NESTLING GROWTH AND THERMOREGULATORY DEVELOPMENT IN SUBALPINE DUSKY FLYCATCHERS

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ABSTRACT.—The Dusky Flycatcher (*Empidonax oberholseri*), a small, open-nesting Neotropical migrant, is a relatively common summer inhabitant of subalpine environments in the western and southwestern United States. Nestling growth and development of thermoregulation were studied in a population at Tioga Pass (3,000 m) in the eastern Sierra Nevada of California. Despite the selective advantages that might be expected from accelerating rates of growth and thermoregulatory development, in an environment where the season was relatively short and cold temperatures and inclement weather were common, there was little evidence of adaptive modification in either of those parameters; growth rates were comparable to those of other tyrant flycatchers. Feather eruption began around day 5, brushing in dorsal and ventral tracts began two days later, and brushing of the flight feathers around day 9. Asymptotic body masses were attained around day 12, but nestlings did not fledge for another 4 to 5 days. The physiological development of endothermy was closely correlated with increases in body mass and accompanying decreases in surface-area-to-volume ratio and age, but was not significantly correlated with changes in plumage development, when mass and age were statistically controlled. On exposure to ambient temperatures between −3 and 5°C for 10 min (roughly twice as long as the average female bout of inattentiveness), individual nestlings were unable to prevent deep hypothermia until after day 7. Homeothermy, at 80% of adult levels, was not attained until after day 12, although broods of nestlings maintained relatively stable body temperatures as early as day 5. Whereas clutch sizes in this population generally ranged from two to four eggs, the most stable thermal environments were provided by broods of three or four chicks. Although broods of nestlings were generally able to maintain temperatures within 5°C of adult levels, temperature profiles during storms indicated a remarkable capacity for nestlings to tolerate temperatures in the nest as low as 15°C for periods as long as 4 h without apparent ill effect. *Received 19 May 1999, accepted 8 August 2000.*

IN MANY VERTEBRATES, accelerated growth is positively correlated with vulnerability during the juvenile stage (Williams 1966, Case 1978). In birds whose young develop in relatively exposed nest sites, this is often reflected in early thermoregulatory development and early mobility (Morton et al. 1972, Austin and Ricklefs 1977, Finch 1984). Altricial birds are particularly vulnerable during the nestling period, depending completely upon parental care for warmth, food, and protection from the elements. To escape predators or weather, chicks of open-nesting species must quickly develop in size and degree of neuromuscular development and mature physiological function that is necessary for survival outside the nest. The ability to maintain elevated body temperatures is an important correlate of this, enabling efficient physiological responses and the rapid, co-ordinated movements needed for locomotion and feeding. Homeothermy tends to occur at a lower percentage of asymptotic body mass than in cavity nesters of similar adult body size (Visser 1998). Emerging adult capabilities in those areas do not come without costs, however. The energy invested in activities such as thermoregulation is unavailable for growth and tissue development, as indicated by the slower growth rates that occur in tissues with a high degree of mature function (Ricklefs 1979, Visser and Ricklefs 1993, Hohtola and Visser 1998, Ricklefs et al. 1998).

The geographical trends for rapid growth in temperate-zone birds, as compared with tropical and subtropical species (Nice 1954, Lack 1968, Ricklefs 1968, Klaasen and Drent 1991) and in species breeding in areas where they are relatively exposed to predators or weather, form the basis of the view advocated first by Lack (1948, 1954, 1968) and others since (Ricklefs 1968), that environmental factors are the

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driving selective force behind those patterns. Further, those ecological hypotheses postulate that growth rates are shaped by environmental pressures such as predation, weather, and food supply, largely through their effects on nestling mortality (O'Connor 1977, 1978; Ricklefs 1983).

Tests of those ideas are often complicated, however, by the taxonomic biases that accompany geographical comparisons (see, for example, Ricklefs et al. 1998). Regional comparisons between growth rates in temperate and tropical zones can be biased by the zoogeographical dominance of some families in certain regions (Vuilleumier 1975). Shared attributes within families often extend to types of nest sites, foraging modes. and anatomical specializations for feeding and locomotion (see, for example, Traylor and Fitzpatrick 1982, for the Tyrannidae) further obscuring effects of environmental factors on development. Perhaps in part due to those factors, attempts to test the validity of the ecological hypotheses have sometimes yielded equivocal results. In some studies, there is evidence to support the idea that rates of mortality and development are related (Bosque and Bosque 1995, Ricklefs et al. 1998); in others, fledging age but not growth rates appear to be related to nestling mortality rates (Maher 1964; Ricklefs 1969a, b; King and Hubbard 1981); and in still others, there is no support at all (Ricklefs 1969a, c, 1976, 1982). As a result, alternative hypotheses have been developed to explain interspecific variability in growth. Of those, one set revolves around constraints on development imposed by energetics of parental effort (Ricklefs 1968, Drent and Daan 1980), and another focuses on potential effects of anatomical and physiological constraints upon development (Ricklefs 1969c, 1983, 1984; Ricklefs et al. 1998).

Because the nestling period and age of fledging depend on a number of growth-related parameters, including overall rates of development and tissue maturation and the levels of functional maturity attained at each stage of growth, studies of natal development in those environments continue to provide information relevant to understanding selective factors that have shaped patterns of avian growth. Data on growth and thermoregulatory development from a greater diversity of species, particularly high-latitude or high-altitude members of tropical groups and tropical members of predominantly temperate-zone families, enable interspecific comparisons that can be helpful in differentiating between those hypotheses.

