Adult birds maintain high body temperature in cold environments by the insulating properties of their plumage, particular behaviours such as huddling and communal roosting (Ancel et al. 1997), and a high capacity for thermogenesis. In nestlings, the capacity for thermoregulation is limited by constraints specific to young organisms. For example, compared to adults, chicks have a less favourable surface-to-volume ratio (Visser 1998) and their immature and underdeveloped muscles contribute little to thermogenesis (Hohtola & Visser 1998).

In altricial birds, newborn chicks are poikilothermic, physically helpless and therefore dependent on parental care for heat, food, and protection. Normal development, shown by age at fledging and body mass, is achieved when these three factors are optimal. Heat transferred by brooding adults is necessary during incubation and the initial period of post-hatching growth, until homeothermy is achieved. Thereafter, homeothermy is maintained by thermogenesis and thus is dependent on parental food provisioning. However, heat transfer by brooding parents may alleviate the energetic costs of chick homeothermy. Chicks from large broods can benefit from the thermal inertia of their siblings (Westerterp et al. 1982), which decreases the amount of food required for thermoregulation, permitting parents to forage for longer periods (Clark 1982). The energetics of altricial chicks are difficult to characterise and such studies have therefore been done mainly in the laboratory. Hatching asynchrony complicates the issue by creating a size hierarchy amongst siblings (Newton 1979). A size hierarchy often results in

The influence of hatching order on the thermoregulatory behaviour of barn owl Tyto alba nestlings

Joël M. Durant

The behavioural responses of barn owl Tyto alba chicks to variation of ambient temperature were investigated in relation to hatching order. Four broods of wild barn owls were video-monitored during their postnatal growth. During the foraging trips of the adults, nest temperature and the behaviour of the chicks were recorded. The results show an influence of hatching order on the individual behavioural responses to variation in ambient temperature.

The average temperatures at which the chicks showed specific thermal behavioural responses depend on the position in the size hierarchy. This result may indicate a difference in development among siblings in relation to the hatching order, possibly due to a difference in growth or tissue maturation associated with differences in food availability. That late-hatched chicks showed behavioural responses against cold and heat stress respectively at higher and lower temperature than their older siblings may be, in addition to being a consequence of food restriction, a way to divert part of their energy intake from muscle maturation to growth.

Key words: Nestling growth, thermoregulation, hatching asynchrony, raptor, behaviour.

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a slower growth or death of the last-hatched chick(s) due to sibling competition for food (Stoleson & Beissinger 1997).

In raptors, parents share the task of caring for the chicks. For some days after the eggs have hatched, generally asynchronously as most raptors begin incubation before they complete their clutches, the female broods the chicks and then starts hunting leaving the brood alone (Newton 1979, Taylor 1994). Because of their varying age, the consequence is that chicks are left unattended at different stages of development (Durant & Handrich 1998). The youngest chick is left unattended more often during its growth compared to its older siblings. Consequently, the younger and less developed chicks of a brood are confronted with more constraints, increased thermoregulatory cost and lower food intake, compared to their older siblings at the same age. In order to achieve normal growth and to fledge successfully, the younger chicks must be able to allocate resources differently from their older siblings (Nilsson & Svensson 1996). One hypothesis could be that the younger chicks allocate fewer resources to the maturation of thermogenic tissues than do their siblings. If this hypothesis is correct, there must be a difference in the behavioural responses to ambient temperature, in relation to hatching rank, between siblings at the same age.

To explore this problem, I measured nest temperature and recorded chick behaviour in broods of European barn owl Tyto alba. Barn owls have large broods, on average 4–5 chicks depending on food availability (Taylor 1994). The eggs hatch asynchronously at an average interval of 2.3 days (Durant & Handrich 1998), which creates a size hierarchy among the chicks (Roulin 1998). Body growth and plumage development are relatively slow for a bird of this size (Durant & Handrich 1998). The acquisition of homeothermy is dependent on the amount of energy available to the chicks and thus on food supply (Roulin 1998). Consequently, the hatching order and size hierarchy in a brood may influence the chicks’ thermoregulatory responses. During the brooding period, nestlings experience little variation in body temperature except when both parents leave the nest for extended periods. I studied the behavioural responses of wild broods to natural temperature fluctuations inside the nest when adults were absent. The objective was to investigate under natural conditions the influence of hatching order on the chicks’ behavioural responses to variation in temperature.

