

Thermoregulation in Breeding Crowned Plovers (*Vanellus coronatus*)

By

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Preface

The experimental work described in this dissertation was carried out in the School of Botany and Zoology, University of Natal, Pietermaritzburg, from February 1998 to November 1999, under the supervision of Dr Colleen T. Downs.

These studies represent original work on my part and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text. Each chapter is written in the format of the journal it has been submitted to.



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Abstract

Ground-nesting birds nesting in the open have to cope with an extreme thermal environment. Their nests, eggs and chicks are often located within the boundary layer and are exposed to direct solar radiation. In preventing eggs and chicks from overheating, adult incubating birds expose themselves to severe heat loads. This study looked at two aspects of this system. Firstly, we examined the role of behaviour in the thermoregulation of breeding crowned plovers (*Vanellus coronatus*). We then examined the development of independent thermoregulation in hatchling crowned plovers.

This study assessed the role of shading behaviour in the thermoregulation of incubating crowned plovers (*Vanellus coronatus*). Shading behaviour was shown to have no direct benefit for eggs, at times even causing eggs to rise close to lethal levels. Instead, shading behaviour played an important role in maintaining incubating bird temperatures at a constant level. We therefore suggest changing the term “shading” to “standing” behaviour.

In addition, core body temperatures of free-ranging adult incubating birds and their eggs were examined on both a daily and a seasonal scale. A range of core bird temperature of 8.8° C was measured during the course of the study. Both daily and seasonal differences in core bird temperature occurred. Daily differences are a result of daily circadian rhythms while seasonal differences are explained by changes in ambient temperature. Both daily and seasonal differences in egg temperatures also occurred. The concept of optimum incubation temperature for a species is therefore reconsidered. Differences between and within species may not be as a result of phylogenetic differences as previously reported, but may be as a result of relatively short-term changes in response to ambient temperature changes.

The validity of using taxidermic models in thermoregulatory studies was assessed by comparing data collected using both real and model birds. No direct correlations were found

between real and model eggs and birds. This suggests that the patterns seen in models may not adequately reflect short term changes that occur in the real system, thus reducing the ability to use such data to make broad generalizations about thermoregulation in general. The models are, however, useful in providing insight into the heat load an animal carries under different environmental conditions, and in estimating the overall, long-term effects of metabolic heat production in a real bird and egg.

Secondly, we looked at the development of thermoregulation in a ground-nesting shorebird. An issue of general importance with regard to the ontogeny of precocial chicks is the timing of the onset of independent thermoregulation. We wanted to determine the mass at which crowned plover (*Vanellus coronatus*) chicks are able to thermoregulate independently in both the laboratory and the field, and to compare this to predicted values previously reported. Laboratory reared chicks attained independent thermoregulation at a mass of 65 g, while chicks in the field did so at a mass of 55 g. This is 33 - 39% of adult body mass, or approximately twice that predicted for a 167 g shorebird chick. Development of homeothermy represents a trade-off between growth rate and development of thermoregulation. Efficient use of behavioural thermoregulation, coupled with predation risks, allows more energy to be channelled into growth early on in the development of crowned plover chicks. Development of homeothermy in any one taxonomic group may not, therefore, always be described by a single function. Instead, differences reflect a balance between growth rate, development of physiological thermoregulation, use of behavioural thermoregulation, predation risk, and environmental factors.

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The Role of Behaviour in the Thermoregulation of Breeding Crowned Plovers

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Abstract

This study assessed the role of shading behaviour in the thermoregulation of incubating crowned plovers (*Vanellus coronatus*). Shading behaviour was shown to have no direct benefit for eggs, at times even causing eggs to rise close to lethal levels. Instead, shading behaviour played an important role in maintaining incubating bird temperatures at a constant level. We therefore suggest changing the term “shading” to “standing” behaviour.

In addition, a range of core bird temperature of 8.8° C was measured during the course of the study. Both daily and seasonal differences in core bird and egg temperature occurred. Daily differences in core bird temperature are probably a result of daily circadian rhythms while seasonal differences are explained by changes in ambient temperature. The concept of optimum incubation temperature for a species is therefore reconsidered. Differences between and within species may not be as a result of phylogenetic differences as previously reported, but may be as a result of relatively short-term changes in response to ambient temperature changes.

Finally, the validity of using taxidermic models in thermoregulatory studies was assessed by comparing data collected using both real and model birds. No direct correlations were found between real and model eggs and birds. This suggests that the patterns seen in

models may not adequately reflect short term changes that occur in the real system, thus reducing the ability to use such data to make broad generalizations about thermoregulation in general. The models are, however, useful in providing insight into the heat load an animal carries under different environmental conditions, and in estimating the overall, long-term effects of metabolic heat production in a real bird and egg.

Introduction

Ground-nesting birds and their thermal environment

Most ground-nesting birds select nest sites in open ground, free of vegetation, and therefore free of visual obstructions (Maclean 1967; 1985). This allows good visibility and hence early nest departure in the face of predator disturbance (Maclean 1985). The nest is often merely a scrape in the ground (Purdue 1976; With & Webb 1993) and eggs are usually very cryptic (Maclean 1984; 1985).

The thermal environment in such natural habitats is generally complex. Factors influencing the thermal environment of natural habitats are: direct solar radiation, infrared radiation, air and soil temperature, and water vapour pressure (Porter et al. 1973). Scattered and reflective heat gain and radiative heat gain by long wave radiation from objects in the environment also play an important role in influencing the heat load on organisms (Withers 1992). In addition, there is also conductive heat transfer between the animal and the ground through the feet and sometimes the body, and convective heat transfer by forced and/or free convection (Schmidt-Nielsen 1990). In windy conditions an atmospheric boundary layer exists near the ground surface (Porter et al. 1973; Lovegrove 1993). Day-time thermal conditions in this boundary layer are most extreme, with the effect of wind higher up reducing temperature by allowing more convective and evaporative cooling (Bennett et al. 1981).

Nests, eggs and chicks of ground-nesting birds all lie within the boundary layer and are very susceptible to hyperthermia (With & Webb 1993). Hyperthermia reduces egg survival more strongly than hypothermia (Webb 1987) and is thus a critical factor in breeding success. Exposure of eggs to high radiant heat loads may produce rapid overheating and embryonic death (Barrett 1980; Bennett et al. 1981). Risks of such lethal exposure may be particularly high in ground-nesting species breeding in low latitudes. Exposure of double-banded courser (*Smutsornis africanus*, previously *Rhinoptilus africanus*) eggs for 15 minutes killed the embryos (Maclean 1967). Exposure time of just two minutes caused lethal overheating of eggs at the Salton Sea area, USA (Grant 1982). In hot climates, incubating birds must therefore play a role in preventing eggs from overheating. In such cases a reversal of the normal incubation process occurs, and eggs need to be cooled rather than warmed by the incubating bird (Grant 1982; Walsberg & Voss-Roberts 1983; Burton 1987; Rahn 1991; Turner 1991; Downs & Ward 1997). In the process the adults themselves may be exposed to substantial heat loads and must therefore prevent themselves from overheating.

Several physiological adaptations exist in some ground-nesting birds which increase tolerance to high ambient temperatures (Maclean 1996). These include a lower than expected basal metabolic rate (Thomas & Maclean 1981); a salt-secreting nasal gland (Maclean 1974; 1976*b*; 1984; Thomas & Robin 1977; Ward 1990) and a counter-current cooling system, involving the rete ophthalmicum (Pinshow et al. 1982; Ward 1990).

The role of behavioural thermoregulation

Behaviour is an important avenue for hyperthermia avoidance and reduction in ground nesting birds (Maclean 1996). At environmental temperatures exceeding 39° C, the parent must dissipate heat to maintain eggs at sub-lethal temperatures (Walsberg & Voss-Roberts

1983; Rahn 1991; Turner 1991). When ambient temperatures surpass those of the thermal neutral zone, adult ground nesting birds employ one or a number of behaviours to facilitate heat loss (Bartholomew & Dawson 1979; Grant 1982; Ward 1990).

A widely used behaviour employed by incubating ground nesting birds is shading (Dawson 1974; Maclean 1976*a*; Grant 1982; Ward 1989*a, b*, 1990; Buttemer & Astheimer 1990; Downs & Ward 1997), whereby the incubating bird straddles the nest, squatting on it's tibiotarsi with the body raised above the nest (Ward 1990; Downs & Ward 1997). This effectively shades the eggs from direct solar radiation while possibly elevating the incubating bird out of the boundary layer (Ward 1990; Downs & Ward 1997). The role of shading in ground-nesting birds has, however, been little studied (Grant 1982; Ward 1990; Downs & Ward 1997) and empirical data on real birds are not available. Some authors suggest that shading behaviour is of primary importance in cooling eggs by convective cooling (Dixon & Louw 1978; Bennett et al. 1981), but more recent work suggests that shading behaviour provides direct cooling benefits to the adult bird and only secondarily (as a result of a cooler brood patch) to the eggs (Ward 1990; Downs & Ward 1997).

A number of studies have examined the relationship between behavioural thermoregulation and incubating bird and egg temperatures using taxidermic models (Bakken 1989; Ward & Pinshow 1995; Downs & Ward 1997). Criticism of these studies suggest that trends seen in models may not reflect the situation found in real birds (Bakken 1991; Walsberg & Wolf 1996) and that models that closely represent the living animal are difficult and expensive to make (Walsberg & Weathers 1986). Studies examining changes in real bird temperature in the field are few, and have mostly employed body-temperature measurements using cloacal (Howell & Bartholomew 1962; Schmidt-Nielsen et al. 1969; Spellerberg 1969; Walsberg & Voss-Roberts 1983; Buttemer & Astheimer 1990) or brood-patch temperature

(Ward 1990; Zann & Rossetto 1991). Studies of core body temperature of birds in the wild are few. Grant (1982) measured the temperature of an incubating male black-winged stilt (*Himantopus himantopus*) by surgically inserting a temperature-sensitive transmitter into the left abdominal air sac. His results were affected by panting behaviour which reduced air sac temperature. Bligh & Hartley (1965) recorded the deep body-temperature of an unrestrained ostrich (*Struthio camelus*). To the best of our knowledge, no study has examined the seasonal differences in both egg and core bird temperatures of free-ranging birds.

Aims of this study

Despite much work done on individual aspects of this complex system, more detailed studies are required to provide a common understanding of the complete relationship between climate, nests, eggs, and parent birds (Barrett 1980). Here we determine:

- i) The role of shading behaviour in the thermoregulation of incubating ground-nesting birds and their eggs.
- ii) Measurement of core body temperatures and egg temperatures of free-ranging adult incubating birds on both a daily and a seasonal scale.
- iii) Comparison between real and model bird and egg temperatures to assess the usefulness of thermal models in thermoregulatory studies of birds.

