How does the bird-nest incubation unit work?

D. Charles Deeming

School of Life Sciences, University of Lincoln, Joseph Banks Laboratories, Lincoln, LN6 7DL, UK

Corresponding author email: cdeeming@lincoln.ac.uk

Abstract

The bird-nest incubation unit was proposed as a means of explaining the functionality of incubation in most avian species where the egg is in direct contact with the incubator. Subsequent work resulted in revision of this idea to suggest that large birds act as incubators and the nest is a location for incubation; by contrast, in small species the interaction between the bird and its nest played a key role in ensuring efficiency of incubation. This paper briefly reviews what we know about the incubation environment within nests and considers how small birds can contact-incubate eggs whilst ensuring appropriate levels of respiratory gas exchange. A hypothesis is proposed that the incubating bird does not 'sit tight' on its nest to maintain egg temperature at a minimal energy expenditure but, rather, it allows warmed air to escape from the nest cup. This convection flow draws air into the cup from the nest walls, providing oxygen for developing eggs and diluting carbon dioxide that they produce. Evidence supporting this idea of an 'open' nest during incubation is presented. Further experimentation is required to understand the environment within the nest cup better and this paper presents a hypothesis that can be tested in future studies. Investigations of how nests interact with their immediate environment should no longer be biased towards the effects of temperature on nest dimensions or composition. Instead, they should address all of the environmental factors that could affect the composition and function of a bird nest.

Keywords: Bird nest, convection, humidity, insulatory value, respiratory gas exchange

1. INTRODUCTION

Incubation of avian and reptilian eggs can be described in relatively simple terms (Ar and Sidis, 2002): (1) eggs need to be kept at the appropriate temperature for embryonic development (Deeming and Ferguson, 1991; Turner, 2002; Birchard, 2004); (2) the humidity in the nest chamber should ensure that there is an appropriate loss of water vapour from the eggs during incubation (Ar and Deeming, 2009; Belinsky *et al*., 2004); (3) there should be adequate provision of oxygen and removal of sufficient carbon dioxide for normal embryonic development (Ar *et al*., 2004; Ar and Deeming, 2009); and (4) if required, eggs should be turned (Deeming, 2002a, 2009). Although various taxa of reptiles and birds differ in crucial characteristics of the nest microclimate, these four basic conditions underpin the process of incubation mediating embryonic development to completion (*i.e.* hatching).

In reptiles egg temperature simply reflects the prevailing nest temperature, which in turn, depending on species, can reflect the degree of insolation of the soil, presence of microbial degradation of vegetation, or geothermal heat sources (Ackerman and Lott, 2004). By contrast, adult birds use contact-incubation to warm eggs with metabolic heat raising the temperature above ambient to levels required for embryonic development (Turner, 2002). In light of this, I proposed the concept of the 'bird-nest incubation unit' (Deeming, 2002b), suggesting that effective incubation of eggs cannot be achieved by the bird outside of its nest, although under

normal circumstances this is very difficult to test. Moreover, unlike in reptiles (and Megapode birds; Booth and Jones, 2002) where ambient temperatures are sufficient to allow normal embryonic development, in birds the nest structure alone cannot generate heat that is sufficient for normal embryonic development. In effect, maintenance of the egg temperature requires both the bird to provide metabolic heat input and the nest to ensure that there are not excessive rates of heat loss.

The 'bird-nest incubation unit' concept was modified following investigations of the allometric relationships between avian body mass and nest dimensions (Deeming, 2013). As birds increased in body mass their nests became larger but shallower. Moreover, egg size increases in absolute terms with larger birds but decreases in relative terms (Bennett and Owens, 2002; Deeming, 2007). For example, a species, such as the Mute Swan (*Cygnus olor*), which weighs 7.8 kg, lays a clutch of 7 eggs each weighing 345 g so that its total clutch mass is only 31% of the female's body mass. Its nest is 150 cm wide but with a nest cup that is only 10 cm deep (Cramp, 1977). By contrast, a 10.8 g Blue Tit (*Cyanistes caeruleus*) lays a clutch of 10 eggs weighing a total of 14.4 g (133% of body mass) in a nest that is 3.6 cm deep (Cramp, 1988; C.R. du Feu, unpublished observations). Hence, I reasoned that the Mute Swan can be considered as the 'incubator' because it encloses its eggs within its feathers and the nest is primarily where contact-incubation takes place, although where the nest is located may be important in the process of incubation, for instance in the provision of ambient humidity. The Blue Tit, by contrast, needs the nest surrounding the clutch to ensure that there is maintenance of nest temperature – the bird and the nest form the 'incubator'. In light of these observations, I refined the concept of 'bird-nest incubation unit' to apply only to smaller species and considered larger species to be 'birds as incubators' (Deeming, 2013). Whether there is a specific adult mass at which one system changes to another is unknown but it is likely that, given the diversity in nest structure and location (Hansell, 2000), there will be a range of different strategies to ensure successful contact-incubation.

Ar and Sidis (2002) considered how the nest walls affected the microclimate within the nest in terms of energy budgets – in some species at least nest walls appear simply to offer shelter from wind (Ar and Sidis, 2002); for instance, the Common Eider (*Somateria mollissima*) nesting in the Arctic (D'Alba *et al.*, 2009). Ar and Sidis (2002) provided a simple model for required nest insulation based on maintenance of parental body temperature but this has not been further investigated.

Here, I consider the implications of my revised proposal for the role of the nest within the incubation process with particular reference to smaller species, typically passerines. Previous research into the nest microclimate has focussed on two key maintenance elements, namely that of temperature and humidity. The species studied to date have been limited in number and biased towards some taxa, such as waterfowl and seabirds (reviewed by Rahn and Paganelli, 1990; Ar and Sidis, 2002). The recent interest in research focussing on nest construction and function (see reviews by Healey *et al.*, 2015; Deeming & Mainwaring, 2015) has meant that functional properties of nests need to be more carefully considered. Here, I consider: (1) the concept of nest insulation; (2) what we know about the microclimate of the nest cup; and (3), most crucially, what we know about the microclimate of nests of small bird species. I go on to propose a hypothesis that the bird-nest incubation unit is actually functioning as a true 'incubator' in that it not only controls egg temperature but also acts to provide an appropriate gaseous environment to regulate humidity and respiratory gases.

2. THE NEST MICROCLIMATE

Avian incubation has been studied for millennia, primarily so we could replicate the process and artificially incubate eggs of domesticated birds (Sykes, 1991). Over the past 150 years, modern biology has studied the development of avian embryos, typically using the chick as a model, and various environmental factors (*e.g.* temperature or humidity), have been manipulated to determine the impact of such changes on the typical pattern of embryonic development (see for example Romanoff, 1960, 1967). Much of this research was carried out under artificial conditions so our understanding of the natural incubation environment was rather limited. During the 1970s and 1980s the research focus of some zoologists switched to studies of the factors affecting embryonic development in relation to nest structure. In particular, Hermann Rahn, Charles Paganelli and Amos Ar led the way in documenting the ecophysiology of avian embryos during natural incubation. Development of the idea of water vapour conductance of eggshells as a perspective to understand the humidity microclimate, and the metabolism of embryos, within a nest was insightful. This allowed Rahn and his colleagues to develop ideas about the water balance and respiration of avian embryos in a range of avian species, although the emphasis was often on relatively large waterbirds (see reviews by Rahn and Paganelli, 1990; Ar and Sidis, 2002; Deeming, 2002c).

