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Development of a stable body temperature and growth rates in nestlings of three ground nesting passerines in alpine tundra

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While in the nest, altricial nestlings are provided with food and warmth. The food provides the energy for the maturation of the body, the increase in body mass, which leads to a better balance between heat gain and heat loss, and the development of a better insulating coat of feathers. As the nestling matures, its own heat generating capacity improves so that the warmth that the brooding parent provides becomes gradually less important. The rate of development of body mass, feather growth and the attainment of homeothermy varies among species (e. g. DAWSON & EVANS 1960, MAHER 1964, MORTON & CAREY 1971, DUNN 1975, CONRY 1978, MISHAGA & WHITFORD 1983).

Ground nesting passerines generally have shorter incubation and nestling periods than closely related species that nest off the ground (LACK 1968). In some species, such as larks (Alaudidae), the young leave the nest well before they can fly (HARTLEY 1946, VERBEEK 1967, MACLEAN 1970). One might expect such young to be homeothermic at an early age. However, as DUNN (1975) showed in a comparative study, the age of endothermy is closely tied to growth rate, which in turn is related to body size (RICKLEFS 1968, DUNN 1975). MISHAGA & WHITFORD (1983) cautioned that although body temperature may provide the most practical basis for comparing different species, these temperatures are not just the result of metabolic heat production and growth.

This paper compares the growth and the development of a stable body temperature under natural conditions of three coexisting, ground-nesting passerines, which differ in the placement of their nests.

Study Area and Methods

The study was conducted above tree line in the Cirque d'Anéou, Parc National des Pyrénées, France, at an altitude between 1800 and 2100 m. The three species studied were the Skylark (*Alauda arvensis*), which has an open cup nest, Water Pipit (*Anthus spinoletta*), which nests in niches so that the nest is partly concealed from above, and Wheatear (*Oenanthe oenanthe*), which nests in a short tunnel under ground.

When a brooding parent leaves the nest, the nestlings begin to cool. However, as the young lie against each other, thereby decreasing their combined surface area, the rate of cooling is slower than if they were kept as single individuals (ROYAMA 1966, MERTENS 1969, YARBROUGH 1970). Upon arrival at the nest, I quickly measured the body temperature of each young to the nearest 0.1 °C with a SCHULTHEIS quick-reading thermometer inserted orally into the proventriculus, after which the young were placed separately in the shade on the turf and protected against the wind. Sometimes, especially when the young were still small, the brooding parent flushed from the nest, but at other times the adult had been off the nest for an unknown period. To obtain the effect of exposure after the young were placed on the turf, where they remained 24 min, their temperature was read at 3 min intervals. At the end of the session each young was weighed with a pesola balance to the nearest 0.1 g and the ambient temperature was measured at about 1 cm above the ground. The length of the first primary was measured with a millimeter rule. The day of hatching was designated day 0. The data partain to 8 nestling Skylarks, 10 Water Pipits and 10 Wheatears. All birds were measured once a day at about 24 h intervals.

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Results

Body temperature of nestlings in the nest.

The mean body temperature of Skylarks and Wheatears was above 30 °C as early as day 1 (Fig. 1) and rose steadily on subsequent days. No body temperatures were obtained for 1-day old Water Pipits, but by extrapolating the data, they conformed to