Methods

The study was conducted in eastern France (48°20’N, 7°45’E) on four barn owl broods each with 4 chicks. The nest chamber (73 x 42 x 43 cm), a wooden nest box regularly used by breeding barn owls, was equipped with an infrared video camera linked to a video recorder (Durant et al. 1996). Ambient temperature inside the chamber was monitored to the nearest 0.5°C every second at two points on opposite walls of the nestbox. The average of the two temperatures was recorded on a computer (there was no significant difference in temperature between the two spots). The computer and video-recorder clocks were synchronised, making it possible to associate temperature and behaviour. Both recordings were run continuously during the rearing period. The amount of time the chicks were left unattended was calculated each day from video analysis.

Nestlings were identified by video at hatching and followed individually throughout their development thanks to differences of development (size, feather growth). The chicks and their parents were not manipulated nor were they aware of human presence. Chick behaviour was recorded during the periods when both parents were outside the nest box. Recording was done over 2 min periods starting 2 min after the adult left, which was assumed to be long enough to observe any behavioural responses to the change in the chick’s thermal environment. Five behavioural responses to temperature were considered, classified in a rank order according to their intensity, from cold to warm:

1) Huddling and/or shivering: In huddling, the chick tries to put its head under the wing or belly of an older sibling and pushes its body against that of the other. Shivering is a tremor of the body that is usually observed when huddling is not possible.

2) Leaning together: The first stage of cold stress behaviour: the chick leans against the body of one or more other siblings. In contrast to the previous behaviour, the chick does not actively try to put itself under its sibling.

3) Staying alone: The chick is alone and shows no tremor. Its wings are kept against the body and its beak is closed. It is indifferent to ambient temperature.

4) Wings spread and/or fluttering: The first stage of heat stress behaviour: the chick increases its body surface by opening its wings and/or fluttering them, and lying on the floor.
Table 1. Average ambient temperature (± s.e.) at which different thermal behaviours of barn owl chicks are observed in relation to their rank order of hatching. Behaviour categories are: 1 = huddling/shivering; 2 = leaning together; 3 = staying alone; 4 = wings spread/fluttering; 5 = panting.

