the Lower Lethal Temperature (LLT) and simultaneously maintain their own temperature. The buffering effect was positive overall, as observed in other species (Szentirmai et al. 2005), and it should contribute to a reduction in incubation costs (Petteri et al. 2002, Cresswell et al. 2004). However, this effect was reduced at dawn when ambient temperature began to increase, which is less critical because it leads to a more favourable thermal situation (Drent 1975) and is closer to a situation of less thermal stress.

As expected, the presence of an adult during the night in enclosed nests increased the nest temperature, adding to the buffering effect of the nest. The temperature inside the occupied nest was significantly higher than that outside, with an average difference of almost 9° C. Surprisingly this variation was not related to the variation in the ambient temperature. This contrasts with previous results for unoccupied nests and suggests that the presence of an adult in enclosed nests is sufficient to smooth the nest chamber temperature and compensate for the effect of ambient temperature oscillations. This is especially important in the Spanish sparrow because the male will stay in or around the nest in the absence of the foraging female, but it cannot incubate properly because of the lack of a brood patch (Marques 2004). Thus it takes advantage of the insulation effect to prevent the egg temperature dropping below critical values. This difference constitutes a positive insulation effect of the nest structure, which retains part of the heat released by the adult, thereby contributing to a smoothing of the impact of the ambient temperature on nest temperature. A similar effect was observed in Cactus wrens (Ricklefs and Hainsworth 1969). This effect may contribute to a reduction in the costs of incubation (Petteri et al. 2002; Magrath et al. 2005). Interestingly, this effect also had a positive impact on the adult, reducing the exposure to the effect of wind cooling, which may have negative consequences (Pinowski et al. 2006; D'Alba et al. 2009; Tulp et al. 2012).

As expected, the temperature of the nest floor in occupied enclosed nests was significantly higher than the nest temperature (approximately 12°C). The nest floor temperature corresponds to the temperature when eggs or parts of them are not in direct contact with the brooding patch of adults, and it reflects the incubation effort of the female measured on the nest floor. Interestingly, the average value of 30°C was well above the PZT but below the LLOD (Haftorn 1988, Conway and Martin 2000). This situation may promote slower development without putting the embryo at thermal stress or survival risk (Drent 1975).

## Open-cup nests

A different picture emerged from our study of open-cup nests. As in the enclosed nests, the nest floor temperature was significantly higher during night compared with the ambient temperature (approximately 17°C). However, we found only a weak correlation between the floor temperature and the ambient temperature. During the daytime, there was a smaller but significant difference between the nest floor temperature and ambient temperature (plus *circa* 5°C), with also correlating variation. The night-time and daytime correlations with ambient temperature suggest that adults incubating in open-cup nests cannot completely compensate for the effects of ambient temperature oscillations at the nest floor level. The nest floor temperature was similar during the day and night (above 30°C) and very close to the lower limit of the optimal incubation temperature but within the hatchability temperature range (French 1997, Conway and Martin 2000). The egg temperature in the open-cup nests was surprisingly low (approximately 34°C) and below the optimal incubation temperature (French 1997), while at times it dropped below 26°C. This situation is more suited to species with a slow rather than a fast embryonic development (Haftorn 1988, Martin et al. 2007). However, a larger dataset is needed to classify the development of Iberian azure-winged magpies embryos. Not surprisingly, the egg temperature was not related to the oscillations in the ambient temperature. This is an interesting result because the adults compensate the effect of ambient temperature oscillations only at the egg level, and hatchability would be affected if eggs were subjected to these oscillations (French 1997). This fact limits the female's possibility of leaving the nest during incubation without undermining the breeding success.

In the context of temperature regulation, our results highlight two advantages of enclosed nests compared with open-cup nests, i.e. a buffering effect against the ambient temperature and the retention of heat produced by adults when inside the nest (an insulation effect). Overall, this shows that open-cup nests are more susceptive to ambient temperature oscillations and that the resulting effect is only compensated for at the egg level, whereas we found no correlation in enclosed nests. Therefore, the absence of an incubating parent would more rapidly endanger hatchability in open-cup nests than enclosed nests. The life histories of our investigated species correspond to these results. In both species, only the female incubates, although it is fed by the male (or helpers) (de la Cruz et al. 2003) in the case of the Iberian azure-winged magpie (open-cup nest) whereas females can leave the nest to forage in the Spanish sparrow (enclosed nest) (Marques 2004). Overall, the different types of nests have advantages and disadvantages in specific ecological situations, and the nest type depends on balancing of multiple factors (Collias 1997).

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## REFERENCES


Ardia D.R., Pérez J.H., Chad E.K., Voss M.A., Clotfelter E.D. 2009 – Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behaviour – J. Animal Ecol., 78: 4-13.

Both C., Visser M.E. 2005 – The effect of climate change on the correlation between avian life-history traits – G. Change Biol., 11: 1606-1613.

Bryan S.M., Bryant D.M. 1999 – Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major* – PRSB, 266: 157-162.