In all of the above, we use crowned plovers (*Vanellus coronatus*) as a model. They are a suitable model species as they are widespread in sub-Saharan Africa, prefer short grass habitats and are often found in hot environments (Ward 1989*a, b*).

Materials and Methods

All observations were made at Scottsville Racecourse, Pietermaritzburg (29° 30' S 30° 30' E).

The site is approximately 20 ha in extent and is mown weekly, making it suitable habitat for vanelline plovers throughout the year (Ward 1989a). At this site birds breed more than once a year. This facilitated comparison between different seasons at a single site. Nests were located by observing adult behaviour and were usually found during the laying phase. All nests were marked with numbered dowling poles placed within 2 m of the nest. Data were collected within 10 days of laying to minimise the effects of embryonic heat production on egg temperatures, and to standardise measurements made between nests.

Measurement of temperatures

Incubating birds were captured on the nest using a spring-loaded trap. Temperature sensitive telemeters (Model XM, Mini-mitter Co., Sunriver, Oregon) encased in wax and weighing 1.4g (~ 0.74% of body mass) were surgically implanted into the intra-peritoneal cavities of the four incubating birds under inhalation anaesthesia (Isoflurane in O₂; induction and maintenance, 3%; flow rate, *ca* 1l.min⁻¹) to determine patterns in adult body temperature. Mini-mitters were calibrated against a standard mercury thermometer (0.05° C) in a water bath at temperatures from 5 - 45° C. After insertion of the mini-mitter and banding with standard aluminium and colour rings (SAFRING), birds were returned to their territories within 1 h of capture. All birds returned to incubating duties within two days. A circular antenna (25 cm diameter) placed around the nest linked to a medium-wave receiver (radio temperature monitor, Electronics Centre, UNP) recorded the signal from the mini-mitter while the bird was on or just above the nest.

Egg temperatures were recorded using copper-constantin thermocouples. A small hole was drilled into the egg, the thermocouple inserted \pm 2mm beneath the surface of the shell, and the hole sealed using super-glue. This position of the thermocouple should closely reflect

the temperature experienced by the embryo, especially in early stages of development when the embryo is situated in a similar position (Haftorn 1978; 1979). Although none of the implanted eggs survived, all un-tampered eggs in the clutch hatched successfully. Mean egg size for crowned plovers is 40.0 mm x 28.9 mm (n = 274; Maclean 1993).

Soil surface and ambient temperatures were recorded using standard thermocouple probes. Ambient temperatures were measured at 5 cm and 30 cm off the ground using both shielded (from above and below) and unshielded thermocouples (Walsberg & Weathers 1986). This allowed us to estimate the effect of direct solar radiation on the heat load of an organism.

A model bird and eggs were placed in exposed areas near the nests of real birds as a measure of the standard operative temperature (the sum of air temperature, radiative and convective factors, Walsberg & Wolf 1996). The model plover (a skinned specimen stuffed with aluminium foil) was the same as that used by Downs & Ward (1997). A thermocouple was inserted into the abdominal cavity of the model plover in a position similar to the mini-mitter placed in real birds. Contents of a crowned plover egg were carefully removed and replaced with plaster-of-paris. The thermal conductivity of plaster-of-paris ($0.432 \text{ W m}^{-1} \text{ }^{\circ}\text{C}^{-1}$; Weast 1986) is similar to that of an authentic egg (Henderson 1963). A copper-constantin thermocouple was inserted 2 mm beneath the shell surface in the same position as in the real egg. Model bird and egg temperatures represent the standard operative environmental temperature, which is the equilibrium temperature an organism would attain with no metabolic heat production or evaporative water loss, and serves as a measure of heat load (Bakken 1980). All themocouples were calibrated at 0° and 90° C against a standard mercury thermometer.

Field apparatus was, in all cases, set up at least half an hour before recording sessions

began. Real bird temperatures, real egg temperatures, ground exposed and air at 5 cm exposed temperatures were recorded on a MCS 120-02EX data logger (MC Systems, Cape Town) 10-15 m from the nest. The remaining temperatures were recorded with a MCS 120-02EX data logger (MC Systems, Cape Town) approximately 200 m from the nest where behavioural observations were made. All temperatures were recorded every two minutes. A motor vehicle, at a distance of 200-250 m away, was used as a hide, and birds resumed incubation duties within 30 minutes of nest disturbance in most cases. Temperature measurements were taken for up to five day-time periods (10 am - 3 pm) and two night-time periods (8 pm - 6 am). The only exception was nest S10 (summer) which was not monitored at night.

Measurement of behaviour

Behavioural measurements were made on a total of 24 birds. Each nest was observed continually for up to four hours during the hottest part of the day (10 am - 3 pm) for five days. Shading behaviour, its duration, and the time implemented was recorded to discern how it is used under different ambient conditions.

Measurement of wind speed

Wind velocities have been identified as playing major roles in the thermoregulatory ability of ground nesting birds (Bartholomew and Dawson 1979). Wind speed was measured every two minutes at 10cm above the ground with a MC Systems 177-03 anemometer, and correlated with temperature and behavioural data in an attempt to identify any behavioural changes made as a result of wind. Wind speed has no effect on eggs of ground-nesting birds (Downs & Ward 1997). We were therefore mainly interested in the effect of wind speed has on bird temperature when shading or incubating.

Results

A total of 41 nests was located and observed over an 18 month period (06/98 - 11/99). Of these, 78% were found in spring, 10% in summer, 7% in winter and 5% in autumn. Mean adult body mass of the four implanted birds was $189 \pm 9.8\text{g}$. Nest S10 was studied in November 1998 (summer), S15 in May 1999 (autumn), S18 and S20 in early and late September 1999 (spring). A further 20 birds were observed for behavioural data collection to determine seasonal changes in behavioural patterns.

Daily Data 10am - 3pm

i) Correlations between environmental variables

Effects of shade and distance from the ground on ambient temperature for summer, autumn, early spring and late spring are shown in Table 1. Distance from the ground had a highly significant effect on temperature, with temperature decreasing with increasing distance from the ground. All exposed ambient temperatures were significantly higher than shaded ones. We decided, on the basis of differences in seasonal correlations of environmental variables (see below) to keep data as separate seasons, and to show that environmental conditions affect birds differently on a seasonal basis.

In summer (S10), exposed ground temperatures were significantly positively correlated with shaded ground temperatures and exposed air temperatures at 5 cm ($r^2 = 0.92$; $P < 0.0001$ and $r^2 = 0.92$; $P < 0.0001$). Exposed air temperatures at 30 cm were significantly positively correlated with shaded air temperatures at 5 cm and at 30 cm ($r^2 = 0.92$; $P < 0.0001$ and $r^2 = 0.92$; $P < 0.0001$). These correlations prevented use of all temperature variables as independent variables in data analysis. To avoid this problem, two new variables were independently created using Principal Components Analysis. PCground was the first principle

component of exposed ground temperatures, shaded ground temperatures and exposed air temperatures at 5 cm. The PC I axis explained 94% of the variance in these three variables. PCair was the first principal component of exposed air temperatures at 30 cm and shaded air temperatures at 5 cm and at 30 cm. This explained 97% of the variation in these three variables. The component loadings of these two variables were as follows:

$$Pcground = 0.980 * Tgroundus + 0.973 * T5cmus + 0.954 * Tgroundsh \quad (1)$$

$$PCair = 0.982 * T30cmus + 0.987 * T5cmsh + 0.985 * T30cmsh \quad (2)$$

In autumn (S15), exposed ground temperatures were significantly positively correlated with all other ambient temperatures ($r^2 = 0.747$; $P < 0.0001$). Principal Components Analysis was therefore used to create a new variable (PCambient) that was a linear combination of all ambient temperatures. This was the PC I axis and explained 68% of the variation in these six variables. The component loadings for this variable was:

$$PCambient = 0.735 * Tgroundus + 0.835 * T5cmus + 0.932 * T30cmus + 0.491 * Tgroundsh + 0.918 * T5cmsh + 0.944 * T30cmsh \quad (3)$$

In both early (S18) and late (S20) spring, exposed air temperature at 30 cm was significantly positively correlated with shaded ground, air at 5cm and air at 30 cm temperatures ($r^2 = 0.82$; $P < 0.0001$). Principle Components Analysis was used to create two new variables (PCshade and PCshade2) that were linear combinations of these four correlated ambient temperatures for early and late spring. These were the PC I axes for early and late spring and explained 86% and 88% of the variation in these four variables respectively. Component loadings for these two variables were as follows:

$$\text{PCshade} = 0.924 * T_{30\text{cmsh}} + 0.902 * T_{\text{groundsh}} + 0.950 * T_{5\text{cmsh}} + 0.951 * T_{30\text{cmsh}} \quad (4)$$

$$\text{PCshade2} = 0.922 * T_{30\text{cmsh}} + 0.924 * T_{\text{groundsh}} + 0.945 * T_{5\text{cmsh}} + 0.951 * T_{30\text{cmsh}} \quad (5)$$

Table 1: Results from an ANOVA showing the effect of solar exposure and distance from the ground on ambient temperature on a seasonal basis during the study of crowned plovers

Season	Thermocouple variable	df error	MS error	<i>F</i>	<i>P</i>
summer	shade vs exposed	334	12.19	3034.35	<0.0001
	distance from ground	668	5.23	3010.37	<0.0001
autumn	shade vs exposed	592	12.14	5240.39	<0.0001
	distance from ground	1184	2.72	2866.58	<0.0001
early spring	shade vs exposed	448	13.04	3493.33	<0.0001
	distance from ground	896	6.77	1691.69	<0.0001
late spring	shade vs exposed	515	6.87	11987.63	<0.0001
	distance from ground	1030	2.51	6171.58	<0.0001

ii) Effect of direct solar exposure on environmental temperatures

An index of the effect of direct solar radiation on heat load was created using the equation:

$$\text{Solar Index} = T_{\text{exposed}} - T_{\text{shaded}} / T_{\text{shaded}} \quad (6)$$

The greater the effect of direct solar radiation on heat load, the higher the index. The solar index reflects the effects of direct solar radiation on ambient conditions at various levels within the microclimate of the nesting plovers. This effectively pin points areas that are most affected by direct solar radiation. Seasonal solar indices for ground, air at 5 cm and air at 30 cm are summarised in Figure 1. Indices were highest for ground temperatures, followed by air temperatures at 5 cm and air temperatures at 30 cm. Ground temperatures were most affected by direct solar radiation (Figure 1). The greatest mean difference between shaded and exposed

temperatures occurred in late spring when exposed ground temperatures were $19.21 \pm 3.71^\circ$ C higher than shaded temperatures. The smallest difference between shaded and exposed temperatures also occurred in late spring when exposed air temperatures at 30 cm were only $0.89 \pm 0.9^\circ$ C higher than shaded temperatures. The solar index shows us that incubating birds can release some of the thermal stress present by merely standing up to a level of 5cm, where the effect of direct solar radiation is significantly reduced.