This study focuses on growth and development of thermoregulation in the Dusky Flycatcher (*Empidonax oberholseri*), a small (ca. 10 g), insectivorous Neotropical migrant that breeds in montane environments throughout western North America (Johnson 1963, Sedgwick 1993). This species builds open-cup nests in a variety of habitats ranging in elevation from around 1,000 m in the northernmost parts of its range, to over 3,000 m in the south (Johnson 1963). In the eastern Sierra Nevada of California, it is the only tyrant flycatcher that routinely breeds above 3,000 m (Gaines 1988). Thus, an interesting opportunity is provided for investigating the relationship between ecological setting and patterns of growth and thermoregulatory development. Assuming that risk of mortality during the nestling period is an important selective factor in the evolution of growth patterns, several predictions might be made with regard to the pattern of growth and thermoregulatory development that should be most advantageous in a high-altitude environment. If growth rates are sensitive to such selection, they should be more rapid in this species than in low-latitude or low-altitude congeners, and the nestling period should also be shortened. Similarly, because ambient temperatures decrease with altitude, the age at which homeothermy is attained might be expected to occur earlier in this species than in those of the same size in more favorable environments. If, however, growth is not sensitive to those factors but is constrained by internal factors as suggested by Ricklefs et al. (1998), the pattern of development in *E. oberholseri* should be more similar to that in other tyrannids, irrespective of environment. Growth and thermoregulatory development in this species is presented in the contexts of individual physiological development, the brood environment, and environmental factors such as inclement weather.

MATERIALS AND METHODS

Growth and thermoregulation were studied in 192 nestling *E. oberholseri* from May through August over a 5 year period (1981 through 1985) at Tioga Pass, Mono County, in the eastern Sierra Nevada of California. The study site consisted of two glaciated, con-

TABLE 1.   List of abbreviations used in text.

Abbrev.	Definition
T_b	Core body temperature, °C
T_a	Ambient temperature, °C
ΔT_b	Temperature difference between body and ambient $(T_b - T_a)$, °C
T_s	Skin temperature, measured beneath wing, °C
$T_{brood-1}$	Brood temperature at start of experiment, after flushing female, °C
$T_{brood-2}$	Brood temperature at end of 10 min of cold exposure, °C
ΔT_{brood}	Change in brood temperature over 10 min testing period $(T_{brood-2} - T_{brood-1})$
T_{egg}	Nest temperature, as measured by thermocouple-implanted egg, °C
$P6_T$	Total length of left 6th primary (counted from outermost, 10th primary in)
$P6_{Pin}$	Length of ensheathed portion of left 6th primary
$P6_B$	Brush length of left 6th primary
Md_T	Average total length of mid-dorsal feathers
Md_{Pin}	Average length of ensheathed portion, mid-dorsal feathers
Md_B	Average brush length of mid-dorsal feathers
Vt_T	Average total length of mid-ventral feathers
Vt_{Pin}	Average length of ensheathed portion, mid-ventral feathers
Vt_B	Average brush length of mid-ventral feathers
$R1_T$	Total length of left central rectrix
$R1_{Pin}$	Length of ensheathed portion of left central rectrix
$R1_B$	Brush length of left central rectrix

necting valleys that run roughly north–south and east–west. The area ranges in elevation from 2,857 m at its lowest boundary (Ellery Lake) to about 3,150 m part way up the slopes of the ridges surrounding the two valleys, with an abundance of habitat suitable for *E. oberholseri* throughout the area. Nests were situated in a variety of plant species, including willow (*Salix* spp.), aspen (*Populus tremuloides*), wild currant (*Ribes* spp.) and pine (*Pinus contorta, P. albicaulis*), and varied considerably in height, position, and degree of exposure to the elements.

Growth was monitored in nestlings during each of the five years of the study and thermoregulatory development was documented from 1981 to 1984. Nests were located during construction, and after completion were checked daily for clutch starts. Hatching generally occurred on the fifteenth or sixteenth day of incubation, and was preceded a day ahead by pipping, which began with small star-shaped extrusions on the surface of the shell. In most cases, the first visit on the day of hatching (designated day 0) was made within 3 h of emergence. In nests that already contained day 0 chicks when visited, the probable time of hatching could be established within a few hours by comparison with descriptions of a reference group of nestlings for which hatching times were known for certain.

Each hatchling was marked with a waterproof felt-tipped marker and the center or rear toenail of either the right or left foot clipped to correspond with its hatching order. Toenails were reclipped later if necessary, but in most instances, were clearly distinguishable until fledging at day 16 or 17. Chicks were weighed to 0.01 g on an Ohaus triple-beam balance at the time of discovery and on alternate days for the rest of the nestling period. Measurements of plumage were taken to the nearest 0.5 mm, from the base of the feather to the tip, using a thin, flexible, plastic millimeter ruler. In 1983 and 1985, chicks were sexed by laparotomy and banded with numbered aluminum bands obtained from the U.S. Fish and Wildlife Service. Weights obtained after sexing were not included in analyses of growth.

Nestlings were cold stressed for 10 min at ambient temperatures (T_a) as solitary individuals (1981, 1982) or as broods (1983, 1984). All abbreviations and symbols for measurements are defined in Table 1. Broods used as controls for effects of temperature stress on growth rates were weighed and measured daily or at 2–3 day intervals. No differences in growth were seen between nests that were visited daily and those visited at longer intervals. However, in order to minimize any possibility that growth might be affected, nestlings used in cold stress experiments were tested on alternate days. Because mean weights and feather lengths for each day of age were not significantly different between cold-stressed and control chicks (*t*-tests, $P > 0.05$), the two groups were combined for analysis. Visits to each nest were made between 0530 and 0800 PDT when T_a were between −3 and 5°C. Chicks being tested individually for physiological development of endothermy were removed from the nest and placed in separate cardboard boxes (7 × 11 × 4 cm). Behavior and posture were noted and at the end of 10 min, deep body (T_b) and skin temperatures (T_s) were recorded along with body weights and feather lengths. In 1981, temperatures of nestlings were taken orally with a telethermometer (Yellow Springs) and thermistor probe coated with vaseline and threaded into the proventriculus. In 1982 and

1983, temperatures were taken with a quick-register-ing, small diameter thermocouple (Bailey RET-3 ball-tipped probe) inserted into the cloaca. In addition, beginning in 1982, skin temperatures were taken with a Bailey SST-2 skin probe (surface diameter of 0.5 cm) pressed flat against the ilium until a stable temperature registered.