Canário F., Vicente L.M. 2000 – Nest placement, structure, composition and size in the Azure-winged Magpie – Arq. Museu Bocage (NS), 3: 377-388.

Collias N.E. 1997 – On the origin and evolution of nest building by passerine birds – Condor, 99: 253-270.

Conway C.J., Martin T.E. 2000 – Effects of ambient temperature on avian incubation behaviour – Behav. Ecol., 11: 178-188.

Cooper C.B., Hochachka W.M., Butcher G., Dhondt A.A. 2005 – Seasonal and Latitudinal Trends in Clutch Size: Thermal Constraints during Laying and Incubation – Ecology, 86: 2018-2031.

Cresswell W., Holt S., Reid J.M., Whitfield D.P., Mellanby R.J., Norton D., Waldron S. 2004 – The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper – Behav. Ecol., 15: 498-507.

D'alba L., Monaghan P., Nager R.G. 2009 – Thermal benefits of nest shelter for incubating female eiders – J. Thermal Biol., 34: 93-99.

De La Cruz C., Solís E., Valencia J., Chastel O., Sorci G. 2003 – Testosterone and helping behavior in the azure-winged magpie ( *Cyanopica cyanus*): natural covariation and an experimental test – Behav. Ecol. Sociobiol., 55: 103-111.

Drent R. 1975 – Incubation – In: Farner, D.S. & King, J.R. (Ed.) – Avian Biology. pp. 333-420, Academic Press. New York.

Durant S.E., Hopkins W.A., Hawley D.M., Hepp G.R. 2012a – Incubation temperature affects multiple measures of immunocompetence in young wood ducks (*Aix sponsa*) – Biol. Letters, 8: 108-111.

Durant S.E., Hopkins W.A., Wilson A.F., Hepp G.R. 2012b – Incubation temperature affects the metabolic cost of thermoregulation in a young precocial bird – Functional Ecol, 26: 416-422.

French N. 1997 – Modelling incubation temperature: the effects of incubator design, embryonic development, and egg size – Poultry Sci., 76: 124-133.

Haftorn S. 1988 – Incubating female Passerines do not let the egg temperature fall below the 'Physiological Zero Temperature' during their absences from the nest – Ornis Scand., 19: 97-110.

IPCC 2001 – Climate change 2001: the scientific basis. Contribution of working group I to the third assessment report of the Intergovernmental Panel on Climate Change – Cambridge University Pres. Cambridge.

Magrath M.J.L., Overveld T.V., Komdeur J. 2005 – Contrasting effects of reduced incubation cost on clutch attendance by male and female European starlings – Behaviour, 142: 1479-1493.

Marques P.A.M., Marques A.F., Vicente L.M. 2004 – Measurements and weights of Spanish sparrows *Passer hispaniolensis* during the breeding season in southern Portugal – Airo, 14: 121-125.

Marques P.A.M. 2004 – Parental care during incubation in Spanish sparrows *Passer hispaniolensis*: sex roles and effect of male mate desertion – Bird Study, 51: 185-188.

Marques P.A.M., Vicente L.M., Márquez R. 2002 – Nest placement in the Spanish sparrow *Passer hispaniolensis* – Int. Stud. Sparrows, 29: 21-31.

Martin T.E. 2008 – Egg size variation among tropical and temperate songbirds: An embryonic temperature hypothesis – PNAS, 105: 9268-9271.

Martin T.E., Auer S.K., Bassar R.D., Niklison A.M., Lloyd P. 2007 – Geographic variation in avian incubation periods and parental influences on embryonic temperature – Evolution, 61: 2558-2569.

Nord A., Nilsson J.-Å. 2011 – Incubation temperature affects growth and energy metabolism in blue tit nestlings – Am. Nat., 178: 639-651.

Petteri I., Terho T., Dennis H. 2002 – Are incubation costs in female pied flycatchers expressed in humoral immune responsiveness or breeding success? – Oecologia, 130: 199-205.

Pinowski J., Haman A., Jerzak L., Pinowska B., Barkowska M., Grodzki A., Haman, K. 2006 – The thermal properties of some nests of the Eurasian Tree Sparrow *Passer montanus* – J. Thermal Biol., 31: 573-581.

Ricklefs R.E., Hainsworth F. R. 1969 – Temperature regulation in nestling cactus wrens: the nest environment – Condor, 71: 32-37.

Szentirmai I., Szekely T., Liker, T.A. 2005 – The influence of nest size on heat loss of penduline tit eggs – Act Zool. Acad. Scientiarum Hungaricae, 51: 59-66.

Tulp I., Schekkerman H., Leeuw J.D. 2012 – Eggs in the freezer: Energetic consequences of nest site and nest design in arctic breeding shorebirds – PLoS ONE, 7: e38041.

Visser M.M.E., Lessells C.M. 2001 – The costs of egg production and incubation in great tits (*Parus major*) – PRSB 268: 1271-1277.

Webb D.R. 1987 – Thermal tolerance of avian embryos: a review – Condor, 89: 874-898.