The thermal environment of the nest has been studied in a variety of ways (reviewed by Smith *et al.*, 2015). Thermistors embedded in dummy eggs placed within a clutch during incubation have provided details of the temperatures maintained in nests and how they fluctuate in species ranging from the Ostrich (*Struthio camelus*; Swart and Rahn, 1988) to small passerines (Weathers and Sullivan, 1989). Embryonic development in birds is only possible within a relatively narrow range of temperatures, which is often higher than ambient (Webb, 1987; Deeming and Ferguson, 1991). Heat is provided by direct contact between the eggs and the brood patch (Lea and Klandorf, 2002) and the temperature that can be maintained by different species depends in part on the body mass of the incubating bird (Deeming, 2008). Whilst maintenance of temperature in artificial incubators heated by convection is relatively well understood (Owen, 1991; Meijerhof, 2009), the thermal characteristics of naturally incubated eggs have been described as changes in temperature recorded by dummy eggs (*e.g.* Weathers and Sullivan, 1989). Only Turner (1991, 2002) has considered the effects of contact-incubation on egg temperature in any detail. That heat is provided by incubating adults means that the energetics of incubation have long been considered from a sitting adult's perspective (reviews by Tinbergen and Williams, 2002; Nord and Williams, 2015), but how the nest contributes to the thermal conditions remains far from clear.

We have a relatively good understanding of the control of humidity in a nest. Incubating birds do not actively regulate nest humidity but, instead, they raise the nest humidity above that of ambient by trapping water vapour in the air around the eggs. This can be achieved by using feathers to surround the eggs, as is the case in scrape-nesting species that lack a nest, or by use of nest walls that isolate the cup microclimate from the ambient conditions (Deeming, 2011). Fluctuations in humidity of the nest air simply reflect that of the humidity in the ambient air surrounding the nest (see Rahn, 1991). In cup nests the wall prevents loss of water vapour, especially in dry, cold environments where thermal insulation of the nest wall is presumably high (Figure 1). Elevated humidity in the nest cup has acted to select for an increase in water vapour conductance of the eggshells to ensure an appropriate level of weight (water) loss from the egg during incubation (Figure 2; Deeming, 2011).

The number of species in which nest humidity has been recorded in less than 50, with a predominance of larger species of waterfowl and seabirds. Those species in which we know about other gases in the nest

environment (*e.g.* oxygen and carbon dioxide) is less than 10 (Walsberg, 1980; Rahn, 1991). Data for the gaseous environment of even the Domestic Fowl (*Gallus gallus*) are almost a century old (see Rahn, 1991). This reflects the technical difficulties in measuring these gases accurately in a natural environment but the result is a poor understanding of how nesting birds regulate such respiratory gases.

Nesting in a burrow, or other enclosed cavity, lends itself to studies of the gaseous environment. While nesting in a cavity can have advantages, such as minimising exposure of nest contents to predators, it poses difficulties in maintaining an appropriate nest humidity, and oxygen and carbon dioxide concentrations if the nest walls are impermeable to gases. Data collected from the five species studied to date confirm that oxygen concentration is reduced and that of carbon dioxide is increased relative to ambient, with changes being moderate (1-2%) towards the end of incubation (Birchard *et al.*, 1984; Lill and Fell, 2007; Mersten-Katz *et al.*, 2013). The movement of the bird in and out of the nest chamber appears fundamental in ensuring that there is frequent exchange of gases within the nest (Mersten-Katz *et al.*, 2013). A failure to introduce fresh air could lead to hypoxia, which may have important adverse effects on the survival of the incubating adults (Mersten-Katz *et al.*, 2013) and their embryos (Tullett and Deeming, 1982).

3. THE NEST AS A FUNCTIONAL UNIT

The nest has long been considered as a receptacle for eggs during incubation and, in many cases, for nestlings until fledging (Hansell, 2000). Various roles have been postulated for nests – defence, sexual signalling, signals of parental fitness, *etc.*, and often are considered to reflect conflicting demands of the adults (Moreno, 2012; Mainwaring *et al.*, 2014a, 2015). In some instances, factors affecting nest characteristics appear to be opposed. For instance, bigger nests can be associated with higher reproductive success because of thermoregulatory benefits but these are counterbalanced by costs incurred from greater conspicuousness to predators (Møller, 1990). However, recently developed ideas have changed perspectives from the nest simply containing eggs or nestlings, to one of it taking a more active role in incubation.

Britt and Deeming (2011) suggested that the nest may be built by the incubating birds to minimise the energy expenditure of the incubating adult rather than impacting directly on regulation of temperature of the eggs or nestlings. Plasticity in nest construction behaviour is increasingly seen as being typical in birds because nest composition is variable between individuals and locations (Walsh *et al.*, 2010, 2011; reviewed by Deeming and Mainwaring, 2015). Ambient temperature has been shown to affect nest construction behaviour in a variety of passerines (Crossman *et al.*, 2011; Britt and Deeming, 2011; Deeming *et al.*, 2012; Mainwaring *et al.*, 2012, 2014b). Nest construction is important because the insulatory properties of the nest wall (a measure of insulation offered by a structure – see Deeming and Gray, 2016a) inversely correlate with reproductive success of Blue Tits (Deeming and Pike, 2015). In addition, removal of air trapped within the nest walls by vacuum-packing reduced the insulatory value of the nests by 20% in a variety of small species (Deeming and Biddle, 2015). Heat loss from nests in a moving airstream is significantly increased above that of a nest in still air (Heenan and Seymour, 2012).

The emphasis on nest construction being primarily associated with its insulatory properties can be re-considered in light of recent studies. Although Heenan and Seymour (2011) suggested that structural considerations were more important than insulation in passerine nests, their arguments have been challenged (Deeming and Mainwaring, 2015). Although insulatory values, measured as a difference in cooling rates

(°C·20s^{-1}; McGowan *et al.*, 2004), were shown in Blue Tits and Common Blackbirds (*Turdus merula*) to be related to environmental temperature (Mainwaring *et al.*, 2012, 2014b; Deeming *et al.*, 2012), there are other reports which fail to demonstrate any clear relationship between insulatory values of nest walls and environmental temperature (Biddle *et al.*, 2016; Taberner Cerezo and Deeming, 2016), although this may reflect limited sampling. Whilst nest attentiveness during incubation negatively correlates with insulatory values of nests (Deeming and Gray, 2016b), perhaps it is premature to assume that the nest wall solely insulates against drops in temperature.