<table>
<thead>
<tr>
<th>Brood</th>
<th>Hatching order</th>
<th>Thermal behaviour 1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1</td>
<td>13.0 ± 0.5</td>
<td>15.5 ± 0.7</td>
<td>25.1 ± 0.5</td>
<td>31.6 ± 1.2</td>
<td>37.6 ± 1.5</td>
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<td></td>
<td>2</td>
<td>13.7 ± 0.7</td>
<td>16.6 ± 0.8</td>
<td>24.6 ± 0.7</td>
<td>29.4 ± 1.3</td>
<td>35.2 ± 1.5</td>
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<tr>
<td></td>
<td>3</td>
<td>14.2 ± 0.8</td>
<td>17.6 ± 0.7</td>
<td>25.5 ± 0.6</td>
<td>29.5 ± 1.7</td>
<td>34.5 ± 1.4</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>15.1 ± 0.8</td>
<td>17.9 ± 0.8</td>
<td>25.4 ± 0.6</td>
<td>30.4 ± 1.8</td>
<td>35.7 ± 1.6</td>
</tr>
<tr>
<td>B</td>
<td>1</td>
<td>19.9 ± 0.7</td>
<td>21.0 ± 0.4</td>
<td>22.7 ± 1.1</td>
<td>29.9 ± 1.3</td>
<td>33.6 ± 1.0</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>20.4 ± 0.3</td>
<td>21.9 ± 0.7</td>
<td>21.7 ± 1.1</td>
<td>27.4 ± 1.0</td>
<td>30.8 ± 1.0</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>20.7 ± 0.5</td>
<td>21.8 ± 0.7</td>
<td>25.2 ± 0.7</td>
<td>26.8 ± 1.9</td>
<td>30.0 ± 1.1</td>
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<tr>
<td></td>
<td>4</td>
<td>20.6 ± 0.3</td>
<td>22.0 ± 0.8</td>
<td>25.9 ± 0.3</td>
<td>26.8 ± 1.9</td>
<td>29.3 ± 1.0</td>
</tr>
<tr>
<td>C</td>
<td>1</td>
<td>20.5 ± 0.4</td>
<td>22.4 ± 0.7</td>
<td>25.0 ± 0.8</td>
<td>30.0 ± 0.4</td>
<td>34.3 ± 2.7</td>
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<tr>
<td></td>
<td>2</td>
<td>20.5 ± 0.4</td>
<td>22.5 ± 0.7</td>
<td>24.7 ± 0.9</td>
<td>28.4 ± 0.7</td>
<td>30.7 ± 2.6</td>
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<td></td>
<td>3</td>
<td>20.9 ± 0.4</td>
<td>22.6 ± 0.7</td>
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<td></td>
<td>4</td>
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<td>25.9 ± 0.9</td>
<td>27.7 ± 1.0</td>
<td>30.0 ± 4.5</td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td>18.0 ± 0.6</td>
<td>20.2 ± 0.8</td>
<td>27.8 ± 1.2</td>
<td>30.4 ± 2.4</td>
<td>32.6 ± 2.6</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>17.9 ± 0.5</td>
<td>19.9 ± 0.8</td>
<td>27.5 ± 1.6</td>
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</tr>
</tbody>
</table>

(5) Panting: The chick exhibits a high respiratory frequency visible by movements of the belly, the beak is open and the tongue protruding.

Each behaviour recorded was associated with the corresponding ambient temperature measured during the 2 min period. Thus, for each chick two columns of data (of c. 100 lines) were obtained relating ambient temperature (°C) and response behaviour index (1–5). The average temperature at which each behaviour was shown was calculated for each chick (Table 1). Comparisons were made using one-way repeated measures ANOVA.

**Results**

**Nest attendance and temperature**

In barn owls, only the female broods the eggs and young chicks. The first significant break in continuous brooding occurs when the female makes her first hunting trip. In this study, this happened on average 15 ± 1 days after the hatching of the first egg, which was on average 8 ± 1 days after the hatching of the fourth and last egg (Fig. 1). Before this date females rarely left the nest box. On average chicks were first left alone for the whole night 20 days after hatching of the first egg.

Nest temperature during the study ranged from 8° to 43°C and outside temperatures from 4° to 37°C.

**Behavioural responses to ambient temperature**

The average temperatures at which different thermal behaviours were observed are presented in Table 1. The pooled values for chicks of the same hatching order are presented in Figure 2. Average temperatures were significantly different between behaviour categories for every chick (Brood A, $F_{3,12} = 538.93$; Brood B, $F_{3,12} = 91.696$; Brood C, $F_{3,12} = 98.466$; Brood D, $F_{3,12} = 143.368$; all $P < 0.001$).

The cold stress responses (Behaviours 1 and 2) were observed at a significantly higher ambient temperature in the younger chicks of a brood compared to their elder siblings (Behaviour 1, $F_{3,9} = 6.157$, $P = 0.015$; Behaviour 2, $F_{3,9} = 6.643$, $P = 0.012$, Table 1 and Fig. 2). On the other hand, the heat stress responses (Behaviours 4 and 5) were observed at significantly lower ambient temperature in the younger chicks compared to their elder siblings (Behaviour 4, $F_{3,9} = 12.929$, $P = 0.001$; Behaviour 5, $F_{3,9} = 9.588$, $P = 0.004$, Table 1 and...
Fig. 2). No difference was found between siblings in the temperatures at which they showed Behaviour 3 ($F_{3,9} = 2.509$, ns).