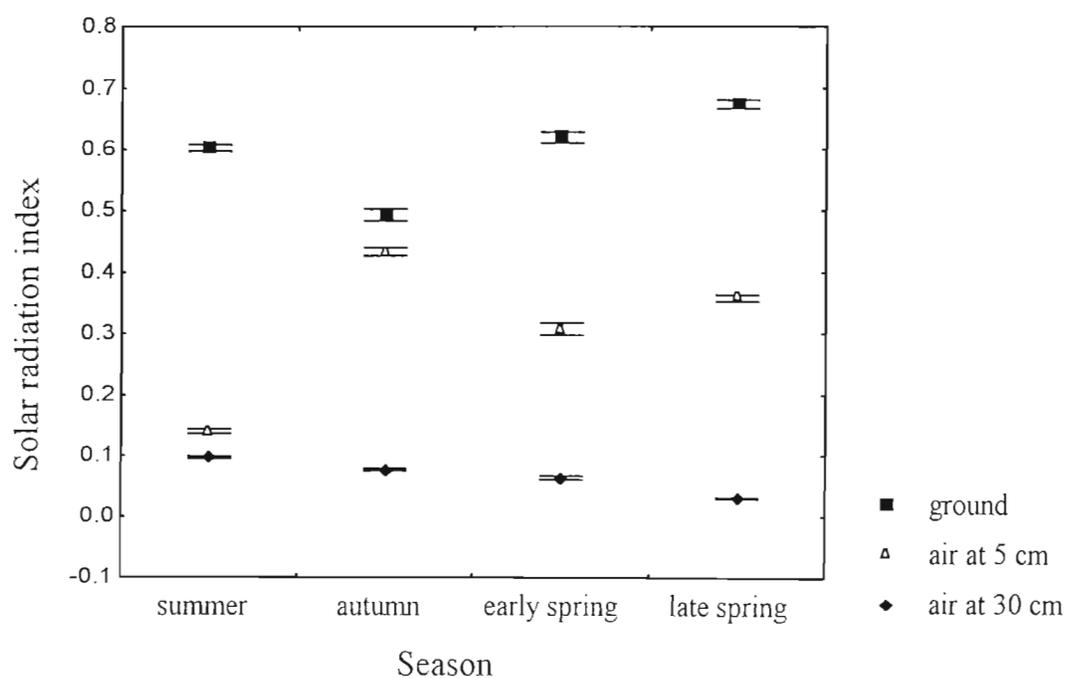


Figure 1: Seasonal solar indices for all environmental temperatures measured to show the effect of solar radiation on ambient conditions experienced by nesting crowned plovers ($\bar{x} \pm S. E.$)

iii) Overall effect of bird position on bird and egg temperature

Summer egg temperatures were significantly lower when incubated than when either shaded or exposed ($F_{2, 343} = 34.54, P < 0.0001$). Shaded egg temperatures were not significantly

different from exposed egg temperatures, but were lower. Summer bird body-temperatures were significantly lower when shading than when tightly incubating (ANCOVA with PCground, PCair and wind speed as covariates; $F_{1, 294} = 4.979, P = 0.026$).

Autumn egg temperatures were significantly higher when exposed than when shaded or tightly incubated ($F_{2, 610} = 21.11, P < 0.0001$). No significant difference was found between egg temperatures when tightly incubated or shaded. Autumn bird body temperatures did not differ when the bird was shading from when it was tight incubating (ANCOVA with PCambient and wind speed as covariates; $F_{1, 250} = 0.41, P = 0.522$).

Early spring bird position did not affect egg temperature ($F_{2, 457} = 2.74, P = 0.065$) or bird body temperature (ANCOVA with PCshade, windspeed, ground exposed and air at 5 cm exposed temperatures as covariates; $F_{1, 175} = 2.74, P = 0.0997$).

Late spring egg temperatures were significantly higher when exposed than when shaded or incubated ($F_{2, 426} = 202.83, P < 0.0001$), and significantly higher when shaded than when incubated. Late spring shading bird temperatures were significantly higher than incubating bird temperatures ($F_{1, 341} = 9.468, P < 0.01$).

iv) Effect of wind speed and ambient temperature on egg temperature, bird temperature, and bird position

Summer incubated egg temperatures were only significantly correlated with PCground ($r^2 = 0.305, P < 0.0001$). Shaded egg temperatures were weakly but significantly correlated with both PCground ($r^2 = 0.077, P < 0.0005$) and PCair ($r^2 = 0.077, P < 0.01$), with PCground having the greater effect (standardised regression co-efficient $B = 0.579$). Exposed summer egg temperatures were only significantly correlated with PCair ($r^2 = 0.52, P < 0.01$). Wind speed had no effect on egg temperatures in summer. Summer bird body temperature when

incubating was significantly affected by PCground, PCair and wind speed ($r^2 = 0.249$, $P < 0.0001$; $r^2 = 0.249$, $P < 0.0001$ and $r^2 = 0.249$, $P < 0.005$ respectively), with PCair having the greatest effect on bird temperature (standardised regression co-efficient $B = 1.182$; increased wind speed resulted in lowered body temperature). When shading, summer bird body temperature was only weakly affected by PCair ($r^2 = 0.092$, $P < 0.05$).

Incubated egg temperatures in autumn were weakly affected by PCambient ($r^2 = 0.061$, $P < 0.005$). Exposed egg temperatures were affected by both PCambient and wind speed ($r^2 = 0.259$, $P < 0.0001$ and $r^2 = 0.259$, $P < 0.05$ respectively), with PCambient having the greater effect (standardised regression co-efficient $B = 0.487$). Autumn shaded egg temperatures were not significantly correlated with either ambient temperatures or wind speed. When shading, bird body temperature was significantly correlated with PCambient ($r^2 = 0.635$, $P < 0.05$) in autumn.

In early spring, incubated egg temperatures were only significantly affected by exposed ground temperatures ($r^2 = 0.594$, $P < 0.0001$), while shaded egg temperatures were highly correlated with PCshade ($r^2 = 0.914$, $P < 0.01$). Exposed egg temperatures were significantly correlated with exposed ground, exposed air at 5 cm, and PCshade temperatures ($r^2 = 0.521$, $P < 0.0001$; $r^2 = 0.521$, $P < 0.0001$ and $r^2 = 0.521$, $P < 0.01$ respectively), with exposed ground temperatures having the greatest effect (standardised regression co-efficient $B = 0.819$). Although early spring bird temperature when shading showed no correlation to environmental temperature or wind speed, bird temperature when incubating was significantly correlated with exposed ground temperature, exposed air at 5 cm temperature and PCshade ($r^2 = 0.43$, $P < 0.0001$ for all three environmental parameters). Exposed early spring ground temperatures had the greatest effect on bird temperature (standardised regression co-efficient $B = 0.527$) when incubating.

Late spring incubated and shaded egg temperatures were significantly correlated with exposed ground temperatures ($r^2 = 0.158$, $P < 0.0001$ and $r^2 = 0.118$, $P < 0.05$ respectively). Late spring exposed egg temperatures were significantly correlated with exposed ground temperatures, PCshade2 and wind speed ($r^2 = 0.299$, $P < 0.0001$; $r^2 = 0.299$, $P < 0.0005$ and $r^2 = 0.299$, $P < 0.05$ respectively). Exposed ground temperatures showed the highest correlation with exposed egg temperatures (standardised regression co-efficient $B = 1.033$). Bird temperatures when incubating were significantly correlated with exposed ground temperatures and PCshade2 ($r^2 = 0.451$, $P < 0.0001$ for both parameters), with exposed ground temperatures having the stronger correlation (standardised regression co-efficient $B = 0.434$). When shading, late spring bird temperature was significantly correlated with exposed ground temperatures, exposed air at 5 cm temperatures and wind speed ($r^2 = 0.398$, $P < 0.001$; $r^2 = 0.398$, $P < 0.001$ and $r^2 = 0.398$, $P < 0.01$ respectively), with exposed air at 5 cm temperatures showing the stronger correlation (standardised regression co-efficient $B = 0.36$).

Differences between ambient temperatures when the nest was tightly incubated, shaded and exposed for all seasons are shown in Figure 2. Exposed ground temperatures are likely to have the greatest effect on egg temperature, whilst shaded-air temperatures at 5 cm are likely to have a high effect on bird body temperature. Ambient conditions were significantly higher when the bird was shading the nest than when it was tightly incubating or the nest was exposed. Ambient temperatures were lowest when the nest was exposed.

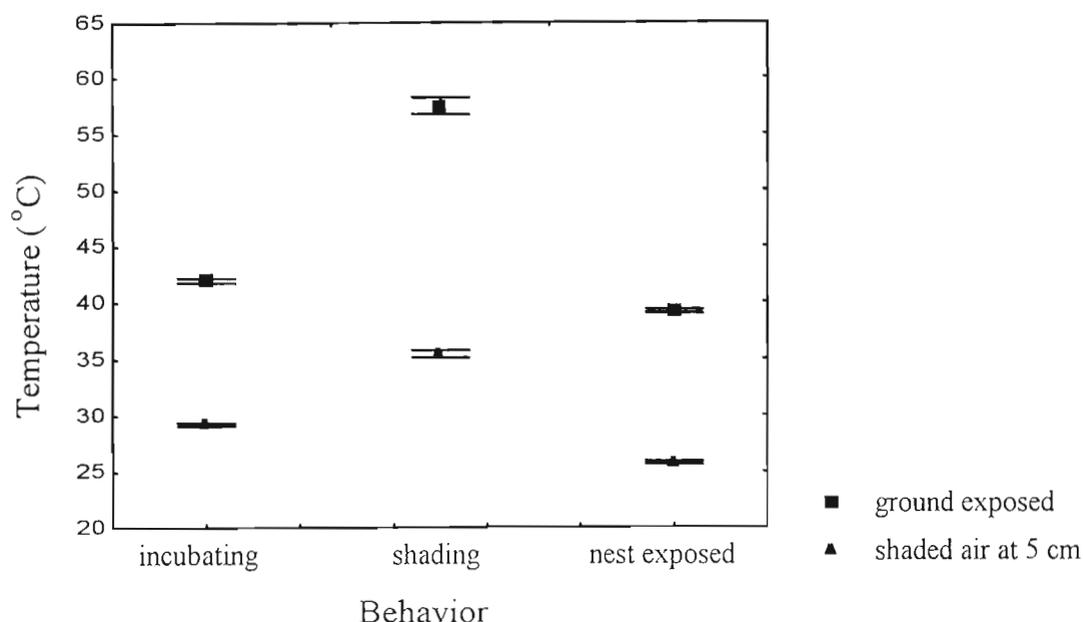


Figure 2: Overall daily ambient temperatures (ground exposed and shaded air at 5 cm) encountered during different incubating behaviours of crowned plovers ($\bar{x} \pm S. E.$).

v) Effect of bird position on bird and egg temperatures when ambient conditions are controlled for

Data from summer were used to determine the net effect of shading behaviour on the temperatures of real eggs and birds. Shading behaviour was more prominent in summer than other seasons (see below), and provided enough data in order to allow comparison between shaded and incubated birds and eggs at various temperature ranges. Ambient temperatures were grouped into 3 categories, temperatures between 30° and 35° C; temperatures between 35° and 40° C; and temperatures above 40° C. Table 2 summarises the results of ANOVA's used to test for significant differences between shaded and unshaded eggs and shading and incubating bird body temperatures. In all cases, shaded egg temperatures were significantly higher than incubated egg temperatures. Bird body temperature while shading was significantly lower than when incubating, also in all cases (see appendix 2).