The role of the nest wall in regulating the nest's gaseous environment has not been well studied. Rahn *et al.* (1983) studied the microclimate of Common Eider nests and suggested that nest wall insulation not only retained heat but also humidity. Deeming (2011) showed that nest humidity is retained within the nest cup by the presence of nests walls in many species and that this effect is not observed in scrape nests (Figure 1). In dry, cold environments there is a particular isolating effect of the nest wall probably caused by thermal insulation, leading to elevated nest humidity relative to the ambient conditions. This appears to have resulted in co-evolution between mass-specific nest water vapour conductance and ambient humidity (Figure 2). In walled nests this is an inverse relationship whereas in scrape nests it is positive, suggesting that as humidity increases in the nest environment the eggs need a higher water vapour conductance (Figure 2; Deeming, 2011). This pattern is typical for avian eggs where wetter environments are associated with higher water vapour conductance values, and *vice versa* (Rahn and Paganelli, 1990). Perhaps such patterns reflect how the nest wall has evolved to regulate the nest cup environment more generally rather than simply acting to insulate the incubating adult, eggs and/or chicks.

4. THE BIRD-NEST INCUBATION UNIT

During evolution avian reproduction must have been subjected to a range of selection drivers, such as adult body size, nest location, predation pressure, clutch size and brood size (Lack, 1968), and perhaps such factors have acted upon nest architecture. In light of this the approach of considering nest wall composition and structure as being the sole contributors to a nest's thermal properties is not instructive. Despite the other possible roles of a nest, a physical location for contact-incubation of eggs is fundamental. This involves maintenance and regulation of not only temperature but also humidity and respiratory gases. Recent research on nest composition, insulation, the functional role of air gaps in the nest wall, all in relation to the wider environment, has encouraged me to re-consider the functional properties of bird nests. As a result, here, I consider two scenarios that reflect the bird-nest incubation unit as a 'closed' structure with the sole aim of minimising the energetic demands of the process. The second approach downplays the thermal aspects of incubation but, rather, considers the role of the nest in providing an appropriate incubation environment – in this scenario the nest is 'open' and can be considered as more dynamic because it is not physically sealed and it is influenced by more factors than simply the incubator's energy budget.

4.1. The nest cup as a 'closed' structure
If the nest structure is primarily constructed to conserve heat then the bird should be acting to minimise its energetic demands during incubation. Under these circumstances, the nest structure should serve only to minimise heat loss and so there should be minimal conductance and convection of heat from the bird and eggs,

and the nest walls should be characterised by good insulation. A consequence of this situation will be that the adult bird should 'seal' off the cup with its body to stop convective heat loss (Figure 3A). This means that, in addition to the eggs, the nest walls and air in the cup will be warmed and nest wall insulation will be crucial in minimising energy loss from the structure as a whole. Insulation should serve to minimise conduction and convection of heat through the wall's structure.

Whilst this arrangement may maintain the appropriate egg temperature at minimal energy expenditure, there is a significant disadvantage. If the cup is sealed off by the bird and the walls are well insulated then the amount of fresh air that can be introduced into the nest cup whilst the bird is present is greatly reduced (Figure 3A). Under such circumstances, oxygen consumption by the clutch of embryos in the cup will lead to a decrease in oxygen concentration and concomitant increases in carbon dioxide and water vapour concentrations released from the respiring egg. Eventually, hypoxic conditions will be produced as a result, particularly in the later stages of incubation. This may be deleterious for the embryos leading to a reduction in growth, a water imbalance, and a prolonged incubation period (see Tullett and Deeming, 1982; Burton and Tullett, 1983, 1985). Of course, this deleterious set of conditions will be relieved by the bird leaving the nest during an incubation recess, allowing aeration of the cup and its contents. However, nest attentiveness varies from ~50% to 100% in passerine species (Deeming, 2002d) so some species are potentially in contact with the eggs for a relatively long time and this may induce hypoxic hypercapnia within the egg immediately beneath the brood patch (Ar and Sidis, 2002). High rates of egg turning (Deeming, 2002a) may counter this by increasing the extent of nest cup aeration but artificially elevated oxygen concentrations do not alleviate the adverse effects of failure to turn eggs (Deeming, 1991). Whilst this may be effective during daylight hours when the bird is active, at night evidence from temperature recordings suggests that the incubating bird sits tight on the eggs throughout (*e.g.* Weathers and Sullivan, 1989) and there is minimal gaseous exchange between the nest cup and the ambient air.

4.2. The nest cup as an 'open' structure

A second possibility is that whilst the bird is incubating, the nest cup is not sealed off and so gaseous exchange can occur more freely (Figure 3B). If the incubating bird does not 'sit tight' on the nest cup and allows heated air to leave the nest cup by convection, escaping air must be replaced. The bird will be blocking ingress of air from above (as well as the upward loss of heated air) and so fresh air will enter the nest from the surrounding nest wall. The movement of air driven by convective heat loss would introduce fresh air into the cup thereby introducing oxygen. Carbon dioxide and water vapour released by the eggs would be lost from the cup as air moves upwards. Under this scenario the functional significance of the nest wall does not simply involve thermal insulation, albeit an important role, but also aeration of nest contents that assists incubation effectiveness.

4.3. Supporting evidence for the nest as an open structure during incubation

The scenario described above offers a new hypothesis that can be tested in future investigations of nest function. The idea is based on synthesis of a variety of observations that offer some support for the bird-nest incubation unit as an 'open' structure. This evidence is outlined below.

The nest walls undoubtedly offer thermal insulation (see above) but the nest cup is not sealed off from heat loss, in some species at least. In Blue Tits and Great Tits (*Parus major*) infrared thermography reveals that the anterior of an incubating bird is much warmer than its posterior (Figure 4; Deeming and Pike, 2015). Such a

nest will be losing heat through convection during incubation but we do not yet appreciate the impact of such heat loss on the energetics of the incubating adult bird.

We know that embryos are sensitive to high temperatures, birds can transfer heat from eggs and their thermoregulation acts to cool eggs. Franks (1967) manipulated the temperature of dummy eggs incubated by African Collared Doves (*Streptopelia risoria*) by infusing them with cold or warm water. It was demonstrated that the birds exhibited thermoregulatory behaviours commonly observed at hot ambient temperatures but only when the eggs (but not ambient temperature) were warmed above body temperature. Moreover, in the Palestine Sunbird (*Nectarinia osea*) incubation attentiveness is dependent on ambient temperature with it steadily declining as the temperature increases to around 35 ℃. At higher temperatures, however, birds sit on eggs to the same extent as they do at very low temperatures, *i.e.* < 5 °C (Ar and Sidis, 2002).

The walls of the nests of some passerines are full of air because of their perforated physical structures and the materials used in their construction. Hence, nests of the Common Bullfinch (*Pyrrhula pyrrhula*) are composed of twigs that are interwoven in an open lattice structure (Biddle *et al.*, 2016). Light can be observed through the loosely woven structures that form the walls of Eurasian Blackcap (*Sylvia atricapillus*) nests (D.C. Deeming, personal observation). In other species with more substantial nest walls vacuum-packing reduced nest volume by 90% (Deeming and Biddle, 2015).