Brood temperatures ($T_{brood-1}$) were taken (1982–1984) immediately after the female was flushed from the nest. A quick-registering ball-tipped probe was inserted into the center of the clump of chicks and pressed against the ventral surface or side of each one, beneath the wing and above the lung. In 1982, cloacal temperatures measured before the chicks were removed for cold stress were also used to rep-resent $T_{brood-1}$. By either method, temperatures did not vary among chicks as long as measurements were taken quickly. In 1983 and 1984, the ability of whole broods to thermoregulate was tested as a function of brood size, nest environment, and brood age. Brood age was defined as mean age of all chicks in the brood, rounded to the nearest integer, and expressed as "brood age x" or "age x" to distinguish it from the actual age of individual nestlings (day x). Nests were visited between 0530 and 0800 PDT as in pre-vious work, but as soon as the female was flushed, the maximum temperature of the chicks was record-ed ventrally and beneath the wings. Following 10 min of exposure to T_a, their temperature was again recorded ($T_{brood-2}$). The temperature differential that occurred during that time period (ΔT_{brood}) was used to assess the thermoregulatory development of chicks in the context of their natural nest environ-ment. Ten min of cold exposure was longer than av-erage maternal absence, but still remained well with-in the range of observed off bouts; the average time off the nest for a female with chicks being about 6 min (calculated from nests where egg temperatures in nests with chicks were being recorded). Only fe-males were observed to brood, although both sexes fed chicks.

Measurements of primary 6 (P6), rectrix 1 (R1), and average measurements of mid-dorsal (Md) and mid-ventral (Vt) contour feathers were used to de-scribe plumage development. P6 was counted from the outermost (10th) primary in, and R1 represented the central pair of rectrices. Measurements of mid-dorsal and mid-ventral contour feathers represent an average length of feathers in those regions because it was difficult to get the same ones repeatedly. Feather lengths for all tracts were divided into brush length ($P6_B$, Md_B, Vt_B, $R1_B$) and pin length ($P6_P$, Md_P, Vt_P, $R1_P$). Brush length was defined as the length of the unfurled portion of the feather terminus, to the near-est millimeter, taken with a flat ruler. Pin length was defined as that portion of the growing feather still ensheathed. Total length ($P6_T$, Md_T, Vt_T, $R1_T$) was the sum of both. Analyses of body temperature were performed on both absolute body temperature (T_b)

and the temperature difference between nestling T_b and T_a after 10 min of exposure (ΔT_b).

Partial correlation analyses of T_b and ΔT_b with age, body mass, and feather development were conduct-ed on nestlings grouped by each of three stages of thermoregulatory development, in order to deter-mine the amount of variance in T_b that was attrib-utable to each of those factors. The first (phase I: in-ertial stage) consisted of nestlings from 0.9 to 5.5 g, the second (phase II: early regulation stage) consist-ed of nestlings from 5.5 to 8.5 g, and the third (phase III: late regulation) encompassed nestlings heavier than 8.5 g. Each nestling was generally represented only once during each phase of growth. Statistical analyses were performed using SPSS, BMDP, and SYSTAT statistical software packages. Means are re-ported as ±SD in text, or as ±2 SE in figures, unless otherwise noted. Two-segmented linear regressions (Yeager and Ultsch 1989) were used to determine transition points from thermal conformity to regulation.

<center>RESULTS</center>

GROWTH

Accumulation of body mass.—Growth was sig-moidal in young *E. oberholseri*, increasing from a mean mass (±SD) of 1.19 ± 0.14 g on day 0, roughly 10% of the mean adult mass of 11.5 ± 0.9 g ($n = 15$ females, 2 males), to a mean mass of 11.1 ± 0.8 g on day 12 (Fig. 1A). Because most birds had achieved over 90% of their as-ymptotic mass by this age, day 12 was used as a cutoff date in the calculation of logistic growth rate constants (see below). Between days 12 and 16, further increases were slight, and weight profiles for individuals indicated that masses usually stabilized by day 14, un-dergoing small daily fluctuations until fledging two or three days later. Fledging generally took place on day 16 or 17, but could occur as early as day 14 if broods were disturbed. In one brood of three, the youngest was day 12 when fledging occurred, but it was not known whether that chick survived.

Using the method of Ricklefs (1967), the growth curve in Figure 1A was transformed into a straight line using logistic conversion factors based on an asymptotic estimate of 11.7 g, which yielded the linear regression of best fit. The logistic growth rate constant (K) deter-mined for *E. oberholseri* from those data was 0.425, with rates calculated for separate years ranging from 0.387 to 0.448. Using the same as-
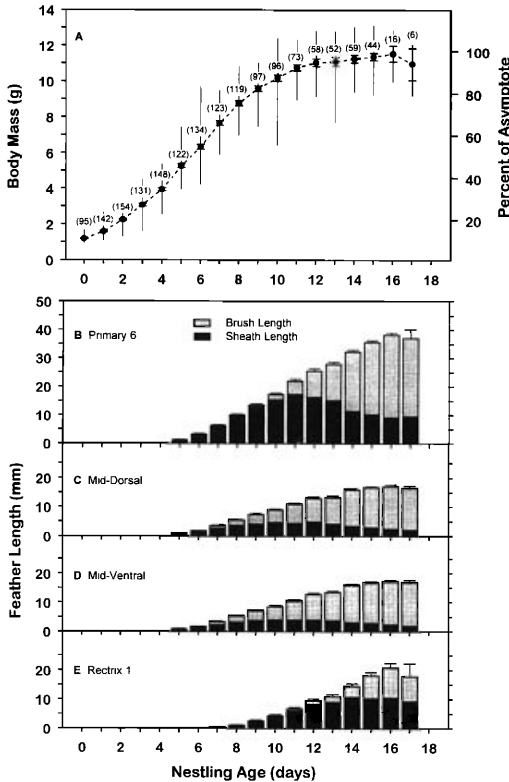
FIG. 1. Mean body mass (A), feather growth in primary 6 (B), mid-dorsal and mid-ventral contour tracts (C,D), and rectrix 1(E) for nestling *E. oberholseri* by day of age. Uncapped vertical lines (A) indicate range of values observed at each age, capped vertical lines represent ±2 SE above and below the mean (A) or above the mean (B–E) and values in parentheses indicate the sample size of nestlings weighed and measured at each age. Black bars (B–E) indicate the length of the ensheathed portion of feathers, light shading indicates the length of the brush.