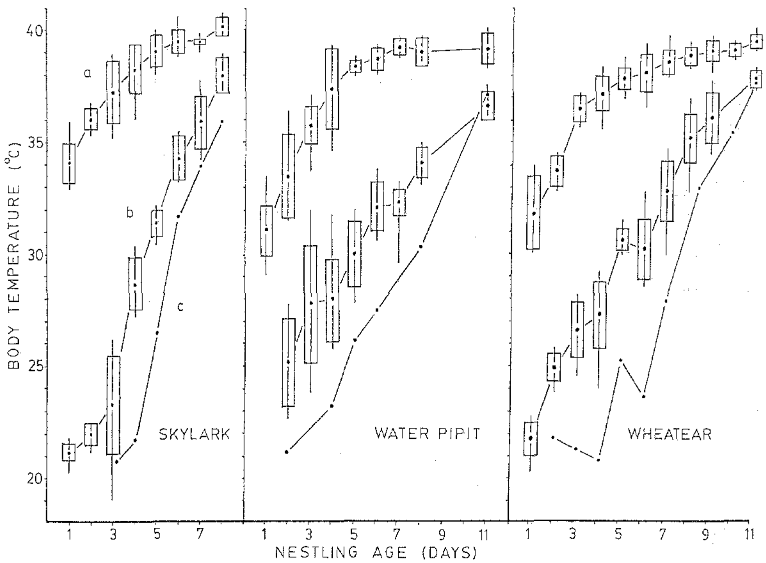

Fig. 1. Daytime body temperatures of Skylark, Water Pipit and Wheatear nestlings (a) sitting together in the nest, (b) after 12 and (c) 24 min of exposure of single birds to prevailing ambient temperatures while out of the nest (see text). The vertical line indicates the range, the black dot indicates the mean and the box represents ± 2 SD of the mean. For clarity of the figure, no range and SD are shown for curve c.

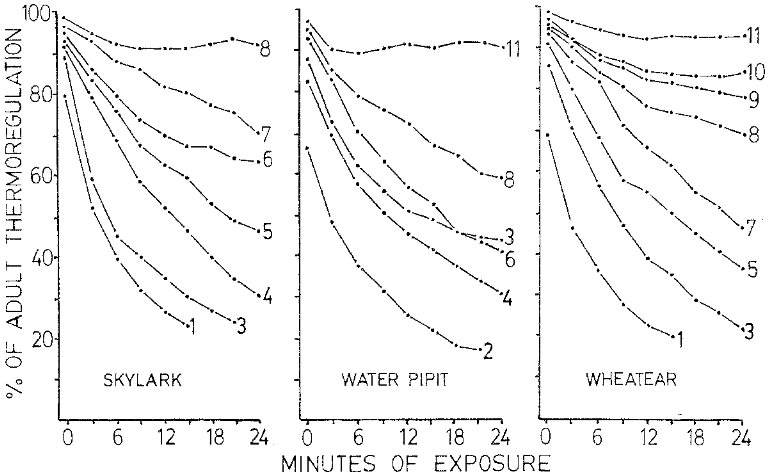

Fig. 2. Development of a stable body temperature in nestling Skylarks, Water Pipits and Wheatears exposed to low ambient temperatures. Each point is the mean temperature of 8 to 10 individuals. The data are expressed as a percentage of adult thermoregulation ability (see text). The number at the lower end of each curve indicates the age of the nestlings.

the other 2 species. The nestling temperature of Skylarks on day 1 (mean 34.1 ± SD 0.88 °C) was significantly ($p < 0.01$) higher than that for Wheatears (31.8 ± 1.62 °C), even though the ambient temperature (12.5 °C) at the time the Skylarks were measured was lower than for the Wheatears (14.7 °C). The body temperatures of the nestling Skylarks were consistently higher at all ages than those of the other two species (Fig. 1), probably because at hatching Skylark nestlings are the biggest and those of the Water Pipits the smallest of the three species. Nestling Skylarks thus retained their body heat better after the female left the nest than the nestlings of the other two species.

Body temperature of nestlings following exposure outside of the nest.

The ability to thermoregulate was standardized by calculating the difference between the body and the ambient temperature during the period of exposure and expressing this as a percentage of the adult body temperature (assumed to be 40 °C) at the prevailing ambient temperature (Dunn 1979). This avoids the effect of differences in ambient temperature at each nest and on different days. Although all 3 species showed marked improvement over time, there were clear differences.

As soon as the nestlings were taken from the nest their body temperature dropped (Fig. 2). After 12 min of exposure on day 1 the mean body temperature of two of the three species dropped to slightly above 20 °C. The body temperature in all 3 species dropped further after an additional 12 min of exposure but the total drop in temperature for each species was less than in the first 12 min. The cooling curves thus leveled off, indicating that the young were able to maintain their body temperature above ambient temperature even after 24 min of exposure.