In some species there seems to be active behaviour to maintain the volume of the nest walls. 'Tremble-thrusting', a behaviour where incubating birds repeatedly penetrate nest materials with their bills and rearrange how they are positioned (Haftorn 1994), is considered to be a critical nest maintenance behaviour (Møller, 1984). Tremble-thrusting is observed in various small passerines from temperate and tropical regions (Haftorn, 1982, 1984, 1994; Greeney, 2004; Dobbs *et al.*, 2005; Greeney and Gelis, 2005; Greeney and Sornoza, 2005; Greeney *et al.*, 2006; Underwood and Sealy, 2011), and has even been described in the much larger Sickle-winged Guan (*Chamaetetes goudotii fagani*; Greeney, 2005). When a Great Tit nest was artificially compressed during an incubation recess, the female was observed subsequently to restore the nest's infrastructure by tremble-thrusting (Haftorn and Slagsvold, 1995). Goldcrests (*Regulus regulus*) only exhibit tremble-thrusting after hatching when nestlings are brooded by the adult but not during later stages of the nestling period (Haftorn, 1982).

Activities by incubating birds, such as tremble-thrusting, are thought to introduce more air into nest walls that appears to augment the insulatory properties of the nest (Deeming and Biddle, 2015). Given that humans use trapped air as an effective insulator in, for example, duvets and double glazing, it is surprising that the air in nest walls does not offer greater insulation. Although the species where insulatory values of nests are known are few in number (Deeming and Mainwaring, 2015; Deeming and Gray, 2016b), qualitatively many other bird species build nests that visually seem to offer little thermal insulation. For instance, the 'stick' nests of Columbiformes seem to be mere platforms where incubation takes place (Ferguson-Lees *et al.*, 2012) and it would be good to determine what thermal insulation the nest walls offer in some of the smaller species in this order.

The effect of nest wall insulation on humidity within the cup has already been described above. The lack of data on the respiratory gases within nests means that there is no direct evidence to support the ideas outlined above (Figure 3). However, it is possible to estimate the amounts of oxygen available in nests at peak oxygen consumption by a clutch of eggs by determining the volumes of the nest cup, the clutch and that

occupied by the bird as it sits within the cup and contacts the eggs. Data are limited for species with cup nests where we know both rates of pre-internal pipping oxygen consumption (Vo_2) and nest dimensions but Table 1 provides values for six species of British passerines. In general terms, if the nest cup was sealed off, the smaller the nest (and bird), the less air is available for oxygen exchange by the embryos and the time that available oxygen would last is markedly less than 480 minutes (Table 1). There is a positive relationship between nest cup volume and the time that oxygen will last but this only approaches significance (Spearman's $rho_4 = 0.71$, $P = 0.07$), which perhaps reflects the small sample size. It would seem illogical that birds sitting 'tight' on their nests during the night could be depriving their embryos of oxygen. Whilst it is possible that incubating adults might stand up during the night to aerate the nest contents, data collected from thermistors in dummy eggs in nests generally suggest that this does not happen (or if it does, the effect on recorded egg temperature is imperceptible). The limited amount of oxygen in a nest cup offers indirect support for the idea that nest aeration is a key aspect of nest function. There is a pressing need for more research to gather empirical data for the gaseous environment of nest cups during incubation.

The simple model for the role of nest insulation proposed by Ar and Sidis (2002) was based on the energetic requirements of the adult birds. However, the main role of a bird's nest is to provide the appropriate microclimate for the eggs during incubation (and in many cases for chicks). The incubating adult is absolutely crucial to this process but when considering nest function we should always consider how it impacts on the viability of the embryos being incubated. Failure to hatch eggs has a significant adverse effect on the adults' fitness. From this perspective studies of nest function should focus on the impacts on the eggs (or chicks) rather than the adult.

5. CONCLUSIONS

A nest with an 'open' cup would be a dynamic structure that is an integral part of the incubation process. This situation would resemble that we have attempted to mimic in artificial incubators (Owen, 1991; Meijerhof, 2009). Commercial incubators are boxes with insulated walls in which temperature is thermostatically controlled as the eggs are heated to the appropriate temperature. The volume of 'spare' air is minimal because the eggs occupy much of the space. Fresh air has to be introduced into the cabinet and then circulated between the eggs by fans (a consequence of the large numbers of eggs that can be accommodated). Poor aeration, or air movement, can lead to hypoxic and hypercapnic conditions, which are deleterious to embryonic survival (D.C. Deeming, personal observations). Humidity is monitored via a wet bulb temperature and water vapour is introduced as a spray or as evaporation from water-filled pans to supplement water vapour lost from the eggs.

The hypothesis presented in this paper is the first to attempt to explain nest function in terms of all aspects of incubation. Hence, it offers a novel framework for future investigations of the role of the nest in avian incubation, irrespective of the size, species and type of nest. Future studies of nest function need to address all aspects of the environment (*e.g.* temperature, rainfall and wind), when considering the factors determining how a nest fulfils its role as a place to incubate eggs. Whilst Mainwaring *et al*. (2014b) failed to demonstrate that precipitation correlated with insulatory values of Common Blackbird nests, the amount of water such nests absorb during rain and their rate of drying may be important aspects of nest function and/or location. It is hoped by providing a testable hypothesis that there will be a renewed interest in research into the functional properties of nests and in contact-incubation within a natural environment.

REFERENCES

Ackerman, R.A. and Lott, D.B. (2004). Thermal, hydric and respiratory climate of nests. In: Deeming, D.C. (ed.), *Reptilian incubation: environment, evolution*, and behaviour, pp. 15–43. Nottingham University Press, Nottingham.

Ar, A. and Deeming, D.C. (2009). Water and gas exchange in determining hatchability success. *Avian Biol. Res.*, **2,** 61–66.

Ar, A., Belinsky, A., Dmi'el, R. and Ackerman, R.A. (2004). Energy provision and utilisation. In: Deeming, D.C. (ed.), *Reptilian incubation: environment, evolution*, and behaviour, pp. 143–186. Nottingham University Press, Nottingham.

Ar, A. and Sidis, Y. (2002). Nest microclimate during incubation. In: Deeming, D.C. (ed.), *Avian incubation: behaviour, environment, and evolution*, pp. 143–160. Oxford University Press, Oxford.

Belinsky, A., Ar, A., Dmi'el, R. and Ackerman, R.A. (2004). Water in reptilian eggs and hatchlings. In: Deeming, D.C. (ed.), *Reptilian incubation: environment, evolution*, and behaviour, pp. 125–142. Nottingham University Press, Nottingham.

Bennett, Peter M. and Owens, Ian P. F. (2002). *Evolutionary ecology of birds - life histories, mating systems and extinction*. Oxford University Press, Oxford.

Biddle, L.E., Goodman, A.M. and Deeming, D.C. (2016). Patterns of construction of nests provide insight into nest-building behaviour. *Behav. Proc.,* (in press).

Birchard, G.F. (2004). Effects of incubation temperature. In: Deeming, D.C. (ed.), *Reptilian incubation: environment, evolution*, and behaviour, pp. 103–123. Nottingham University Press, Nottingham.

Birchard, G.F., Kilgore, D.L. Jr and Boggs, D.F. (1984). Respiratory gas concentrations and temperatures within the burrows of three species of burrow-nesting birds. *Wilson Bull.*, **96,** 451–456.