ymptote (11.7 g), the ratio of asymptotic to adult mass was 1.02.

Feather development.—External indications of plumage development began with light pigmentation under the skin in some tracts as early as late day 2, followed by the appearance of beading and darkening pigmentation as feathers approached eruption. Eruption of the primaries and feathers of the mid-dorsal and mid-ventral regions did not begin until late day 4, but had occurred in nearly all day 5 chicks (Fig. 1B–D). Variation in time of feather emergence may have been partly a function of imprecise aging; nestlings that hatched during the night

or the previous evening were up to 8 h older than those hatching the next morning.

Eruption in primaries and contour feathers occurred simultaneously, reaching maximum growth rates by day 11, although only the contour feathers had completed development by fledging five or six days later. After eruption, the 6th primary (P6) lengthened at a rate of about 1 mm per day between days 4 and 6, increasing to roughly 3.5 mm per day for the rest of the nestling period. By fledging, its length was still only 58% of yearling lengths (1963), although more than 70% of the primary was unsheathed (Fig. 1B). Contour feathers (Fig. 1C, D) lengthened at around 2 mm per day, but were fully grown and brushed over 75% of their lengths, by days 13 and 14. At this age, overall body coverage by brushing was almost complete. Because the mid-ventral and mid-dorsal contours erupted at the same time and closely paralleled each other in rates of growth and brushing, the mid-dorsal contours were used to represent overall contour development in subsequent analyses. The rectrices were the last major feathers to erupt (Fig. 1E). The central pair (R1–1) began to emerge between days 6 and 8 and grew at a rate of between 2 and 3 mm per day from day 9 on, attaining roughly a quarter of yearling lengths by day 15.

Relationship between body mass and plumage development.—Two questions were investigated with regard to mass and feather development at a given age. The first was whether heavier nestlings at a given age were developmentally more advanced, leading to accelerated feather growth. The second dealt with the extent to which pin-feather development might influence variation in age-specific body mass through effects on fluid balance.

The first question was addressed by analyzing the partial correlation between body mass and total feather length while at the same time controlling for age. We expected that if plumage development was more advanced in heavier nestlings, then total feather length should positively correlate with mass when age was held constant. Total feather length in each tract was indeed positively correlated with body mass for all three phases of growth, when age was controlled (Table 2). During phase II (5.5 to 8.5 g), between 22 and 30% of variation in feather length was associated with variation in body mass (ventral contours, r =

TABLE 2.   Zero-order, marked with (—) for control column, and partial correlations (r) for body mass with total feather length (Md_T, Vt_T, $P6_T$, $R1_T$) and ensheathed pin feather length (Md_{Pin}, Vt_{Pin}, $P6_{Pin}$, $R1_{Pin}$), while controlling for the effects of nestling age and/or total feather length. Separate analyses conducted for each of the three phases of growth are discussed in text. Tracts represented are the mid-dorsal, mid-ventral, primaries and rectrices. During phase I (0.5–5.5 g), feathers were completely ensheathed, hence pin length was the same as total.

Feather variable	Control var.	Body mass with feather length					
		0.5–5.5 g		5.5–8.5 g		8.5 g+	
		r	P	r	P	r	P
Md_T	—	0.58	<0.001	0.78	<0.001	0.75	<0.001
	Age	0.22	<0.001	0.49	<0.001	0.38	<0.001
Vt_T	—	0.49	<0.001	0.77	<0.001	0.75	<0.001
	Age	0.14	<0.001	0.47	<0.001	0.38	<0.001
$P6_T$	—	0.62	<0.001	0.80	<0.001	0.75	<0.001
	Age	0.27	<0.001	0.55	<0.001	0.40	<0.001
$R1_T$	—	—	—	0.34	<0.001	0.69	<0.001
	Age	—	—	0.02	NS	0.21	<0.001
Md_{Pin}	—	0.58	<0.001	0.69	<0.001	−0.06	NS
	Age	0.22	<0.001	0.44	<0.001	0.21	<0.001
	Age, Md_T	—	—	0.04	NS	0.09	0.025
Vt_{Pin}	—	0.48	<0.001	0.56	<0.001	−0.03	NS
	Age	0.14	<0.001	0.31	<0.001	0.19	<0.001
	Age, Vt_T	—	—	−0.11	0.030	0.05	NS
$P6_{Pin}$	—	0.62	<0.001	0.81	<0.001	0.17	<0.001
	Age	0.27	<0.001	0.57	<0.001	0.29	<0.001
	Age, $P6_{Pin}$	—	—	—	—	0.20	<0.001
$R1_{Pin}$	—	—	—	0.36	0.004	0.72	<0.001
	Age	—	—	0.02	NS	0.35	<0.001
	Age, $R1_T$	—	—	—	—	0.29	<0.001

0.47; primary 6, $r = 0.55$). However, by phase III (8.5+ g), the amount of variation in plumage length that continued to correlate with body mass was only about 4–16%, depending upon the feather tract. The decline in partial correlations between phases II and III indicated that body mass explained less of the variation in plumage development in older chicks and that developmental differences did not persist over the nestling period. They also suggested that some proportion of that correlation may have been influenced by increases in the fluid content of developing feathers.