Table 2: Results from ANOVA's showing the effect of bird behaviour on bird and egg temperatures when ambient temperature is controlled for

Comparison	Ta Range	df error	MS error	F	P
Tb incubating vs Tb shading	30-35	8	0.03	10.37	<0.05
	35-40	35	0.03	26.33	<0.0001
	>40	29	0.02	6.84	<0.05
Tegg incubated vs Tegg shaded	30-35	8	0.77	6.77	<0.05
	35-40	35	1.08	18.04	<0.0005
	>40	29	0.35	5.95	<0.05

24 hour profiles: Differences between day and night ambient, incubating bird and egg temperatures

Minimum, maximum and mean (\pm SE) day (10 am - 3 pm) and night (8 pm - 6 am) respective ambient, bird and egg temperatures, and wind speed, experienced by birds in summer, autumn and spring are shown in Table 3.

In autumn, mean bird body temperature was significantly higher during the day than during the night (1.57°C) as was mean egg temperature (1.99°C), mean ground temperature (17.42°C) and mean air temperature at 5 cm (18.59°C). Bird body temperature at night was significantly correlated with ground temperature and air temperature at 5 cm ($r^2 = 0.617$; $F = 459.27$; $P < 0.0001$ and $r^2 = 0.67$; $F = 579.81$; $P < 0.0001$ respectively). Likewise, in early spring mean bird body temperature was significantly higher during the day than during the night (3.18°C) as was mean egg temperature (2.73°C), mean ground temperature (19.76°C) and mean air temperature at 5 cm (17.45°C). Bird body temperature at night was significantly correlated with ground temperature and air temperature at 5 cm ($r^2 = 0.78$; $F = 645.56$; $P < 0.0001$ and $r^2 = 0.76$; $F = 604.76$; $P < 0.0001$ respectively). Late spring data showed the same trend, with mean bird body temperature significantly higher during the day than during the night (5.65°C) as was mean egg temperature (3.05°C), mean ground

temperature (30.89° C) and mean air temperature at 5 cm (30.38° C). Bird body temperature at night was significantly correlated with ground temperatures and air temperatures at 5 cm ($r^2 = 0.75$; $F = 467.27$; $P < 0.0001$ and $r^2 = 0.87$; $F = 1027.4$; $P < 0.0001$ respectively).

Table 3: Minimum, maximum and mean day (10 am - 3 pm) and night (8 pm - 6 am) temperatures (ambient, bird and egg) and wind speeds encountered during each season that crowned plovers were studied

Season	Temperature measured	n	Mean	S. E.	Minimum	Maximum
summer	Day shielded ground	338	37.99	0.17	30.28	47.30
	Day shielded air at 5 cm	343	38.12	0.23	27.50	49.70
	Day bird body	308	42.70	0.01	42.12	43.50
	Day egg	346	39.14	0.08	36.30	46.80
	Wind speed (m/s)	334	0.128	0.018	0	1.46
autumn	Day shielded ground	606	25.52	0.10	21.00	31.90
	Day shielded air at 5cm	606	26.17	0.11	21.80	33.80
	Day bird body	269	42.13	0.02	41.13	43.15
	Day egg	618	33.60	0.07	28.30	39.00
	Wind speed (m/s)	606	1.70	0.04	0	7.32
	Night air at 5 cm	583	7.58	0.06	4.72	10.51
	Night ground	583	8.10	0.08	4.18	12.39
	Night bird body	286	40.56	0.03	39.70	41.09
	Night egg	583	31.60	0.04	29.40	34.60
early spring	Day shielded ground	472	25.31	0.13	19.68	31.63
	Day shielded air at 5 cm	472	24.99	0.13	19.20	33.30
	Day bird body	192	42.44	0.03	41.63	43.25
	Day egg	475	33.38	0.13	27.30	40.50
	Wind speed	472	2.21	0.08	0	20.40
	Night air at 5 cm	597	7.54	0.18	1.44	14.47
	Night ground	597	5.55	0.22	-1.09	14.16
	Night bird body	188	39.27	0.13	35.87	41.34
	Night egg	597	30.65	0.10	22.60	35.60
late spring	Day shielded ground	529	28.96	0.11	21.58	37.77
	Day shielded air at 5 cm	529	30.74	0.10	23.70	38.80
	Day bird body	351	42.75	0.02	41.76	43.70
	Day egg	518	33.39	0.13	29.20	42.40
	Wind speed (m/s)	529	1.84	0.04	0	6.82
	Night air at 5 cm	602	0.36	0.09	-3.46	6.26
	Night ground	602	-1.93	0.08	-5.45	2.86
	Night bird body	158	37.11	0.17	34.90	41.91
	Night egg	602	30.34	0.08	24.30	36.80

Seasonal differences in thermal properties

i) Seasonal differences in ambient temperature

Shaded air temperatures at 5 cm (Table 4) were compared between seasons. This ambient temperature was chosen as it was a standard air measurement made during day and night recording sessions. Daily summer temperatures were significantly higher than autumn (T-test; $t = 59.96$; $P < 0.013$ after Bonferroni adjustment) or spring ($t = 49.96$; $P < 0.013$ after Bonferroni adjustment) temperatures, and daily spring temperatures were significantly higher than autumn temperatures ($t = -5.65$; $P < 0.013$ after Bonferroni adjustment). Spring night temperatures were significantly lower than autumn temperatures ($t = 36.07$; $P < 0.0001$). Range in temperatures experienced by incubating birds over a 24 hour period was 29.08°C and 42.26°C in autumn and spring respectively.

ii) Seasonal differences in wind speed

Wind speed was highest in early and late spring. Summer had the lowest levels of wind, with autumn only showing moderate levels of wind speed (Figure 3).

iii) Seasonal differences in bird behaviour during the day

Mean percentage time spent incubating, shading and away from the nest between 10 am and 3 pm for summer, autumn and spring are shown in Figure 4. Incubating birds spent significantly more time shading the nest in summer than in autumn ($t = 4.16$; $df = 9$; $P < 0.005$) or spring ($t = 4.08$; $df = 9$; $P < 0.005$). More time was spent tightly incubating in autumn than summer ($t = -2.34$; $df = 9$; $P < 0.05$) or spring ($t = 2.52$; $df = 15$; $P < 0.05$). Nests were left exposed for longer periods of time during autumn than summer ($t = -2.79$; $df = 9$; $P < 0.05$).

Table 4: Shaded air temperatures at 5 cm for each season to show the range of temperatures experienced by nesting crowned plovers.

Temperature	mean	S. E.	min	max
summer day	38.12	0.23	27.5	49.7
autumn day	26.13	0.11	21.8	33.8
spring day	28.03	0.12	19.2	38.8
autumn night	7.58	0.06	4.72	10.51
spring night	2.20	0.14	-3.46	11.9

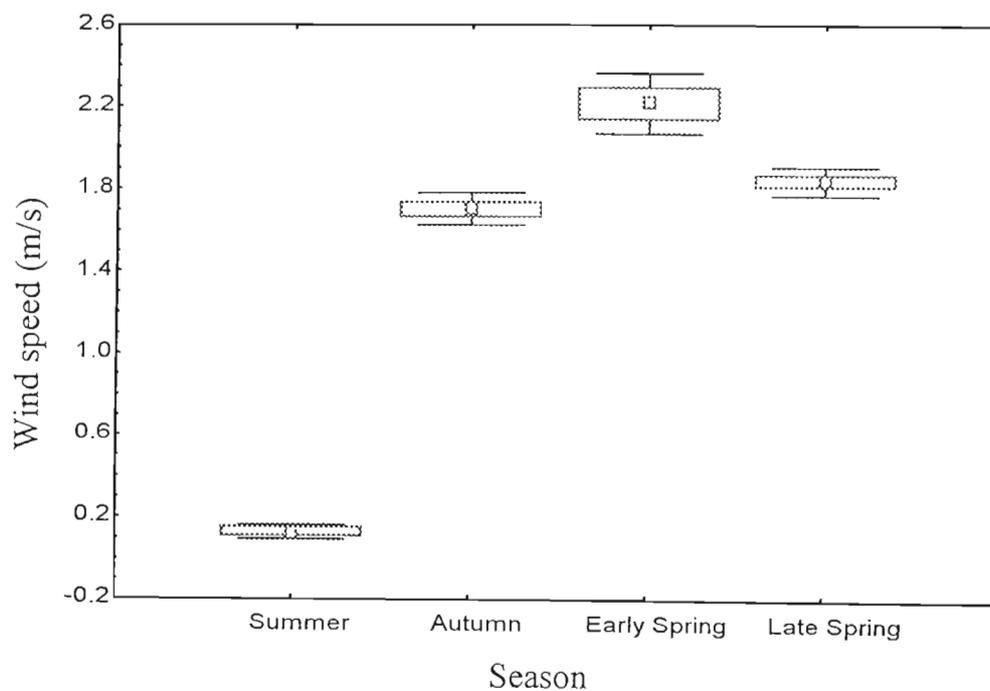


Figure 3: Seasonal differences in wind speed (m/s) at 5 cm above the ground. This is what the adult crowned plover is generally exposed to.