Britt, J. and Deeming, D.C. (2011). First egg date and air temperature affect nest construction in Blue Tits *Cyanistes caeruleus* but not in Great Tits *Parus major. Bird Study*, **58,** 78–89.

Burton, F.G. and Tullett, S.G. (1983). A comparison of the effects of eggshell porosity on the respiration and growth of domestic fowl, duck and turkey embryos. *Comp. Biochem. Physiol.*, **75A,** 167–174.

Burton, F.G. and Tullett, S.G. (1985). The effects of egg weight and shell porosity on the growth and water balance of the chicken embryo. *Comp. Biochem. Physiol.*, **81A,** 377–385.

Cramp, S. (1977). *Handbook of the birds of Europe, the Middle East and North Africa, The birds of the Western Palearctic, Vol. I ostrich to ducks.* Oxford University Press, Oxford.

Cramp, S. (1988) *Handbook of the birds of Europe, the Middle East and North Africa, the birds of the Western Palearctic, Vol. V. tyrant flycatchers to thrushes*. Oxford University Press, Oxford.

Cramp, S. and Perrins, C. M. (1993). *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. Volume VII. flycatchers to shrikes*. Oxford University Press, Oxford.

Cramp, S. and Perrins, C. M. (1994a). *Handbook of the birds of Europe, the Middle East and North Africa, The birds of the Western Palearctic, Vol. VIII. crows to finches*. Oxford University Press, Oxford.

Cramp, S. and Perrins, C. M. (1994b). *Handbook of the birds of Europe, the Middle East and North Africa, The birds of the Western Palearctic, Vol. IX. buntings and new world warblers*. Oxford University Press, Oxford.

Crossman, C.A., Rohwer, V.G. and Martin, P.R. (2011). Variation in the structure of bird nests between northern Manitoba and southeastern Ontario. *PLoS ONE*, 6, e19086.

D'Alba, L., Monaghan, P. and Nager, R.G. (2009). Thermal benefits of nest shelter for incubating female eiders. *J. Therm. Biol.*, **34,** 93–99.

Deeming, D.C. and Ferguson, M.W.J. (1991). Reasons for the dichotomy in egg turning in birds and reptiles. In: Deeming, D.C. and Ferguson, M.W.J. (eds), *Egg incubation: its effects on embryonic development in birds and reptiles*, pp. 307-323. Cambridge University Press, Cambridge.

Deeming, D.C. (2002a). Patterns and significance of egg turning. In: Deeming, D.C. (ed.), *Avian incubation: behaviour, environment, and evolution*, pp. 161–178. Oxford University Press, Oxford.

Deeming, D.C. (2002b). Importance and evolution of incubation in avian reproduction. In: Deeming, D.C. (ed.), *Avian incubation: behaviour, environment, and evolution*, pp. 1–7. Oxford University Press, Oxford.

Deeming, D.C. (2002c). Functional characteristics of eggs. In: Deeming, D.C. (ed.), *Avian incubation: behaviour, environment, and evolution*, pp. 28–42. Oxford University Press, Oxford.

Deeming, D.C. (2002d). Behaviour patterns during incubation. In: Deeming, D.C. (ed.), *Avian incubation: behaviour, environment, and evolution*, pp. 63–87. Oxford University Press, Oxford.

Deeming, D. C. (2007). Effects of phylogeny and hatchling maturity on allometric relationships between female body mass and the mass and composition of bird eggs. *Avian Poult. Biol. Rev.*, **18,** 21-37.

Deeming, D.C. (2008). Avian brood patch temperature: Relationships with female body size, incubation period, developmental maturity and phylogeny. *J. Therm. Biol.*, **33,** 345–354.

Deeming, D.C. (2009). The role of egg turning during incubation. *Avian Biol. Res.*, **2,** 67–71.

Deeming, D.C. (2011). Importance of nest type on the regulation of humidity in bird nests. *Avian Biol. Res*, **4,** 23–31.

Deeming, D.C. (2013). Effects of female body size and phylogeny on avian nest dimensions. *Avian Biol. Res.*, **6,** 1–11.

Deeming, D.C. and Biddle, L. (2015). Thermal properties of bird nests depend on air-gaps between the materials. *Acta Ornithol.*, **50,** 121–125.

Deeming, D.C. and Ferguson, M.W.J. (1991). Physiological effects of incubation temperature on embryonic development in reptiles and birds. In: Deeming, D.C. and Ferguson, M.W.J. (eds), *Egg incubation: its effects on embryonic development in birds and reptiles*, pp. 147-171. Cambridge University Press, Cambridge.

Deeming, D.C. and Gray, L.A. (2016a). Comparison of two methods for determination of insulation of passerine nest walls. *Avian Biol. Res.*, **9,** in press.

Deeming, D.C. and Gray, L.A. (2016b). Incubation attentiveness and nest insulatory values correlate in songbirds. *Avian Biol. Res.*, **9,** in press.

Deeming, D.C. and Mainwaring, M.C. (2015). Functional properties of nests. In: Deeming, D.C. and Reynolds,

S.J. (eds), *Nests, eggs, and incubation: new ideas about avian reproduction*, pp. 29–49. Oxford University Press, Oxford.

Deeming, D.C., Mainwaring, M.C., Hartley, I.R. and Reynolds, S.J. (2012). Local temperature and not latitude determines the design of Blue Tit and Great Tit nests. *Avian Biol. Res.*, **5,** 203–208.

Deeming, D.C. and Pike, T.W. (2015). Nest surface temperature predicts fledging success in Blue Tits *Cyanistes caeruleus* but not in Great Tits *Parus major*. *Acta Ornithol.*, **50,** 247–251.

Dobbs, R.C., Martin, P.R., Batista, C., Montag, H. and Greeney, H.F. (2003). Notes on egg-laying, incubation, and nestling care in the Scaled Antpitta (*Grallaria guatimalensis*). *Cotinga*, **19,** 65–70.

Franks, E.C. (1967). The responses of incubating ringed turtle doves (*Streptopelia* risoria) to manipulated egg temperatures. *Condor*, **69,** 268–279.

Greeney, H.F. (2004). Breeding behavior of the Bicolored Antvireo *(Dysithamnus occidentalis)*. *Ornitol. Neotrop.*, **15,** 349–356.

Greeney, H.F. (2005). Nest, eggs, and incubation rhythms at a nest of the Sickle-winged Guan *(Chamaepetes goudotiifagani)* in western Ecuador. *Bull. Br. Ornithol. Club*, **125,** 113–116.

Greeney, H.F. and Gelis, R.A. (2005). A nest of the Rufous Antpitta *Grallaria rufula* depredated by a Turqoise Jay *Cyanolyca turcosa*. *Cotinga*, **24,** 110–111.

Greeney, H.F., McLean, A., Bucker, A.D.L., Gelis, R.A., Cabera, D. and Somoza, F. (2006). Nesting biology of the long-wattled umbrellabird (*Cephalopterus penduliger*). Part I. Incubation. *Ornitol. Neotrop.*, **17,** 395–401.