The extent to which age-specific body mass might be influenced by fluid content of the pin feathers was addressed by examining the partial correlations between body mass and ensheathed feather length, while controlling for age and total feather length (Table 2). We anticipated that if the correlation between body mass and feather development was largely because of the increased fluid content of the growing plumage, then body mass should continue to positively correlate with ensheathed feather length when age and total feather length were controlled; furthermore, that correlation should decline as feathers began to brush. During phase I, when eruption in most tracts had yet to begin and feather development was still largely confined to areas beneath the skin, only 2–7% of variation in body mass could be attributed to variation in length of the pin-feathers (mid-dorsal contours, $r = 0.22$; mid-ventral contours, $r = 0.14$; primary 6, $r = 0.27$; $P < 0.0001$ for all). During phase II, however, when all tracts were actively erupting or had already emerged, the proportion of variation in mass that correlated with pin development increased to 10% in mid-dorsal contours ($r = 0.31$, $P < 0.0001$) and 32% in primary 6 ($r = 0.57$, $P < 0.0001$). By phase III, partial correlations between body mass and pin length had declined in all three tracts as feathers began to harden ($P6_{Pin}$: $r = 0.20$, $P < 0.0001$; Md_{Pin}: $r = 0.09$, $P < 0.05$; Vt_{Pin}: $r = 0.05$, $P > 0.1$). The rectrices, in which development was most rapid and the shafts still soft during phase III, were the only tract for which there was an increase in the partial correlation for mass and pin length between phase II ($r = 0.02$, $P > 0.1$) and

phase III ($r = 0.29$, $P < 0.0001$). Together, those data indicate that not only was feather development slightly accelerated in larger nestlings, but the extent of pin-feathering during phases I and II in particular appeared to influence variation in age-specific body mass.

THERMOREGULATION

Development of physiological endothermy.—During the first nine days, mean T_b in cold-stressed nestlings increased at a rate of slightly less than $2°$ C per day, from $10.6 \pm 1.0°C$ on day 0 to $26.4 \pm 2.1°C$ on day 9 (linear regression: $T_b = 1.836$ (Age) $+ 10.218$, $r = 0.92$, $F = 980.97$, df = 1 and 159, $P < 0.0005$, Fig. 2A). Daily improvements in T_b between consecutive days were greatest between days 9 and 11, after which temperatures changed more slowly ($T_b = 1.442$ (Age) $+ 16.701$, $r = 0.61$, $F = 40.51$, df = 1 and 66, $P < 0.0005$), peaking at $36.0 \pm 2.0°C$ on day 14, the latest age for which these data could be obtained; this was approximately 86% of the mean adult T_b of $42.6 \pm 0.8°C$ ($n = 15$).

The ability for nestlings to maintain elevated T_b at low T_a (ΔT_b) followed the same pattern ($\Delta T_b = 1.904$ (Age) $+ 5.800$, $r = 0.89$, $F = 604.491$, df = 1 and 159, $P < 0.0005$), increasing from $5.9 \pm 0.86°C$ at day 0 to $29.4 \pm 3.56°C$ by day 11 (Fig. 2B). Significant increases in ΔT_b between adjacent days occurred on days 2, 6, and 8, and then daily through day 11. Roughly 20 to 30% of adult ΔT_b was attained between day 1 and day 2, with relatively small improvements occurring over the rest of the first week. The greatest daily changes occurred between days 9 and 11, with ΔT_b leveling off around $31°C$ ($\Delta T_b = 0.987$ (Age) $+ 18.162$, $r = 0.37$, $F = 10.49$, df = 1 and 66, $P < 0.005$). Relative to total mass accumulated during the nestling period, the steepest increases in ΔT_b occurred when nestlings were between 10–20% and 80–100% of their asymptotic weights (Figs. 1A, 2B). By day 14, the age of earliest fledging when disturbed, ΔT_b was still only 83% of adult levels.

In addition to its relationship with age, T_b was highly correlated with body mass ($r = 0.93$, $P < 0.0005$; Fig. 3) and the ratio of surface area to volume ($r = -0.91$, $P < 0.0005$). The ratio of surface area to volume declined steeply (SA:Vol $= -0.583$ (Age) $+ 7.537$, $r = -0.953$, $F = 849.86$, df = 1 and 86, $P < 0.0005$) until day
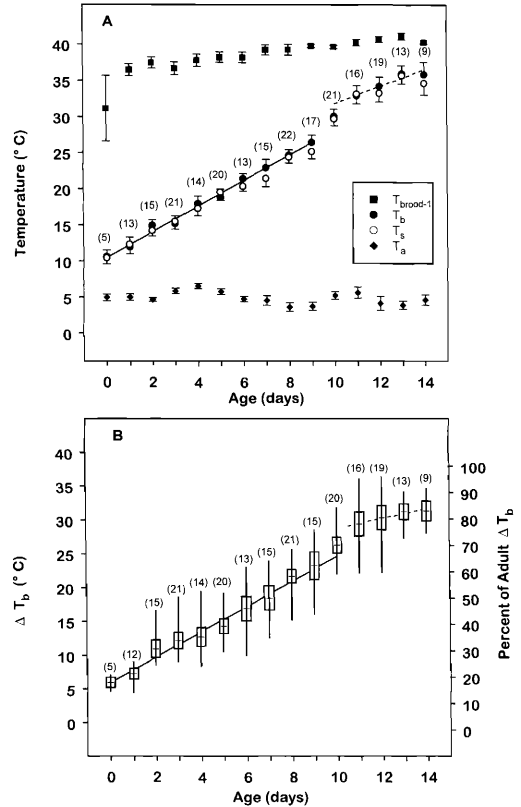