Table 1. Nestling parameters of three ground nesting passerines.

Parameters	*Alauda arvensis*	*Anthus spinoletta*	*Oenanthe oenanthe*
Nestling period (days)	9	14	15
Approximate fledging weight (g)	24	19.5	22.5
Adult mass (g)	34	21	24
(%)[1]	0.70	0.92	0.94
½ fledging weight (days)[2]	4.24	5.03	4.85
Absolute growth rate (g/day)[3]	3.23	1.89	2.08

[1]) Fledging mass divided by adult weight; [2]) Age at which half the fledging mass is achieved; [3]) Slope of regression equation of first 5 days in Fig. 4.

After an initial drop in body temperature, single Skylark nestlings could maintain a steady body temperature (>90 % of adult body temperature) between 7 and 8 days of age. Wheatears and Water Pipits did not reach the same ability until between 10 and 11 days (Fig. 2). By extrapolation, the three curves for the Skylarks (Fig. 1) coincide at about day 10 which is the reported time of fledging in this species (Glutz & Bauer 1985). Water Pipits and Wheatears reach this point at about day 14 and 15, respectively (Glutz & Bauer 1985, Menzel 1964).

Feather growth

At hatching the skin of nestling Skylarks was blackish and much darker than the pinkish skin of Water Pipits and Wheatears. The nestling down of Skylarks was straw

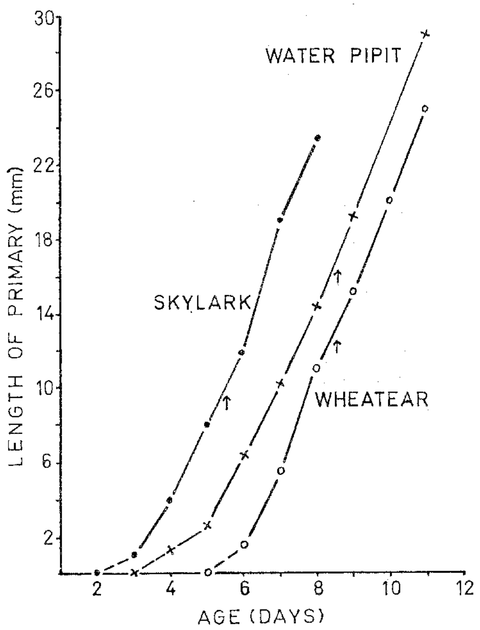

Fig. 3. Mean lengths of the innermost primary of nestling Skylarks, Water Pipits and Wheatears in relation to age. The arrow indicates the day on which the primaries emerged from the sheaths.

coloured, much paler than the light grey down feathers of Water Pipits and the dark grey ones of Wheatear nestlings. In all three species, body feathers emerged from their sheaths earlier than those of the primaries and secondaries. The emerged primaries were measurable between day 2 and 3 in Skylarks, 3 and 4 in Water Pipits and 5 and 6 in Wheatears.

The primaries of nestling Skylarks broke their sheaths 3 days earlier than those of Water Pipits and Wheatears, when the nestling Skylarks had grown to half their adult weight (Table 2). Water Pipit and Wheatear primaries emerged from their sheaths relatively late in the nestling period, in contrast to those of Skylarks (Table 2). Although Water Pipit and Wheatear primaries broke their sheaths on the same day, Water Pipit primaries were in their sheaths for 5 days, while those of Wheatears and Skylarks were in sheaths for only 3 days after emergence from the skin (Fig. 3).

Table 2. Mean length (mm) of innermost primary, mean mass (g) of nestlings and percent of adult mass (g) achieved at the age (days) when the primaries emerge from the sheaths.