Greeney, H. F. and Somoza, F. (2005). The nest and egg of the Slate-crowned Antpitta *(Grallaricula nana),* with observations on incubation behavior in southern Ecuador. *Ornitol. Neotrop.*, **16,** 137–140.

Haftorn, S. (1982). Parental care of nestlings by the Goldcrest *Regulus regulus. Ornis Fenn.*, **59,** 123–134.

Haftorn, S. (1984). The behaviour of an incubating female coal tit *Parus ater* in relation to experimental regulation of nest temperature. *Fauna Norv. Ser. C, Cinclus*, **7,** 12–20.

Haftorn, S. (1994). The act of tremble-thrusting in tit nests, performance and possible function. *Fauna Norv. Ser. C Cinclus*, **17,** 55–74.

Haftorn, S. and Slagsvold, T. (1995). Egg covering in birds: description of the behaviour in tits (*Parus* spp.) and a test of hypotheses of its function. *Fauna Norv. Ser. C Cinclus*, **18,** 85–106.

Hansell, M.H. (2000). *Bird nests and construction behaviour*. Cambridge University Press, Cambridge.

Healy, S.D., Morgan, K.V. and Bailey, I.E. (2015). Nest construction behaviour. In: Deeming, D.C. and Reynolds, S.J. (eds), *Nests, eggs, and incubation: new ideas about avian reproduction*, pp. 16–28. Oxford University Press, Oxford.

Heenan, C.B. and Seymour, R.S. (2011). Structural support, not insulation, is the primary driver for avian cup-shaped nest design. *Proc. R. Soc. B*, **278,** 2924–2929.

Heenan, C.B. and Seymour, R.S. (2012). The effect of wind on the rate of heat loss from avian cup-shaped nests. *PLoS ONE*, **7(2),** e32252.

Hoyt, D.F. (1979). Practical methods of estimating volume and fresh weight of bird eggs. *Auk*, **96,** 73–77.

Lack, D.L. (1968). *Ecological adaptations for breeding in birds*. Methuen, London.

Lea, R.W. and Klandorf, H. (2002). The brood patch. In: Deeming, D.C. (ed.), *Avian incubation: behaviour, environment, and evolution*, pp. 100–118. Oxford University Press, Oxford.

Lill, A. and Fell, P.J. (2007). Microclimate of nesting burrows of the Rainbow Bee-eater. *Emu*, **107,** 108–114.

Mainwaring, M.C., Deeming, D.C., Jones, C.I. and Hartley, I.R. (2014b). Adaptive latitudinal variation in common blackbird *Turdus merula* nest characteristics. *Ecol. Evol.*, **4,** 851–861.

Mainwaring, M.C., Hartley, I.R., Bearhop, S., Brulez, K., du Feu, C.R., Murphy, G., Plummer, K., Webber, S.L., Reynolds, S.J. and Deeming, D.C. (2012). Latitudinal variation in blue and great tit nest characteristics indicates environmental adjustment. *J. Biogeog.*, **39,** 1669–1677.

Mainwaring, M.C., Hartley, I.R., Lambrechts, M.M. and Deeming, D.C. (2014a). The design and function of birds' nests. *Ecol. Evol.*, **4,** 3909–3928.

Mainwaring, M.C., Reynolds, S.J. and Weidinger, K. (2015). The influence of predation on the location and design of nests. In: Deeming, D.C. and Reynolds, S.J. (eds), *Nests, eggs, and incubation: new ideas about avian reproduction*, pp. 50–64. Oxford University Press, Oxford.

McGowan, A., Sharp, S.P. and Hatchwell, B.J. (2004). The structure and function of nests of Long-tailed tits *Aegithalos caudatus. Funct. Ecol.*, **18,** 578–583.

Meijerhof, R. (2009). Principles and practice of incubator design. *Avian Biol. Res.*, **2,** 81-87.

Mersten-Katz, C., Barnea, A., Yom-Tov, Y. and Ar, A. (2013). The woodpecker's cavity microenvironment: Advantageous or restricting? *Avian Biol. Res.*, **5,** 227–237.

Møller, A.P. (1984). On the use of feathers in birds' nests: predictions and tests. *Ornis Scand.*, **15,** 38–42.

Møller, A.P. (1990). Nest predation selects for small nest size in the blackbird. *Oikos*, 57, 237–40.

Moreno, J. (2012). Avian nests and nest-building as signals. *Avian Biol. Res.*, **5,** 238–251.

Nord, A. and Williams, J.B. (2015). The energetic costs of incubation. In: Deeming, D.C. and Reynolds, S.J. (eds), *Nests, eggs, and incubation: new ideas about avian reproduction*, pp. 152–170. Oxford University Press, Oxford.

Owen, J. (1991). Principles and problems of incubator design. In: Tullett, S.G. (ed.), *Avian incubation*, pp. 205–224. Butterworth-Heinemann, London.

Rahn, H. (1991). Why birds lay eggs. In: Deeming, D.C. and Ferguson, M.W.J. (eds.), *Egg incubation: its effects on embryonic development in birds and reptiles*, pp. 345–360. Cambridge University Press, Cambridge

Rahn, H., Krog, J. and Mehlum, F. (1982). Microclimate of the nest and egg water loss of the eider *Somateria mollissima* and other waterfowl in Spitzbergen. *Polar Res.*, **1,** 171–183.

Rahn, H. and Paganelli, C.V. (1990). Gas fluxes in avian eggs: driving forces and the pathway for exchange. *Comp. Biochem. Physiol.*, **95A,** 1–15.

Romanoff, A.L. (1960). *The avian embryo*. Macmillan, New York.

Romanoff, A.L. (1967). *Biochemistry of the avian embryo*. John Wiley and Sons, New York.

Smith, J.A., Cooper, C.B. and Reynolds, S.J. (2015) Advances in techniques to study incubation. In: Deeming, D.C. and Reynolds, S.J. (eds), *Nests, eggs, and incubation: new ideas about avian reproduction*, pp. 179–195. Oxford University Press, Oxford.

Swart, D. and Rahn, H. (1988). Microclimate of ostrich nests: measurements of egg temperature and nest humidity using egg hygrometers. *J. Comp. Physiol.*, **157B,** 845–853.

Sykes, A.H. (1991). An introduction to the history of incubators. In: Tullett, S.G. (ed.), *Avian incubation*, pp. 297–303. Butterworth-Heinemann, London.

Taberner Cerezo, A. and Deeming, D.C. (2016). Nest insulation in the European Robin (*Erithacus rubecula*): effects of latitude and construction materials. *Avian Biol. Res*, **9,** in press.

Tinbergen, J.M. and Williams, J.B. (2002b). Energetics of incubation. In: Deeming, D.C. (ed.), *Avian incubation: behaviour, environment, and evolution*, pp. 299–313. Oxford University Press, Oxford.

Tullett, S.G. and Deeming, D.C. (1982). The relationship between eggshell porosity and oxygen consumption in the domestic fowl. *Comp. Biochem. Physiol.*, **72A,** 529–533.