FIG. 2. Mean body temperatures for individual *E. oberholseri* chicks in nest, at start of testing ($T_{brood-1}$), body temperature (T_b), and skin temperature (T_s) after 10 min of cold exposure in isolation, (A), and mean difference between body and ambient temperature (ΔT_b) by day of age (B). Mean ambient temperatures (T_a) for testing periods on each day of age are indicated on bottom of (A). Capped vertical lines (A) represent 2 SE above and below the mean. (B) Uncapped vertical lines represent the range of values observed for each day of age, boxes indicate 2 SE above and below the mean, shown by a horizontal dash. Samples sizes for nestlings whose temperatures were measured on each day of age are indicated in parentheses.

6; changes after this continued more slowly until asymptotic masses were attained (transition point determined by the method of Yeager and Ultsch, [1989]). Until this point (8.9 g), T_b was linearly related to mass ($T_b = 1.788$ (Mass) $+ 9.929$, $F = 813.37$, df = 1 and 140, $P < 0.0005$, Fig. 3), and ratio of surface area to volume ($T_b = -3.28$ (SA:Volume) $+ 34.86$, $F = 358.24$, df = 1 and 105, $P < 0.0005$, Fig. 4). As body masses exceeded 8.9 g (approximately day 9) however,
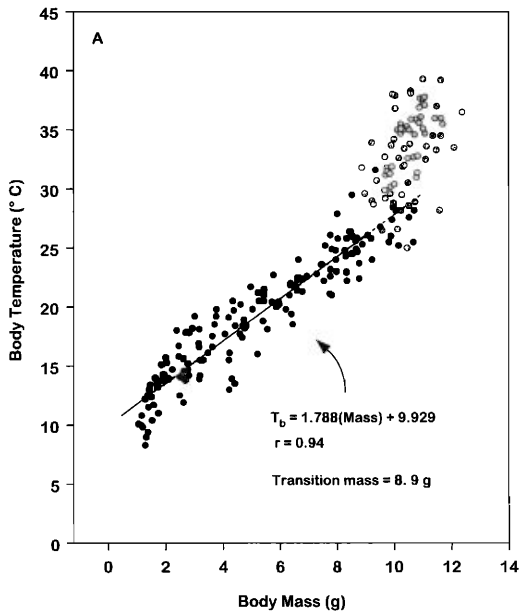
FIG. 3. Individual body temperatures as a function of nestling body mass. Nestlings from day 0 through day 9 are indicated in black, and nestlings day 10 and older are indicated in gray.

FIG. 4. Body temperature as a function of the ratio of surface area (SA, cm² = 8.11 Mass^0.667; Walsberg and King 1978) to volume (estimated by mass, in grams) in nestling *E. oberholseri*. Relationship between declining ratio of surface-area-to-volume and advancing age is indicated by dashed boundary lines indicating the approximate boundaries for each age class. Regression line for T_b (in results) is calculated for nestlings whose ratios of SA:Volume were between 7.8 and 4.2 (4.2 = the transition point between largely passive cooling and when nestlings began to actively regulate T_b). Phase II and phase III nestlings are indicated in gray.

the divergence in T_b between older and younger nestlings falling within the same mass intervals became increasingly visible (Figs. 3, 4).

In the relationship between T_b and mass, potential sources of unexplained variation in T_b included changes in regulatory capacity that were related to age, and in physical features such as feather development (Fig. 2B). To investigate the latter, partial correlation analyses were performed on T_b with mass, age, and plumage components for each of the three phases of thermoregulatory development. Nestlings weighing <5.5 g (phase I), were largely passive in response to cold exposure. Shivering first became visible during phase II, when nestlings were between 5.5 and 8.5 g, and by phase III (8.5+ g), nestlings were actively attempting to maintain homeothermy (see Fig. 3).

Tables 3 and 4 summarize the partial correlations for T_b with mass, age, and plumage development during each of those phases. Because the partial correlations for T_b and ΔT_b with mass, age, and plumage development closely resembled each other, only the values for T_b are reported here. The correlation between T_b and mass declined as nestling development progressed, from 0.83 during the first
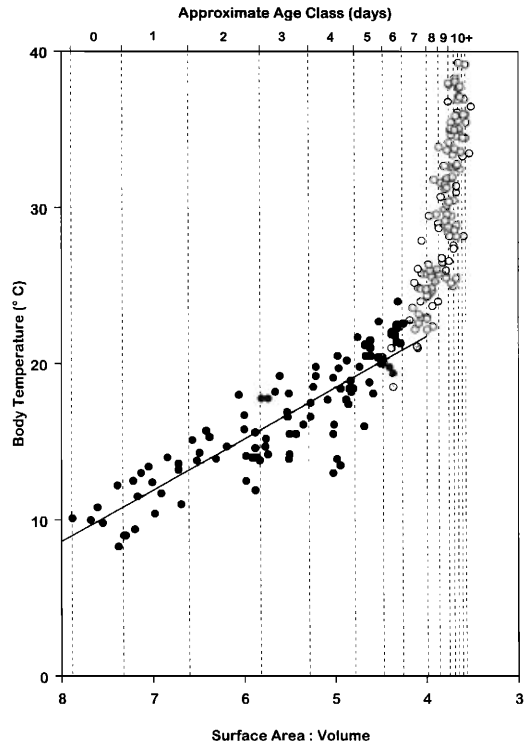
phase of growth, to 0.72 in the second phase, and 0.45 for the last phase of the nestling period (Table 3: $P < 0.0001$ for all three phases). When effects of age and T_a were held constant, partial correlations for T_b with body mass were statistically significant only during the first two phases of growth, when mass was increasing most rapidly (phase I, $r = 0.48$, $P < 0.0001$; phase II, $r = 0.53$, $P < 0.01$). After phase II, body mass increased more slowly, eventually reaching a plateau; at that point, other developmental features clearly superceded mass as explanatory factors (phase III, $r = 0.09$, $P > 0.05$).