**Discussion**

Hatching order in barn owl chicks influences their individual behavioural responses to ambient temperature variation. The younger chicks of a brood showed heat and cold stress responses at less extreme temperatures than did their older siblings (Fig. 2). This result suggests a difference in thermoregulatory capacity depending on hatching position. As food intake directly influences development, differences in food availability between siblings may affect the acquisition of thermoregulatory capacity (Mertens 1977).

**Responses to ambient temperature changes**

The zone of thermal comfort (Mercer 2001) is the range of ambient temperatures within which birds do not show specific behaviours to cope with the thermal environment. It is slightly different from the thermoneutral zone, which is the range of ambient temperature at which temperature regulation is achieved without changes in metabolic heat production or evaporative heat loss (Mercer 2001) and which cannot therefore be determined by behavioural observations. In this study, the chicks were in their zone of thermal comfort when they showed the Behaviour 3. The zone is delimited by the lowest temperature that did not induce a cold stress response (Behaviour 2) and the highest temperature that did not induce a heat stress response (Behaviour 4). Using these behavioural responses to temperature variations, the zone of thermal indifference then ranges between 20 and 31°C for the first born chick and 21 to 28°C for the last one (Fig. 2). These values differ from those found for the thermoneutral zone in fasting adults (23 to 32°C, Thouzeau et al. 1999). This indicates, taking into account the poorer isolation and smaller size of chicks, that under 23°C the chicks should use metabolic heat production to maintain their core temperature. The significant differences between the limits of the zone of thermal comfort for the various age ranks indicated that, in addition to behavioural differences, there might also be a difference in metabolic response to temperature changes. However, in the present study it was not possible to evaluate metabolic responses to temperature fluctuations.
Influence of hatching order

Hatching order is well documented to have an influence on growth (O’Connor 1977, Lesage & Gauthier 1998), as has also been suggested for barn owl chicks (Durant & Handrich 1998, Roulin 1998). In the present study, the influence of the hatching order appeared in the differences in the behavioural response to ambient temperature variations (Fig. 2). At the same age, late-hatched chicks relied more on behavioural responses to temperature variation than older ones did, as shown by the significant differences between them in their zones of thermal comfort (Fig. 2). Resorting to a behavioural response could be either the result of an inability to thermoregulate, e.g., because of poor tissue maturation, or a strategy for saving energy. Why do such differences in behaviour between chicks of different hatching order occur?

Due to the size hierarchy, access to food differs among chicks of an asynchronous brood (Newton 1979). Usually the younger chicks have poorer access to food than their older siblings and have on average a lower energy intake (Stoleson & Beissinger 1997, Roulin 1998). Such food restriction could entail a slower maturation of tissues, i.e., structural and functional changes associated with accumulation of materials such as contractile proteins in growing muscles (Visser 1998), preventing the chick from thermoregulating through heat production. On the other hand, a slower tissue maturation is a means to achieve faster growth (Hohtola & Visser 1998). Indeed in barn owls, the youngest chick of a brood has two growth constraints. During the first period of growth, the last-hatched chick must attain sufficient size to be able to eat entire prey by itself and thus be able to feed when the female is away from the nest. In the present study, females started hunting on average eight days after the hatching of the last egg, although the capacity to eat entire prey is not attained until the age of 20 days (Taylor 1994). As a consequence, the youngest chick was partially deprived of food for 12 days. This partial food deprivation of the youngest chicks is common in barn owls (Taylor 1994) and may lead to death (brood reduction, Lack 1968). However, it has been shown in the laboratory that there exists a margin in which food deprivation has no effect on the linear growth and fledging time (Durant & Handrich 1998). Consequently, partial food deprivation may trigger an increase in growth rate at the expense of tissue maturation.