Turner, J.S. (1991). The thermal energetics of incubated bird eggs. In: Deeming, D.C. and Ferguson, M.W.J. (eds.), *Egg incubation: its effects on embryonic development in birds and reptiles*, pp. 117–146. Cambridge University Press, Cambridge

Turner, J.S. (2002). Maintenance of egg temperature. In: Deeming, D.C. (ed.), *Avian incubation: behaviour, environment, and evolution*, pp. 119–142. Oxford University Press, Oxford.

Underwood T.J. and Sealy, S.G. (2011). Behavior of warbling vireos ejecting real and artificial cowbird eggs. *Wilson J. Ornith.*, **123,** 395–400.

Walsberg, G.E. (1980). The gaseous microclimate of the avian nest during incubation. *Amer. Zool.,* **20,** 363–372.

Walsh, P.T., Hansell, M., Borello, W.D. and Healy, S.D. (2010). Repeatability of nest morphology in African weaver birds. *Biol. Lett.*, **6,** 149–151.

Walsh, P.T, Hansell, M., Borello, W.D. and Healy, S.D. (2011). Individuality in nest building: Do southern Masked weaver (*Ploceus velatus*) males vary in their nest-building behaviour? *Behav. Proc.,* **88,** 1–6.

Weathers, W.W. and Sullivan, K.A. (1989). Nest attentiveness and egg temperature in the Yellow-eyed Junco. *Condor*, **91,** 628–633.

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

Table 1. Nest and egg dimensions for some British passerine species (selected on the basis of available data) together with calculated values for volumes of air within nest cups and the oxygen requirements of embryos measured pre-internal pipping (Rahn and Paganelli, 1990). The number of minutes that the oxygen within the cup would last a clutch of embryos is also shown, assuming that maximum V_{O_2} is maintained as oxygen is diminished.

Species	Blue Tit (*Cyanistes caeruleus*)	Great Tit (*Parus major*)	European Greenfinch (*Cardeulis chloris*)	Yellowhammer (*Emberiza citrinella*)	Song Thrush (*Turdus philomelos*)	Common Blackbird (*Turdus merula*)
Nest cup diameter (cm)	4.5	5.1	5	6.3	9.1	9.8
Nest cup area (cm²) (*i.e.* πr²)	15.9	20.5	19.7	31.2	65.2	75.6
Nest cup depth (cm)	3.6	3.7	4	4.25	6.7	6.7
Cup volume (cm³) [50% of cup area × depth]	57.4	75.8	78.7	132.8	436.8	326.0
Egg length (L, cm)	1.51	1.8	2	2.1	2.7	2.93
Egg breadth (B, cm)	1.17	1.38	1.5	1.6	2	2.1
Egg volume (cm³) (0.56LB²)[A]	1.16	1.92	2.52	3.01	6.05	7.51
Number of eggs in clutch	10	8	4	4	4	4
Clutch volume (cm³) (Egg volume × clutch size)	11.58	15.36	10.08	12.04	24.19	30.06
Volume of air above eggs (cm³) occupied by incubating bird (cup area × [cup depth - egg breadth])	20.1	19.2	19.7	32.8	176.0	183.0
Volume of air around eggs (cm³) (cup volume - clutch volume - volume of air above eggs)	25.7	41.2	49.0	88.0	236.6	113.0
Oxygen consumption (ml hr⁻¹) (V_{O_2})	0.8	1.3	0.9	2.8	2.2	1.6
Clutch V_{O_2} (ml hr⁻¹) [egg V_{O_2} × clutch size)	8	10.4	3.6	11.2	8.8	6.4
Air required to supply oxygen at 21% (ml hr⁻¹) (clutch V_{O_2} × 0.21)	38.10	49.52	17.14	53.33	41.90	30.48
Minutes O₂ all used ([volume around eggs / air required] × 60)	40.5	49.9	171.4	98.9	338.8	222.4

Notes: [A]Hoyt (1979); Data sources: Cramp (1988), Cramp and Perrins (1993, 1994a, 1994b), C. du Feu (personal communication), Rahn and Paganelli, (1990)