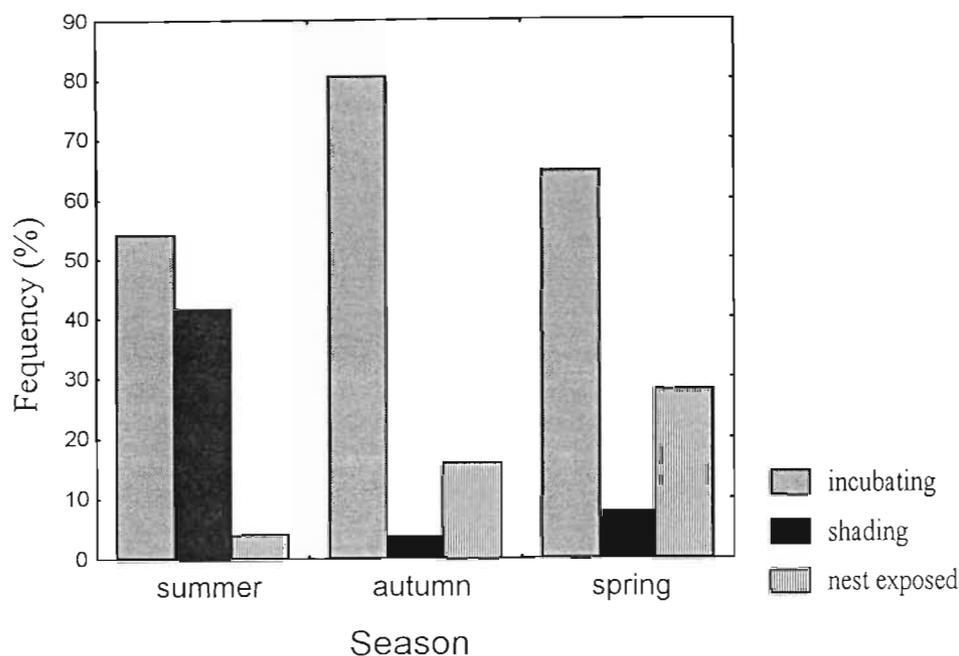


Figure 4: Seasonal differences in the frequency of incubating behaviours in crowned plovers (n=24)

iv) Seasonal differences in egg and bird body temperatures during the day

Bird body temperatures were significantly higher in summer than in autumn ($t = 19.31$; $df = 243$; $P < 0.001$) and spring ($t = 7.12$; $df = 307$; $P < 0.001$), and significantly higher in spring than in autumn ($t = -10.53$; $df = 243$; $P < 0.001$). Bird temperature was on average 0.6°C and 0.23°C higher in summer than in autumn and spring respectively. Egg temperatures were significantly higher in summer than in autumn ($t = 39.93$; $df = 345$; $P < 0.001$) and spring ($t = 42.06$; $df = 345$; $P < 0.001$), and higher in spring than in autumn ($t = 3.37$; $df = 517$; $P < 0.001$). Egg temperature was usually 5.54°C and 4.75°C higher in summer than in autumn and spring respectively.

v) *Seasonal differences in egg and body temperatures at night*

Bird body and egg temperatures were significantly lower in spring than in autumn ($t = 13.98$; $df = 285$; $P < 0.0001$ and $t = 8.95$; $df = 582$ $P < 0.0001$ respectively). Bird and egg temperatures were on average 2.28°C and 0.96°C respectively higher in autumn than in spring.

Comparison between real and model birds and eggs

Daily (10 am - 3 pm) temperatures of real and model eggs and birds for all seasons ($n = 4$ real birds) differed (Figure 5). No strong correlation between real and model bird or eggs was found ($r^2 = 0.037$, $F = 44.02$, $P < 0.0001$ and $r^2 = 0.021$, $F = 32.1$, $P < 0.0001$ respectively). Real bird temperatures were significantly higher (6.8°C) than model bird temperatures ($t = 36.18$; $df = 1119$; $P < 0.0001$). Real egg temperatures were also significantly higher (0.85°C) than model egg temperatures ($t = 7.94$; $df = 1474$; $P < 0.0001$).

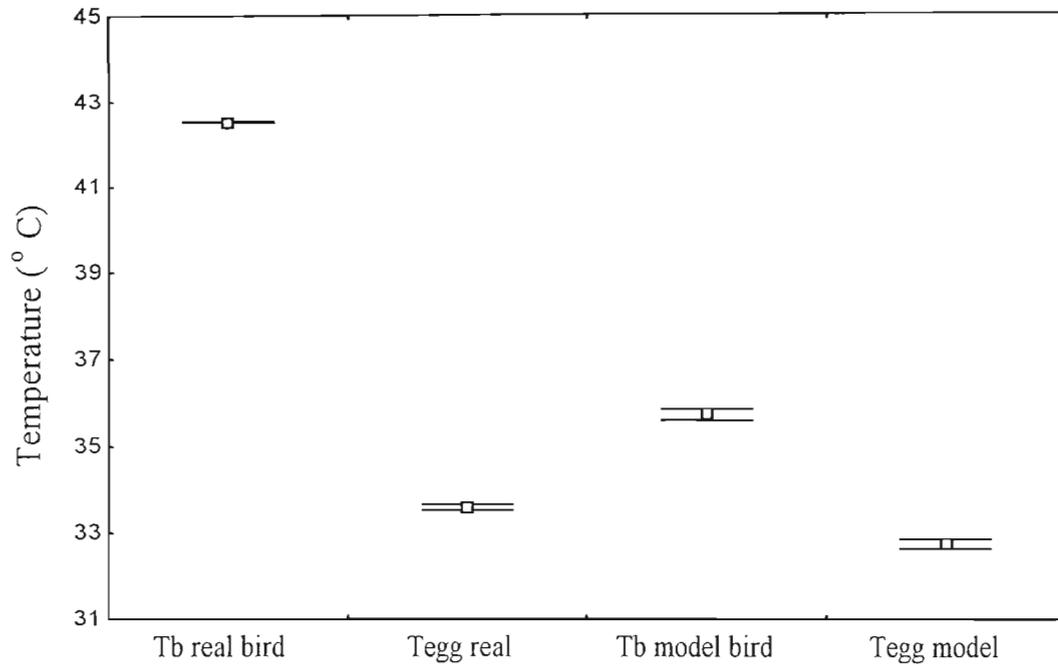


Figure 5: Differences between real and model egg and bird temperatures for crowned plovers for all seasons measured between 10 am and 3 pm ($\bar{x} \pm S. E.$)

Discussion

The role of shading behaviour in thermoregulation

Daily ambient temperatures differed significantly on a seasonal basis, with summer temperatures much higher than spring or autumn temperatures. During this study of crowned plovers, the effect of direct solar radiation on heat load also differed seasonally. Correlations between environmental variables differed substantially on a seasonal basis. Mirroring these trends were significant seasonal differences in the proportion of time an incubating bird spent either incubating, shading, or away from its nest. This prevented us from grouping all data for analyses. Shading behaviour was far more prominent in the hotter summer months, whilst eggs were more often exposed during the cooler autumn months. This supports the notion that behavioural thermoregulation is directly linked to ambient temperature (Purdue 1976; Grant 1982; Ward 1989*b*; 1990). Ward (1990) showed that incubating crowned plovers increased time spent shading eggs from less than 20% between 35 and 40° C, to about 75% at ambient temperatures above 45° C. Therefore, shading behaviour plays a role in thermoregulation at high temperatures.

This study shows that in autumn (mean daily shaded air at 5 cm temperature = 26.2 °C), no difference between shaded and incubated egg temperatures was found, although only 3.5% of incubating time was spent shading and ambient temperatures seldom rose to high levels. However, in summer (mean daily shaded air at 5 cm temperature = 38.12 °C) and late spring (mean daily shaded air at 5 cm temperature = 30.74 °C), shaded egg temperatures were significantly higher than incubated egg temperatures (2.98 and 3.46° C higher respectively). Bird body temperatures when shading in summer were not significantly different from when tight incubating. However, when wind speed, ground and air temperatures were taken into account, bird temperature was significantly higher when incubating than when shading (by

0.05° C). In autumn, bird temperatures did not differ when incubating than when shading, even when wind speed and ambient temperature were accounted for. Spring bird body temperatures were actually higher (by 0.1° C) when shading than when incubating. Downs & Ward (1997) showed, using a model bird, that shading behaviour provides direct cooling benefits for adult birds. However, shading behaviour in all seasons occurred under significantly higher ambient conditions than normal incubation. It is therefore possible that shading behaviour counteracts effects of increased ambient temperature on bird body temperature, and prevents extreme overheating even if bird body temperature itself does not differ much.

When ambient temperature was controlled for (Table 2), bird body temperature was always higher when incubating than when shading, while egg temperature was always higher when shaded than when incubated. In other words, shading behaviour has no direct benefit for eggs, but instead increases the risk of eggs suffering from hyperthermia. This contradicts earlier findings which suggested that egg temperatures are cooled by shading behaviour (Purdue 1976; Dixon & Louw 1978; Bennett et al. 1981), but supports more recent work using taxidermic models which showed that “shading” facilitates cooling of the adult rather than the egg (Downs & Ward 1997). It therefore plays an important role in regulating adult body temperatures when incubating under thermal stress. We therefore recommend changing the term “shading” to “standing” behaviour, as this is more appropriate.

Variation in bird body temperature

Few studies have attempted to measure deep body temperatures of free-ranging birds in the wild (Bligh & Hartley 1965; Grant 1982), and even fewer attempts have been made to examine daily and seasonal changes in free-ranging core body temperatures. This study shows

that body temperature of incubating ground nesting birds differs significantly on both a daily and a seasonal basis. During the course of the study, a range in body temperatures of 8.8°C was measured. The greatest daily range in body temperatures occurred during late spring, when the difference between day and night body temperature was 5.65°C . During this same period, ambient temperatures also showed the highest range (42.26°C). Bird body temperatures in summer and spring were only weakly affected by ambient conditions, and in autumn only night-time body temperatures were weakly influenced by ambient conditions. Thus, even during the breeding season, when energy demands are greatest on an individual (Walsberg & Voss-Roberts 1983), crowned plovers are able to efficiently thermoregulate. Differences between day and night body temperatures are partly explained by natural, daily circadian rhythms (Whittow 1976; Reinersten 1996; **Dawson 2000**).

When compared, seasonal differences in bird body temperature were restricted to a narrower range than daily differences (0.6°C day and 2.28°C night), and were more than likely as a result of changes in ambient temperature. Lowest body temperatures were recorded in late spring, when ground temperatures at night averaged below zero (-1.93°C). It thus appears that the bird's ability to thermoregulate is inversely related to ambient temperature. During the study period most birds nested in spring (78%), when ambient temperatures were most variable. Despite this, spring seems the optimal time to breed. There are a number of reasons why this seems to be the case. Not only is food availability high after the early rains (Ward, 1989), but short grass is predominant after winter and provides ample nest sites for ground nesting birds (Ward 1989a). Also, wind is more prevalent in spring, which is the only season where it has a significant positive effect on bird body temperature (reducing body temperature) when shading and incubating.