TABLE 3. Partial correlation coefficients for body temperature (T_b) with mass and with age, during each of three phases of growth, while controlling for the effects of ambient temperature and plumage variables. Zero order partials (simple correlation) are provided under "no control" category.

	Phase I		Phase II		Phase III	
	r	P	r	P	r	P
			T_b with mass			
No control	0.83	<0.001	0.72	<0.001	0.45	<0.001
Age	0.55	<0.001	0.57	0.001	0.02	NS
T_a	0.84	<0.001	0.72	<0.001	0.50	<0.001
Age, T_a	0.48	<0.001	0.53	0.002	0.09	NS
Age, T_a, Md_T	0.49	<0.001	0.39	0.023	0.12	NS
Age, T_a, Vt_T	0.51	<0.001	0.42	0.014	0.06	NS
Age, T_a, $P6_T$	0.54	<0.001	0.29	NS	0.09	NS
Age, T_a, Md_{Pin}	0.49	<0.001	0.47	0.007	0.13	NS
Age, T_a, Vt_{Pin}	0.51	<0.001	0.53	0.002	0.11	NS
Age, T_a, $P6_{Pin}$	0.54	<0.001	0.29	NS	0.10	NS
Age, T_a, Md_T-$P6_T$	0.56	<0.001	0.30	NS	0.12	NS
Age, T_a, Md-$P6_{Pin}$	0.56	<0.001	0.35	0.048	0.14	NS
			T_b with age			
No control	0.76	<0.001	0.54	0.001	0.70	<0.001
Mass	−0.16	NS	−0.06	NS	0.60	<0.001
T_a	0.79	<0.001	0.57	0.001	0.70	<0.001
Mass, T_a	−0.06	NS	0.05	NS	0.57	<0.001
Mass, T_a, Md_T	−0.06	NS	−0.15	NS	0.41	0.002
Mass, T_a, Vt_T	−0.06	NS	−0.09	NS	0.26	0.033
Mass, T_a, $P6_T$	−0.14	NS	−0.27	NS	0.26	0.038
Mass, T_a, Md_{Pin}	−0.06	NS	−0.09	NS	0.59	<0.001
Mass, T_a, Vt_{Pin}	−0.06	NS	−0.03	NS	0.57	<0.001
Mass, T_a, $P6_{Pin}$	−0.14	NS	0.29	NS	0.58	<0.001
Mass, T_a, Md_T−$P6_T$	−0.15	NS	−0.39	0.028	0.24	0.052
Mass, T_a, Md−$P6_{Pin}$	−0.05	NS	−0.30	NS	0.34	0.011

In contrast to the strong correlation between body mass and T_b (or ΔT_b) when age was controlled, the correlation between age and T_b (while controlling for effects of body mass) was not statistically different from zero until the last phase of growth (phase III, $r = 0.57$, $P < 0.0001$). That suggested that incremental changes in body mass and surface-to-volume relationship were more important during the earlier phases of growth than simple chronological age, but that maturation of control mechanisms predominated during the last phase of development.

Most improvements in thermoregulatory ability might be expected to depend on mass-related changes in thermolysis and thermogenesis. However, changes in plumage development might also affect T_b through effects on heat loss or retention. Plumage development was strongly correlated with T_b and ΔT_b, when nestlings from the entire nestling period were examined (zero order correlations: T_b, ΔT_b, with $P6_T$: $r = 0.91$; Md_T, Vt_T: $r = 0.92$; R_T: $r = 0.81$; $n = 149$, $P < 0.0005$ in all cases). Because

heavier nestlings were more advanced in feather development, and early feather development explained some of the variability in age-specific body mass, we addressed the question of whether early pin development influences thermolysis by analyzing the relationship between T_b, ΔT_b and ensheathed feather length, while controlling for age, mass, and total feather length.

With the start of feather eruption in late phase I nestlings, T_b was negatively correlated with pin lengths in P6, mid-dorsal, and mid-ventral contours, although the correlation was significant only for the primaries (Table 4). Roughly 8% of the variation in T_b was attributable to erupting pin length when the effects of body mass, age, and T_a were controlled ($P6_{Pin}$: $r = -0.28$, $P = 0.018$). During the second phase of growth, T_b continued to correlate with primary and rectrix lengths (Table 4), although the sign of the partial was now positive. During that phase, terminal portions of those feathers began to harden within the sheaths and the cor-

TABLE 4. Partial correlation coefficients for body temperature with pin length, while controlling for the effects of age, T_a, and mass. Dashed line indicates zero order partial. During Phase I (0.5 g to 5.5 g), the entire feather was ensheathed, hence pin length was the equivalent of the entire feather length. During Phases II (5.5 g to 8.5 g) and III (8.5 g +), the "pin" length was a measure of the ensheathed length, which became shorter as the end of the feather began brushing.

		Phase I		Phase II		Phase III	
	Control Vars.	r	P	r	P	r	P
T_b with	—	0.50	<0.001	0.61	<0.001	0.04	NS
Md_{Pin}	Age, T_a, Mass	−0.14	NS	0.11	NS	−0.25	0.037
T_b with	—	0.56	<0.001	0.42	0.010	0.10	NS
Vt_{Pin}	Age, T_a, Mass	−0.20	NS	−0.07	NS	−0.14	NS
T_b with	—	0.58	<0.001	0.72	<0.001	0.07	NS
$P6_{Pin}$	Age, T_a, Mass	−0.28	0.018	0.36	0.032	−0.07	NS
T_b with	—	—	—	0.63	<0.001	0.60	<0.001
$R1_{Pin}$	Age, T_a, Mass	—	—	0.50	0.004	−0.10	NS

relation was essentially equivalent to that between T_b and total feather length.