Figure 1. Relationship between water vapour pressures measured in bird nests and in the ambient environment surrounding the nest for scrape nests (blue symbols, solid line) and cup nests (yellow symbols, dashed line). Solid and dashed lines indicate linear relationships fitted through the data points and the green line indicates parity. Redrawn from Deeming (2011).
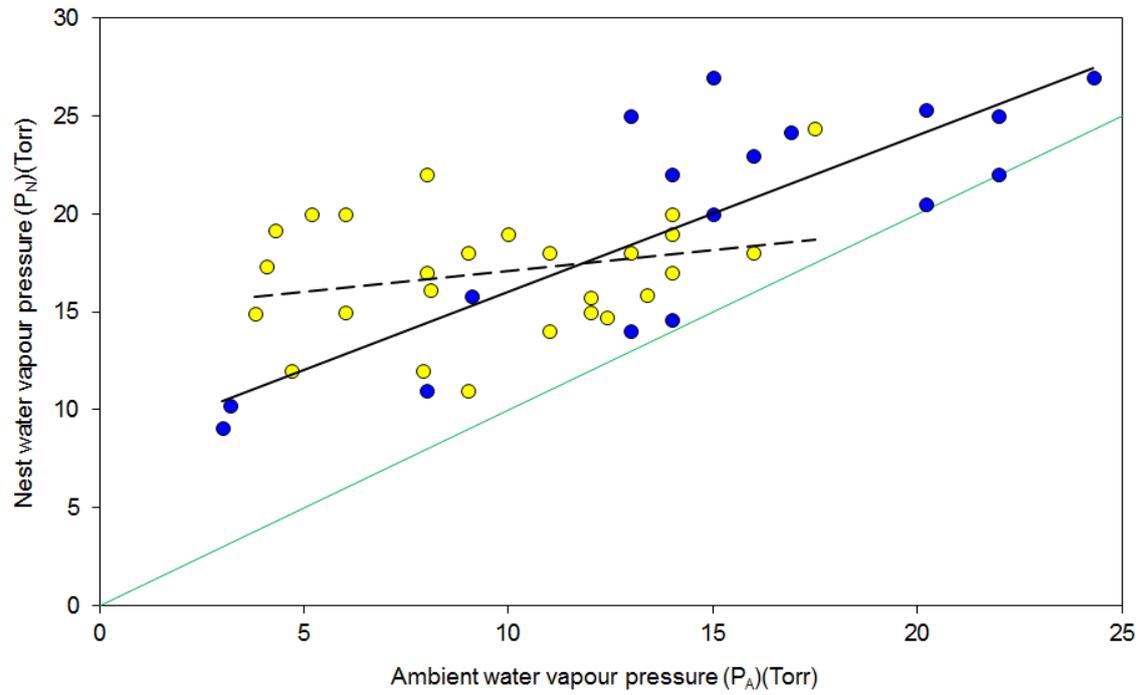
Figure 2. Relationship between mass specific water vapour conductance of the eggshell and water vapour pressures measured in the ambient environment surrounding the nest. Blue symbols and solid line indicate data for species with scrape nests, and yellow symbols and dashed lines indicate data for species with cup nests. Lines are linear relationships fitted through the data points. Reproduced with permission from Deeming (2011).
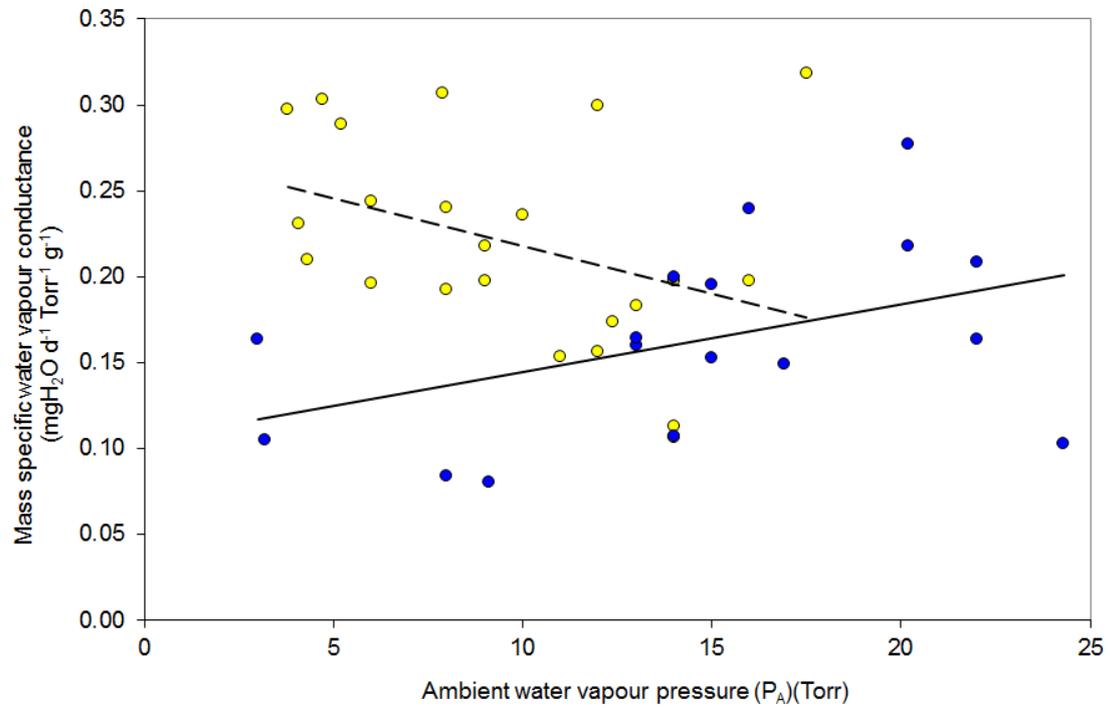
Figure 3. Effects of having a 'closed' (a) or 'open' (b) incubation system on the aeration of the nest cup in a hypothetical small passerine species. Arrows associated with oxygen (O_2), carbon dioxide (CO_2) and humidity indicate whether the partial pressure will decrease (↓) or increase (↑) in the nest cup under the situation illustrated; the number of arrows indicate the extent of the change.
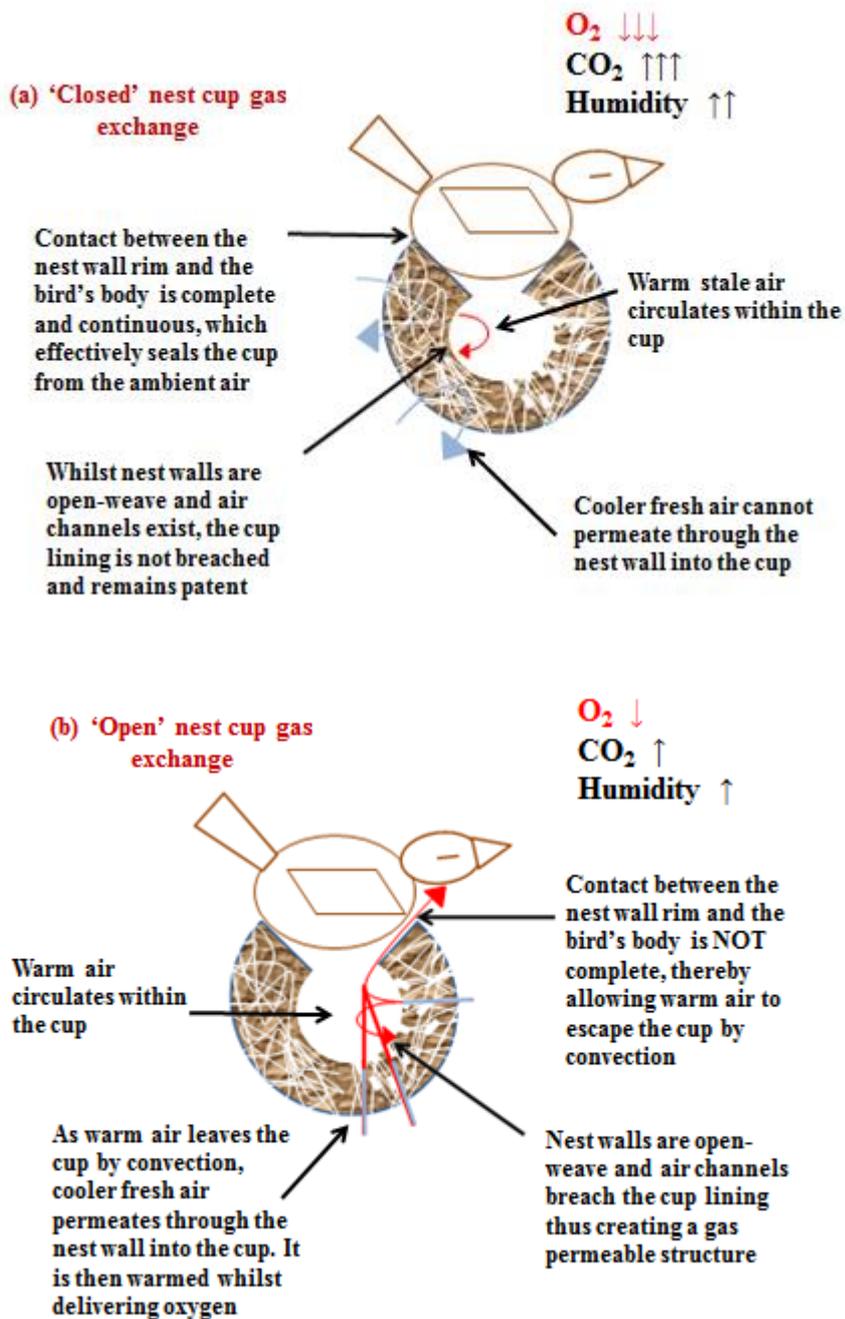
Figure 4. Measurements of surface temperature of a Great Tit (*Parus major*) and its nest *in situ* in a nestbox using infrared (IR) thermography. The hottest parts of the image are indicated by the brightest colours (white: 28 °C and purple: 8 °C). The circle with compass points is the centre of the thermal image while the arrow indicates the direction that the bird was facing (*i.e.* head at the top left of the image).