Variation in real egg temperature

The concept of optimum incubation temperatures has been widely discussed (Bennett & Dawson 1979; Barrett 1980; Webb 1987). Eggs of most bird species are reported to be incubated at internal temperatures around 35-36° C (Drent 1975), and this is often thought to be similar for all species. However, Webb (1987) showed that taxonomic differences in average incubation temperature may occur. No studies have looked at the natural variation of real eggs incubated by free-living birds on both a daily and a seasonal basis. Results from the present study show that real egg temperatures within the first 10 days of incubation differ greatly on a daily basis. In all seasons, egg temperature was significantly higher during the day than at night. The differences were most pronounced in late spring (3.05° C), followed by early spring (2.73° C) and autumn (1.99° C). This differs from some findings that suggest that little variation exists in egg temperatures between day and night (Haftorn 1978; Barrett 1980; Zann & Rossetto 1991). Variations in daily egg temperature have, however, been reported for other species (Haftorn 1979; Bennett et al. 1981; Grant 1982). Closer inspection of these data reveals a definite trend. In cold regions, egg temperatures are lower during the day than at night (Haftorn 1979; Morton & Pereyra 1985). In hot areas, where ambient conditions often exceed bird body temperature, egg temperature is significantly higher during the day than at night (Grant 1982; Walsberg & Voss-Roberts 1983; present study). Moderate regions show no difference in day and night egg temperatures (Haftorn 1978; Barrett 1980; Zerba & Morton 1983; Zann & Rossetto 1991). The present study showed an overall range of egg temperatures of 24.2° C. With the exception of implanted eggs, all monitored nests hatched successfully, indicating that eggs are able to withstand wide fluctuations in ambient temperature.

No references to seasonal changes in egg temperatures could be found in the literature.

This study, however, shows that significant differences in mean egg temperatures occur on a seasonal basis. Summer daily egg temperatures were on average 5.54° C and 4.73° C higher than in autumn and spring respectively. Night-time egg temperature was 0.96° C higher in autumn than in spring. It is possible that egg temperature is moderated at a level dependent on ambient temperature, so as to reduce energy expended on incubation to a minimum while still keeping eggs viable. At high temperatures in summer and spring, this leads to elevated egg temperatures, reducing energy costs spent on cooling eggs to a more reported level (35-36° C). Conversely, at low temperatures during autumn and winter, egg temperatures are moderated at a lower level, reducing costs of warming the egg. Differences in egg temperatures between species may therefore not be as a result of phylogenetic differences as previously reported (Webb 1987), but may be a result of relatively short term changes in response to ambient conditions. Such intra-specific differences should also lead to differences in incubation period.

The validity of taxidermic models in thermoregulatory studies

Studies using both model eggs made of different materials (Yom-Tov et al. 1978; Barrett 1980; Walsberg & Voss-Roberts 1983) and real eggs (Howell & Bartholomew 1962; Spellerberg 1969; Purdue 1976; Haftorn 1978, 1979; Bennett & Dawson 1979; Barrett 1980; Grant 1982; Zerba & Morton 1983; Grant & Paganelli 1984; Morton & Pereyra 1985; Zann & Rossetto 1991) are numerous. Drent (1970) showed that embryonic heat production played a significant role in elevating egg temperature only after the 14th day. In this study, real egg temperatures were on average slightly higher than model egg temperatures (0.85° C). This may indicate that, even early in the incubation period, embryonic heat production plays an important role in the thermodynamics of incubated eggs. Caution must be shown, however, as

none of the implanted eggs studied here survived. It is not known at what age these embryos died. Differences between real and model eggs could also reflect previously unreported differences in the thermal properties of plaster-of-paris and albumin. Model birds were loosely placed over model eggs in a position similar to that of the incubating real bird. Slightly higher real egg temperatures could therefore also be explained by the effect of shading behaviour on the real eggs (see above).

Comparison between real and model bird body temperatures measured simultaneously gives an insight into the effect of metabolism and other thermoregulatory responses on the thermal biology of birds. Model bird temperature was on average 6.8°C lower than real bird temperature. This suggests that even with efficient thermoregulation, metabolic heat production increases body temperature by as much as 6.8°C .

Use of taxidermic models in thermoregulation studies has always depended upon the assumption that models will closely reflect the real organisms that they mimic (Bakken 1980; Ward & Pinshow 1995). However, no direct correlations between real and model egg and bird temperatures were found in this study. This suggests that patterns seen in model birds may not adequately reflect short term changes that occur in the real system, thus reducing the ability to use such data to make broad generalisations about behavioural thermoregulation in general. The models are useful in providing insight into the heat load an animal carries under different environmental conditions, and in estimating the overall, long-term effect of metabolic heat production in a real bird and egg as used above.

Recent progress in telemetry technology now enables us to start experimenting with measuring core bird body temperature in the field in certain circumstances, particularly when the bird is immobile for long periods (when incubating). Although the use of models has led to an increased understanding of the processes working in the thermal system of birds, we feel

it is essential that future research focus on measuring real bird temperatures in order to test some of the theories based on models.

Conclusion

Shading behaviour provides no direct benefit for incubated eggs, but rather plays a role in the regulation of adult body temperatures at high ambient temperatures. Bird body temperature varies on both a daily and a seasonal scale. Daily variation is a function of natural circadian rhythms, while seasonal variation is more likely to be as a result of ambient temperature. Egg temperatures follow similar daily and seasonal variations, and may be a result of an energy-saving mechanism employed by incubating birds. The limitations and uses of taxidermic models is outlined.

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Appendix 1: Symbols used in Chapter 1

T_{groundus} = unshaded ground temperature

T_{groundsh} = shaded ground temperature

T_{5cmus} = unshaded air temperature at 5cm

T_{5cmsh} = shaded air temperature at 5cm

T_{30cmus} = unshaded air temperature at 30cm

T_{30cmsh} = shaded air temperature at 30cm

Appendix 2: Mean, minimum and maximum daily (10 am to 3 pm) temperatures of birds and eggs when nests were exposed, incubated and shaded.

Season	Temperature	n	Mean	S. E.	Minimum	Maximum
Summer	T _b incubating	159	42.71	0.02	42.12	42.95
	T _b shading	149	42.68	0.02	42.22	43.50
	T _{egg} incubated	159	38.50	0.08	36.30	41.90
	T _{egg} shaded	149	39.51	0.09	37.10	44.10
	T _{egg} exposed	38	40.33	0.51	36.50	46.80
Autumn	T _b incubating	255	42.12	0.03	41.13	43.15
	T _b shading	13	42.27	0.06	41.89	42.55
	T _{egg} incubated	456	33.41	0.06	30.50	36.40
	T _{egg} shaded	16	33.19	0.54	29.80	38.30
	T _{egg} exposed	143	34.24	0.19	28.30	39.00
Early Spring	T _b incubating	189	42.44	0.03	41.63	43.25
	T _b shading	3	42.67	0.16	42.46	42.99
	T _{egg} incubated	200	33.24	0.16	30.40	38.10
	T _{egg} shaded	3	37.20	3.10	31.00	40.50
	T _{egg} exposed	270	33.44	0.19	27.30	39.50
Late Spring	T _b incubating	266	42.72	0.02	41.83	43.47
	T _b shading	83	42.84	0.04	41.76	43.70
	T _{egg} incubated	266	31.93	0.12	29.30	37.60
	T _{egg} shaded	88	34.40	0.23	30.90	40.50
	T _{egg} exposed	75	37.30	0.30	31.60	42.40

Chapter 2

Development of Homeothermy in Hatchling Crowned Plovers *Vanellus coronatus*

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Abstract

An issue of general importance with regard to the ontogeny of precocial chicks is the timing of the onset of independent thermoregulation. We wanted to determine the mass at which crowned plover (*Vanellus coronatus*) chicks are able to thermoregulate independently in both the laboratory and the field, and to compare this to predicted values previously reported. Laboratory reared chicks attained independent thermoregulation at a mass of 65 g, while chicks in the field did so at a mass of 55 g. This is 33 - 39% of adult body mass, or approximately twice that predicted for a 167 g shorebird chick. Development of homeothermy represents a trade-off between growth rate and development of thermoregulation. Efficient use of behavioural thermoregulation, coupled with predation risks, allows more energy to be channelled into growth early on in the development of crowned plover chicks. Development of homeothermy in any one taxonomic group may not, therefore, always be described by a single function. Instead, differences reflect a balance between growth rate, development of physiological thermoregulation, use of behavioural thermoregulation, predation risk, and environmental factors.

Introduction

With the exception of extensive work done on gulls (Dawson et al. 1972; Dawson et al. 1976; Bennett et al. 1981; Dawson & Bennett 1980; Salzman 1982), few field studies have looked at the thermoregulatory capacities of chicks of ground-nesting birds. Nestlings in a number of ground-nesting species are precocial or semi-precocial, which allows them to move around and seek protection almost directly after hatching (Maclean 1985; McNabb & Olsen 1996). This may be an adaptation not only to nesting in extreme environments, but in open spaces where altricial chicks found by predators would have little chance of escape. Precocial chicks are generally homeothermic (Snyder et al. 1991; McNabb & Olson 1996), except possibly for the first few days (Visser & Ricklefs 1995). This precociality has distinct advantages in the early post-hatching period, which includes having independent locomotion, the ability to forage for food (McNabb & Olson 1996) and to actively seek shade in the absence of a brooding adult (pers. obs.).

Some precocial chicks show thermoregulatory responses at an early age (Maclean 1967; 1985). Gull chicks are able to thermoregulate at ambient temperatures between 20°C and 35°C, whilst parental attentiveness is necessary at extreme temperatures (Dawson & Bennett 1981). The development of thermoregulation is associated with an increase in the thermogenic capacity of the chick combined with reduced mass-specific thermal conductance (Dunn 1976), which is achieved by improved plumage insulation and decreasing surface-to-mass ratio as the chick grows (Visser & Ricklefs 1993*a*).

An issue of general importance with regard to the ontogeny of precocial chicks is the timing of the onset of independent thermoregulation (Herbert & Prinzinger 1998). Embryos of domestic fowl show no thermoregulatory response to changes in ambient temperature, yet 2 hour-old chicks show clear responses to similar changes (Herbert & Prinzinger 1998). This

suggests that the transition from heterothermy to homeothermy is an immediate post-hatching response in some precocial species (Herbert & Prinzinger 1998). However, birds show a spectrum of post-hatching development with respect to thermoregulatory capacities (Eppley 1996). Beintema & Visser (1989) showed that related species of shorebirds differ in the timing of the development of homeothermy. Furthermore, development of thermoregulation in precocial chicks is at the expense of growth rate, with growth rates of precocial chicks being four times lower than those of altricial chicks of the same adult body mass (Ricklefs 1979). Indeed, body mass plays a major role in the development of homeothermy (Whittow & Tazawa 1991; Visser & Ricklefs 1993*b*; 1995). Neonates of shorebirds have a range in body mass of 4 to 55 g (Visser & Ricklefs 1993*b*). Although all these species are regarded as precocial, differences in the degree of precociality as influenced by body mass at hatching and during growth are not fully accounted for (Visser & Ricklefs 1993*b*).