	Alauda arvensis	*Anthus spinoletta*	*Oenanthe oenanthe*
Age primaries emerge from sheaths	5–6	8–9	8–9
Length of primary ($\bar{x} \pm SD$)	10.3 ± 2.9	15.9 ± 2.6	13.2 ± 2.7
Weight of nestlings ($\bar{x} \pm SD$)	17.2 ± 1.7	17.5 ± 1.1	19.4 ± 1.2
% of adult body weight achieved	50.6	83.3	80.8

Body mass

The nestlings of the three species were not weighed on the last few days before fledging to avoid premature nest departure. Fledgling mass was thus estimated by extrapolation of the growth curves (Fig. 4). Taking the straightest portion of each growth curve (Fig. 4), and regressing the points on the curve, Skylarks added the most mass per day and Water Pipits the least (Table 1). The body mass attained at fledging, ex-

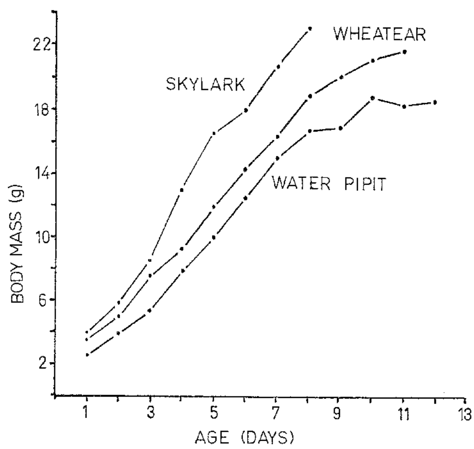

Fig. 4. Mean body mass of nestling Skylarks, Water Pipits and Wheatears in relation to age.

pressed as a percentage of adult mass, was similar in Water Pipits and Wheatears, which fledged close to adult mass, and by comparison much lower in Skylarks, which fledged relatively early (Table 1).

Discussion

Although 50 % of the fledging weight is reached earlier in Skylarks than in Water Pipits, the difference between them (¾ day) is small compared to the range ind fledging age (6 days). Thus, despite differences in the nestling periods, selection for rapid attainment of half the fledging mass in all three species is apparent. Once that point is reached, the three species diverge in the amount of time required until they fledge. While Skylarks stay another 4.8 days before fledging, Water Pipits and Wheatears stay another 8.9 and 10.2 days, respectively. The advantage of gaining mass as soon as possible might be that the young will rapidly fill the nest cup, which is thermally advantageous, because peripheral nestlings will be insulated by the nest. In addition, with any increase in size, the volume to surface area of the nestlings changes in favor of better heat retention. MORTON & CAREY (1971) develop the same argument in their study of White-crowned Sparrows (*Zonotrichia albicollis*).

The early appearance of the primaries, and the early emergence of the feather vanes, provides nestling Skylarks with a steadily improving insulating coat at an earlier age in their development than the other two species. The same rapid growth of feathers and early breaking of the sheaths occurs in Horned Larks (*Eremophila alpestris*; VERBEEK 1967, BEASON & FRANKS 1973, MAHER 1980). This may be adaptive in species with open ground nests, especially in cool regions. However, as Skylarks are widely distributed (HARRISON 1982), inhabiting both cold and warm regions, rapid attainment of better insulation may have evolved not only to conserve body heat but also to keep environmental heat out when the nestlings are exposed to too much direct solar radiation. Careful nest placement (VERBEEK 1967, 1981, MACLEAN 1970) helps to avoid direct solar radiation but it is not fully effective. Water Pipits and Wheatears appear to have evolved a different approach. They delay the growth of primaries, more so in Wheatears than in Water Pipits. The delay may be related to placement of the nest (VERBEEK 1970, 1981), from which the sun and wind are excluded, especially in the Wheatear nest. The body heat presumably is retained longer after the brooding parent departs, thus allowing a relaxation of the need to grow feathers rapidly. The three species thus show different modes of development. In the early stages of development Skylark nestlings appear to shunt relatively more energy into feather growth than body growth, while Wheatears do the reverse and Water Pipits follow an intermediate course.

LINSDALE (1936) noticed a correlation between the color of the nestling down and the nest lining and the degree of concealment of the nest. Nestlings in open nests tended to have light coloured down while those in enclosed nests had dark down. The same correlation is shown in the species reported here. To what extent the dark skin of Skylarks and Horned Larks (DUBOIS 1936) plays a role in absorbing radiant energy is unknown but it may be important.