Another imperative for later hatched chicks is to be able to fledge at the same time as their older siblings, a period when adults begin to give prey to the young owls outside the nest (around 60 days of age, Taylor 1994). At this stage, only the male will bring food directly to the nest. The female, on the other hand, will give the prey to an owlet only if it follows her back to the nest. Thus, unfledged chicks remaining inside the nest get a smaller share of the food supplied. To be treated equal-

![Figure 2. Average ambient nest temperatures (± s.e.) at which different thermoregulatory behaviours of barn owl chicks were observed in relation to hatching order. Data are pooled over 4 broods. Behavioural categories are: 1 = huddling/shivering; 2 = leaning together; 3 = staying alone; 4 = wings spread/fluttering; 5 = panting. * indicates a significant difference (P < 0.05) in mean temperature between the first and last hatched chick for the corresponding behaviour index.](image)
ly, the last-hatched chicks need to be able to fly, that is, to reach adult size and flight feather length at the same time as the first-hatched chicks, i.e., on average 10 days younger. Both of these two constraints require that the last-hatched chicks have a faster growth than their older siblings (Nilsson & Svensson 1996). This could be achieved by channelling part of the energy for thermoregulation to growth, assuming that thermoregulation by modification of behaviour is less expensive than metabolic heat production. To test this hypothesis, it would be necessary to obtain data on tissue maturation and thermogenesis in relation to hatching order.

**Importance of the timing of the female first foraging trip**

During their first days of life, barn owl chicks need to be brooded in order for them to maintain their body temperature. In this species, homeothermy in achieved when chicks are 15–20 days old (Taylor 1994, Durant et al. 1996). As a consequence, the female could not leave the nest before this date without adverse consequences for the chicks. Indeed the first hunting trip of the female during our study began on average 15 days after hatching (Fig. 1). The first time she spent the whole night outside the nest was only 27 days after the first chick hatched, when the youngest was only 20 days old.

What could trigger the female’s exit? As in many birds, growing barn owl chicks become more and more aggressive towards their parents and are calmed only when satiated. The increasing difficulty encountered by the male to supply enough food may accentuate this aggressive behaviour and chase the female from the nest (Durant pers. obs.). Indeed, the food requirement for a brood of 4 chicks is around 8 prey animals of vole size (c. 20 g), when the female makes her first foraging trip, calculated using the average food requirement measured on captive chicks (Durant & Handrich 1998). To this value must be added the food required by both adults, which is also provided by the male. The existence metabolism (i.e. daily metabolised energy at constant body mass) calculated for Strigiformes of 300 g (allometric coefficient 0.58, Wijnands 1984) is 233 kJ 24 h⁻¹, which corresponds to 42 g or two prey items of vole size (assuming a caloric value of 7.7 kJ g⁻¹ and an energy assimilation efficiency of 72.3 %; Durant et al. 2000). As a consequence, the male should hunt c. 12 prey (8 + 2 + 2) every night to fulfil the needs of the brood, his female and himself. The time available to hunt such a quantity of prey could be a threshold for the male. Moreover, male hunting effort may be fixed to a level where his survival is not jeopardised (Wiehn & Korpimäki 1997, Roulin et al. 1999). Consequently, the normal increase in the brood’s requirements will make it impossible for the female to feed on the male’s nest supply. The timing of the female’s first hunting trip may then be adjusted in response to the shortfall between brood requirements and the supply of food to the nest by the male (Whittingham & Robertson 1993, Taylor 1994, Durant & Handrich 1998). Indeed, it was observed that female kestrels *Falco tinnunculus* decreased their hunting effort and prey delivery rate to the nest in response to supplementary feeding (Wiehn & Korpimäki 1997).

This study unravels two important points that should be taken into account for future research. First, intra-clutch competition for access to food imposes a strong selection pressure on the last hatched chicks, which leads to a different growth strategy. Second, the timing of the female’s first exit appears to be a major threshold for the last chicks of a brood as it creates a different thermal and food environment from the one encountered by their older siblings at the same age.

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