The aim of this study was to examine the development of homeothermy in a precocial ground-nesting bird. In particular, we wanted to determine at what mass a precocial ground-nesting shorebird is able to completely thermoregulate independent of ambient temperature, and to relate this to the trade-off between growth rate and the development of thermoregulation. We also wanted to compare this to predicted values from previous studies (Visser & Ricklefs 1993*a*). Mass was used instead of age because, in laboratory conditions, age may be affected by feeding rates and holding conditions. Visser & Ricklefs (1993*a*) found body mass to be a better measure than age when working on homeothermy in neonates of shorebirds. The crowned plover was chosen for this study as it is a relatively common and widespread precocial ground-nesting shorebird species which nests in a range of climatic conditions, often in hot environments (Brown & Downs Chapter 1).

Materials and Methods

The study was conducted on crowned plovers breeding at Scottsville Racecourse, Pietermaritzburg, South Africa (29° 30' S 30° 30' E) over an 18 month period (June 1998 - November 1999). The site is approximately 20 ha in extent and is mown weekly, making it suitable habitat for vanelline plovers throughout the year (Ward 1989). Nests were located by observing adult behaviour and were usually found during the laying phase. All nests were individually marked with numbered dowling poles situated 2 m of the nest. Nests were checked daily until hatching. Chicks were easily caught by hand. Eighteen chicks were removed under permit from the KwaZulu-Natal Nature Conservation Services to the School of Botany & Zoology, University of Natal, Pietermaritzburg. Chicks were housed in individual glass tanks (90 cm X 30 cm X 30 cm) with a sawdust substrate, and were kept in a constant environment room at 28° C. During daylight hours a 60 W lamp provided additional heat in each tank, while at night a standard fan heater was used to heat the room to $\pm 35^{\circ}$ C. Birds were fed a mixed diet of earthworms, mealworms and *Aviplus Mynah* for soft-bills. Water was provided *ad libitum*.

Laboratory study

Measurements were conducted daily between 14:30 and 17:30. Chicks were placed in constant environment rooms and exposed to periods of set ambient temperature (15°C, 25°C, 35°C and 40°C) until body temperature appeared to stabilise. These experimental temperatures were within the range of air temperatures that chicks experience in the field. Experiments were run on a 4-day cycle starting at an age of 2 days with a temperature sequence of 25°C, 15°C, 35°C and 40°C. Cloacal temperatures were measured before and after each trial using a hand-held Fluke 51 digital thermometer (John Fluke MFG. Co., Inc,

Washington) with a 1 mm diameter thermocouple inserted 5 mm into the cloaca.

Measurements were taken within 30 seconds of handling in order to reduce heat gained by handling or stress. Rectal temperatures may show a delayed response to small changes in deep body-temperature (Bligh 1973). Thus, cloacal measurements, although often criticised, may be useful for obtaining accurate measurements of body temperatures without the effect of handling the birds playing a role. Although we were unable to test the effect of handling time on cloacal temperature, we feel that we worked consistently and quickly enough to reduce any effect to a minimum. Change in body temperature at each ambient temperature was used as a measure of the thermoregulatory capacity of the bird. Chick body mass was measured prior to experiments each day. If body temperature dropped below 28°C or rose above 42°C experiments were terminated. This often occurred in young chicks which seemed unable to thermoregulate at all.

Field study

Cloacal body temperatures were taken on an opportunistic basis from 25 chicks at various stages of development using a hand-held Fluke 51 digital thermometer (John Fluke MFG. Co., Inc, Washington) with a 1 mm diameter thermocouple inserted 5 mm. Measurements were taken within 2 minutes of capture. Body mass of the bird, along with unshaded substrate temperatures (taken as the ambient temperature most influencing the chick) were also recorded. Ambient temperatures were divided into ranges (10-20° C; 21-30° C; 31-40° C and > 40° C) to allow comparisons between laboratory and field measurements. It was assumed that chicks in the field were in thermal equilibrium with that particular ambient temperature. Chicks that were being brooded, or who were in shaded or sheltered areas were not used in the study. Unshaded substrate temperatures were used as this is the environmental variable

the chicks are most in contact with and which, presumably, has a large effect on chick temperature. Adult crowned plovers mean body weight is 167 g ($n = 6$; Maclean 1985).

In both the field and laboratory studies, the hand-held digital thermometer was periodically checked against a standard mercury thermometer to check consistency in readings. At no time did the readings differ from a standard mercury thermometer.

Results

A total of 41 nests was found during the study period, of which eggs from 38 clutches (100 eggs) were measured. A total of 66% of the nests consisted of 3 eggs, 24% had 2 eggs, 8% had only 1 egg and 2% (1 nest) consisted of 4 eggs. Mean (\pm S. E.) egg length and breadth was 39.13 ± 0.15 and 28.58 ± 0.08 mm respectively.

The relationship between age and mass for crowned plover chicks reared in the field and in the laboratory is shown in Figure 1. The differences between field and laboratory chicks prevented us from using age as a constant variable. Instead, we used cloacal temperatures at different body masses as a measure of homeothermy development.

Breakpoint regressions (Ward & Pinshow 1994) were used to determine at what mass chicks in both the laboratory and the field were able to thermoregulate (Table 1, Figures 2 & 3). The optimal breakpoint of two regressions on each set of data is the point where chicks go from little control over body temperature to complete, independent thermoregulation. The optimal breakpoint is the point where the pooled error mean square is minimised (pooled error mean square = the sum of the 2 error mean squares for the 2 regressions; Ward & Pinshow 1994). In all cases, our pooled error mean squares was lower than the error mean square for a single regression run on all data, thereby validating the use of breakpoint regressions. Laboratory reared chicks were able to completely thermoregulate at all ambient

temperatures after a body mass of 65 g had been attained. Chicks in the field, however, developed complete homeothermy earlier and were able to maintain body temperature at a body mass of 55 g under most ambient conditions. This equated to an age of about 20 days in the field.

Mean chick body temperature both before and after homeothermy had developed is summarized in Table 2. There were significant differences in chick body temperature between pre-thermoregulatory independence and post-thermoregulatory independence in both the laboratory and in the field ($t = -7.074$; $P < 0.0125$ and $t = -7.70$; $p < 0.0125$ Bonferroni adjustment for multiple t-tests). At low body mass (< 50 g), chicks had an absolute range in body temperature of 11.4 and 12° C in the field and laboratory respectively. Body temperatures were lower at low ambient temperatures (10-30° c) and higher at high ambient temperatures (31-50° C).

Table 1: Breakpoint regression results of the thermoregulatory capacity of crowned plover chicks in the field and in the laboratory

	ambient condition	breakpoint mass	df	Pooled error m.s.
laboratory	15	65	16	2.58
	25	65	19	2.80
	35	65	21	0.63
	40	65	19	1.12
field	10-20	55	4	0.15
	21-30	45	5	0.22
	31-40	55	4	0.04
	41-50	55	4	0.05

* pooled error m.s. represents combined residual m.s. for the two separate regressions

Table 2: Mean, minimum and maximum cloacal temperatures of crowned plover chicks in the laboratory and in the field both before and after complete homeothermy had developed.

Values represent mean of means for all chicks.

		Mean	S.E.	Minimum	Maximum	n
Before complete homeothermy	Lab	36.54	0.251	34.12	38.16	15
	Field	36.74	0.282	35.85	37.81	6
Completely homeothermic	Lab	38.27	0.086	38.06	38.69	7
	Field	38.00	0.196	37.53	38.63	6

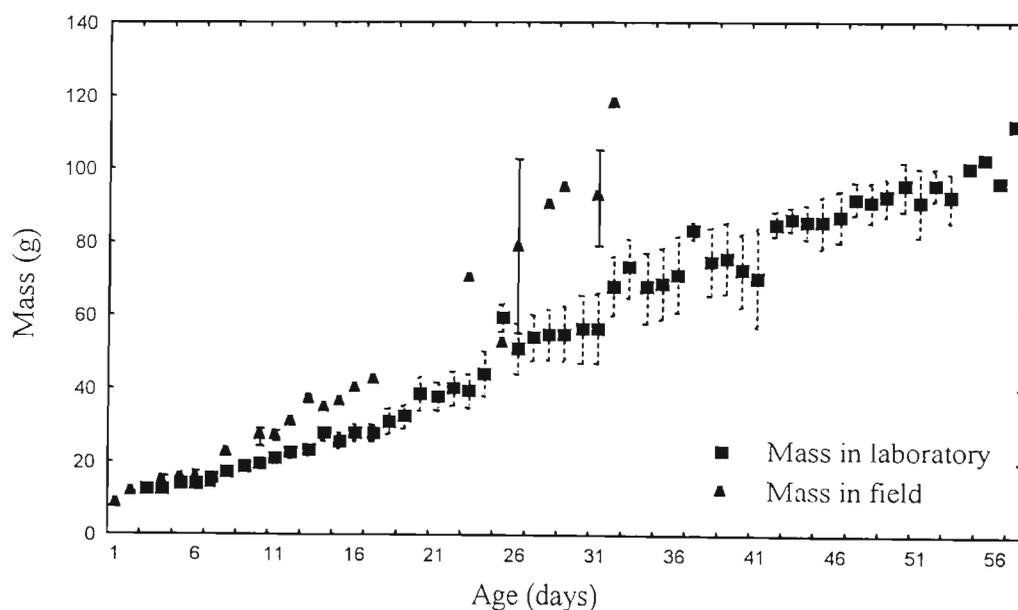


Figure 1: Comparison of growth rates in crowned plover chicks raised in the field and in the laboratory ($\bar{x} \pm \text{S.E.}$).