One presumed advantage of fledging early is to scatter the brood, thus reducing the chance of losing all the young to predation. Fledging prior to the time of full temperature control would be dysgenic, as it would be inefficient to have to brood the young individually out of the nest. The corollary is that young that fledge early relative to their overall development should at least be capable of maintaining their body temperature close to that of the adults. DUNN (1975) refers to the age at which endothermy is reached, while the brood is in the nest, as the "effective age of endothermy". By taking the young out of the nest and exposing them individually to cool ambient temperatures, one can establish the "physiological age of endothermy" (DUNN 1975). Although effective endothermy is attained before physiological endothermy, it is the latter, along with overall maturation of the body, which determines whether a nestling can fledge or not. Early attainment of effective endothermy frees the parents from their brooding duty and allows them to spend more time to gather food, while early attainment of physiological endothermy, which is related to overall growth rate (DUNN 1975), allows the nestlings to fledge as soon as possible. As stated, early fledging may reduce predation, but it also allows the young to search for a better microclimate, which includes both seeking and avoiding certain ambient conditions. Although Skylark nestlings leave the nest as soon as they are homeothermic, nestling Water Pipits and Wheatears stay in the nest several days beyond that stage in their development. The attainment of physiological endothermy (sensu DUNN 1975) thus allows early nest departure but does not dictate it. That some ground nesting species stay in the nest beyond the age of physiological endothermy may be possible because of a safe nest site.

Summary

The mass gain, feather growth and development of a stable body temperature in nestlings of three ground nesting passerines — the Skylark (*Alauda arvensis*), Water Pipit (*Anthus spinoletta*) and Wheatear (*Oenanthe oenanthe*) — were studied in the alpine meadows of the western Pyrenees. When left together in the nest, individual Skylark nestlings had a stable body temperature of about 39 °C by day 5, Water Pipits by day 6—7 and Wheatears by day 7—8. Individual nestlings, taken out of the nest and exposed to low ambient temperatures, could maintain a high body temperature (90 % of adult levels) at an age of between 7 and 8 days (Skylark), and 10 and 11 days (Water Pipit and Wheatear, respectively). Feather growth was fastest in Skylarks. As the young in this species sit in exposed nests, early growth of feathers may help to retain heat or exclude solar radiation depending on the ambient conditions. Body mass gain is fastest in Skylarks and slowest in Wheatears and Water Pipits, which correlates with their nesting mode. All three species attain half their fledging weight between 4.2 and 5.0 days, regardless how long they remain in the nest subsequently.

Zusammenfassung

Massenzunahme, Federwachstum und Entwicklung einer konstanten Körpertemperatur wurde bei den Nestlingen dreier bodenbrütender Singvögel in den alpinen Matten der westlichen Pyrenäen untersucht, nämlich bei Feldlerche, Wasserpieper und Steinschmätzer. Wenn die Jungen zusammen im Nest bleiben, erreichen Feldlerchen am 5., Wasserpieper am 6.—7. und Steinschmätzer am 7. bis 8. Tag eine konstante Körpertemperatur von etwa 39 °C.

Einzelne aus dem Nest genommene und niedriger Umgebungstemperatur ausgesetzte Junge können eine hohe Körpertemperatur (etwa 90 % der ad.) im Alter von 7–8 (Feldlerche) bzw. von 10–11 Tagen (Wasserpieper, Steinschmätzer) aufrecht erhalten. Das Federwachstum war bei der Feldlerche am schnellsten. Da bei dieser Art die Jungen in offenen Nestern sitzen, dürfte ein frühes Federwachstum eine hohe Bedeutung für die Isolation des Körpers gegenüber der Umgebung besitzen. Die Zunahme der Körpermasse ist bei der Feldlerche rascher als bei Wasserpieper und Steinschmätzer. Die Hälfte der Körpermasse zum Zeitpunkt des Ausfliegens wird bei allen drei Arten im Alter von 4,2 bis 5,0 Tagen erreicht, unabhängig von der Länge der Nestlingszeit.

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