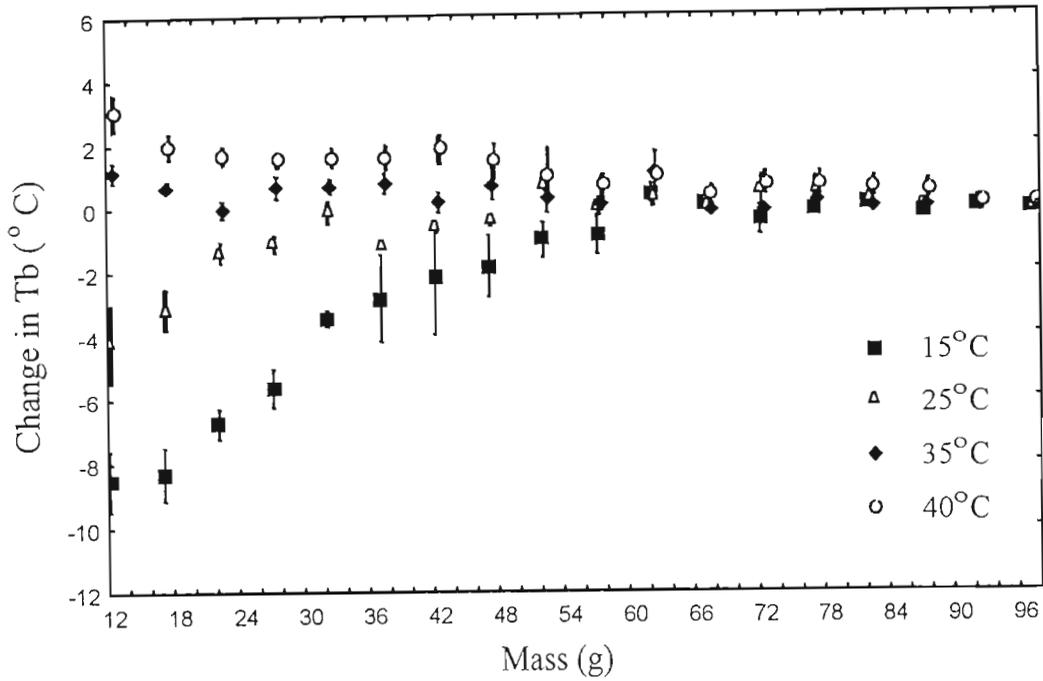


Figure 2: Development of thermoregulation in laboratory reared crowned plover chicks ($\bar{x} \pm$ S.E.). Symbols indicate temperatures at which chicks were exposed to.

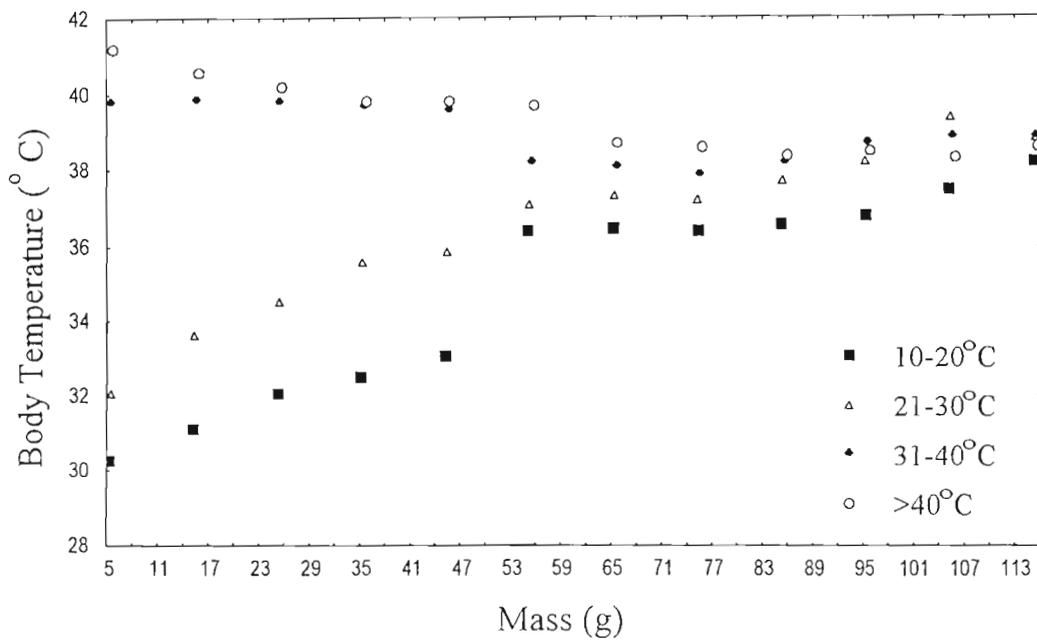


Figure 3: Development of thermoregulation in crowned plover chicks in the field ($\bar{x} \pm$ S.E.).

Symbols indicate the various temperature ranges at which chicks were tested in the field.

Comparison between laboratory and field data

Body temperatures of chicks maintained at 28° C in the laboratory were not significantly different to those of chicks believed to be in thermal equilibrium in the field ($t = 0.068$; $P = 0.948$ and $t = 1.473$; $p = 0.2$ for before and after development of complete homoothermy respectively). This indicates that chicks in the laboratory responded in a similar manner to ambient temperature as did chicks in the field.

Discussion

Numerous studies have examined the development of thermoregulation in both altricial and precocial chicks (Bartholomew & Dawson 1954; Dawson et al. 1972; Dunn 1976; Dawson & Bennett 1981; Chappell et al. 1984; Eppley 1984; Olson 1991; Modrey & Nichelmann 1992; Gdowska et al. 1993; Visser & Ricklefs 1993a, 1995; Finke et al. 1995; Hai et al. 1996), while others have provided comprehensive reviews on the development of thermoregulation in birds in general (Dawson & Hudson 1970; Whittow 1973, 1976; Whittow & Tazawa 1991; Visser & Ricklefs 1995; Eppley 1996; McNabb & Olson 1996). In a comparison between 145 charadriiform species, Eppley (1996) found no significant effect of latitude on egg size, hatchling standard metabolic rate, or growth rate. In other words, climatic differences do not lead to larger, thermally advanced chicks.

Most newly-hatched precocial birds are not fully homeothermic (Visser & Ricklefs 1995). Young birds can pass through this vulnerable period by increasing energy spent on growth rate (Eppley 1996). Growth rate is, however, offset by development of thermoregulation, because this requires energy that could otherwise have been used for growth (Ricklefs 1979; McNabb & Olson 1996). The observed rate of development of homeothermy in neonates therefore reflects a balance between costs (higher catabolic

requirements and slower growth rate) and benefits (increased foraging time and decreased dependency on parents - reduction in time being brooded at extreme ambient temperatures). This balance is different for different taxonomic groups and for different species within each group (Whittow & Tazawa 1991; Visser & Ricklefs 1993a, 1995). Independent thermoregulation in crowned plovers is achieved at 55 g and 65 g in the laboratory and field respectively (this study). This is 33 - 39 % of adult body mass, or approximately twice that predicted by Visser & Ricklefs (1993a) for a 167 g shorebird chick (prediction = 27 g or 16% of adult body mass). Visser & Ricklefs (1993b) also note the importance of ambient temperature on the development of homeothermy. Development of homeothermy in any one taxonomic group (eg shorebirds) may not, therefore, always be described by a single function (Visser & Ricklefs 1993a). Instead, differences may occur as a result of complex interactions between the organism and environmental factors.

Crowned plover chicks show phenotypic plasticity in body temperatures at a young age, before complete homeothermy has developed. All birds are, however, able to run around and forage at this stage, even though body temperatures may be as low as 30° C. Brown & Downs (Chapter 1) recorded a core body temperature of 34.9° C in a free-ranging adult crowned plover, suggesting that adults of this species are also able to tolerate low body temperatures at times. In the past, precociality has often been equated with homeothermy (Snyder et al. 1991; McNabb & Olson 1996), but it is clear from our results that this is not the case. Although crowned plover chicks achieve locomotory and feeding independence almost directly after hatching, complete homeothermy develops only when chicks attain a mass of 55-65 g (33 - 39 % of adult body mass). But why do these chicks take so long to fully develop endothermy if it is so advantageous to do so early on? A clear distinction between physiological and behavioural thermoregulation in these young birds is necessary.

Behavioural thermoregulation is in operation almost directly after hatching, with chicks actively seeking shade and panting (pers. obs.). Efficient use of behavioural thermoregulation, in addition to high predation risks, leads to more energy being channelled into growth early on in the development of crowned plover chicks. This leads to a slower than predicted rate of homeothermy development.

Laboratory studies induce numerous stresses upon young birds, including lack of parental bonding, natural brooding, learnt feeding, and others. These behavioural links to parents may alter the physiological development of young birds and thus may not reflect the natural situation. In our case, using chicks removed from the field, homeothermy developed at a later stage in the laboratory than in the field, suggesting that our laboratory setup was not optimal. Visser & Ricklefs (1993*a*), using chicks incubated artificially, found lower asymptotic chick masses and higher Gompertz growth constants in the laboratory than in the field, suggesting that their experimental conditions were also not representative of the field situation. Differences in results from the laboratory and field studies suggest that previous findings based on laboratory studies alone should be approached with caution. We suggest that more field based studies be used as controls for laboratory studies, as a means of validating results from laboratory studies.

Conclusions

Crowned plover chicks develop complete homeothermy at more than twice the size predicted by Visser & Ricklefs (1993*a*) for a shorebird of 167 g. They also differ in the development of homeothermy in the field and laboratory. Ambient temperature is shown to affect chick body temperature at an early age. These findings suggest that environmental conditions, behavioural thermoregulation, and parental behaviour are major factors in the development of

homeothermy in precocial species, and that the onset of independent thermoregulation cannot be predicted by studying physiology alone. Independent thermoregulation in a species represents a trade-off between growth rate and development of homeothermy.

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Conclusion

This study has provided some insight into ground-nesting systems. Shading behaviour provides no direct benefit for incubated eggs, but rather plays a role in the regulation of adult body temperatures at high ambient temperatures. Bird body temperature varies on both a daily and a seasonal scale. Daily variation is a function of natural circadian rhythms, while seasonal variation is more likely to be as a result of ambient temperature. Egg temperatures follow similar daily and seasonal variations, and may be a result of an energy-saving mechanism employed by incubating birds. Taxidermic models are useful for studying heat load of animals under different environmental conditions, but are limited in their ability to reflect short term changes in response to changing ambient conditions as experienced by real birds.

Crowned plover chicks develop complete thermoregulation at more than twice the size predicted by Visser & Ricklefs (1993a) for a shorebird of 167 g. They also differ in the development of thermoregulation in the field and laboratory. Ambient temperature is shown to affect chick body temperature at an early age. These findings suggest that environmental conditions, behavioural thermoregulation, and parental behaviour are major factors in the development of thermoregulation in precocial species, and that the onset of independent thermoregulation cannot be predicted by studying physiology alone. Independent thermoregulation in a species represents a trade-off between growth rate and development of homeothermy.

It is clear that technology has a major role to play in the future study of bird physiology. The use of models in the past has led to an increased understanding of the heat loads experienced by organisms in extreme environments. I feel it is imperative that future research make more use of technology to try and test the conclusions drawn from model work. It is also clear from this study that we cannot study the thermal physiological systems

of birds as discrete, separate systems, but that we must include aspects of behaviour and environmental factors into account. Only when we take a more holistic approach will we begin to understand the complex ways in which birds interact with their environment.