During phase III, feathers were mostly unsheathed in dorsal and ventral contour tracts, but were still largely unbrushed in primary tracts. As the length of the ensheathed portion declined with continued brushing, partial correlations between T_b and ΔT_b and pin lengths ceased to differ significantly from zero (Table 4). Although brush length increased during this period and simple correlations with feather brush length were significant, neither T_b nor ΔT_b were correlated with brush length when age, body mass, and total feather length were controlled ($P > 0.1$ for all partials). That suggests that although thermoregulatory improvements coincide with plumage maturation and brush development, they are not contingent upon those changes, but depend instead upon the maturation of other physical and physiological factors that also coincide with feather development.

Development of effective endothermy.—In isolated nestlings, development of endothermy was relatively slow, with little ability to maintain stable T_b at adult levels until day 10 or 11. However, we noted visible shivering and thus active attempts to regulate temperature as early as day 5. Because most nestlings occurred in broods larger than one, the extent to which development of homeothermy was influenced by presence and number of brood mates was addressed by measuring temperatures of chicks within the nest, immediately upon flushing the female ($T_{brood-1}$), and then again after 10 min of cold-exposure (T_s, T_b for chicks cold-stressed in isolation, $T_{brood-2}$ for chicks cold-stressed in broods).

Mean temperatures for chicks tested individually in the nest ($T_{brood-1}$) and then subsequently cold-stressed in isolation are shown at the top of Figure 2A, and again after 10 min of exposure in isolation (T_s and T_b). Although obtained immediately after flushing the female, means for $T_{brood-1}$ were below the average female body temperature of 42°C, and increased significantly over the nestling period, from 31.1 ± 5.5°C in day 0 nestlings to 41.2 ± 0.7°C by day 13 (linear regression, $T_{brood-1}$ = 0.427 (Age) + 35.587, $r = 0.71$, $F = 157.508$, df = 1 and 157, $P < 0.0005$). By days 5 and 6, mean $T_{brood-1}$ of 38.2 ± 1.0°C did not differ significantly from those measured on subsequent days (ANOVA, Tukey's test, $P > 0.05$).

The reliability of T_s as an approximation of T_b was tested in isolated nestlings after cold exposure, when the differences should be magnified. Although skin temperatures after cold exposure were significantly lower than core temperatures when isolated nestlings of all ages were pooled (mean difference: 0.7 ± 1.5°C, Wilcoxon-signed ranks test, $P < 0.005$), the differences for most ages were not statistically significant (Wilcoxon-signed ranks test, $P > 0.05$ in 8 of 14 age groups) and were less than 1°C in four of the age groups in which small differences were found (Wilcoxon-signed ranks test, $P < 0.05$). When age, mass, and T_a were controlled, these differences were negatively correlated with the extent of dorsal brushing (Md_b: $R = -0.26$, df = 116, $P = 0.004$; $P6_B$: $r = -0.21$, df = 116, $P = 0.020$). The close correla-

tion between T_s and T_b ($r = 0.98$, df $= 155$, $P < 0.0005$), and the tendency for differences to be small or nonexistent, even on exposed surfaces like the ilium, supported the use of skin temperatures from protected areas as conservative approximations of core temperature. That was particularly important in young nestlings, where cooling at low T_a occurred rapidly and could be exacerbated by the disturbance of handling.

Temperatures of nestlings monitored by this method in broods before and after cold exposure (1983, 1984: Fig. 5A), showed age-related patterns of change comparable to $T_{brood-1}$ obtained for chicks tested individually in nests (Fig. 2A). Brood age, in those analyses, was defined as mean age of all chicks in the brood rounded to the nearest integer. Brood temperatures for the first two days tended to be around 8°C below the female T_b, but were only 4°C below the female T_b by brood age 5 (Fig. 5A). Although $T_{brood-1}$ for that sample increased through the first eight days ($T_{brood-1} = 0.728$ (brood age) $+ 34.074$, $r = 0.71$, $F = 58.230$, df $= 1$ and 58, $P < 0.0005$; Fig. 5A), no further changes occurred beyond that age ($r = 0.24$, $F = 2.01$, df $= 1$ and 23, $P > 0.1$). No $T_{brood-1}$ of 42°C (the T_b of adult females) was measured, even at fledging, although values of 40°C were common after age 5.

For chicks in broods of all ages, temperatures after cold-exposure ($T_{brood-2}$, Fig. 5A) were higher than for isolated nestlings (T_b, Fig. 2A). Mean $T_{brood-2}$ increased from a minimum of 23.8 $\pm$ 1.4°C for broods of age 0–1 days, to 39.1 $\pm$ 1.1°C for broods of age 9 ($T_{brood-2} = 2.01$ [brood age] $+ 22.523$, $r = 0.90$, $F = 252.18$, df $= 1$ and 60, $P < 0.0005$; Fig. 5A). For broods of age 5, the mean $T_{brood-2}$ was 33.0 $\pm$ 1.9°C which was 79% of T_b in adults. Postexposure drops in temperature (ΔT_{brood}, calculated as $T_{brood-1} - T_{brood-2}$) decreased with brood age from a maximum of 10.2 $\pm$ 2.1°C for broods of age 0–1 to 4.8 $\pm$ 0.9°C in broods of age 5 (Fig. 5B). Some broods of ages 4 and 5 underwent declines of less than 3°C. By age 9, brood temperatures did not change, and after 11 days, most broods were consistently showing higher $T_{brood-2}$ after 10 min of testing than at the start, perhaps because of agitation and accompanying increases in metabolic activity.

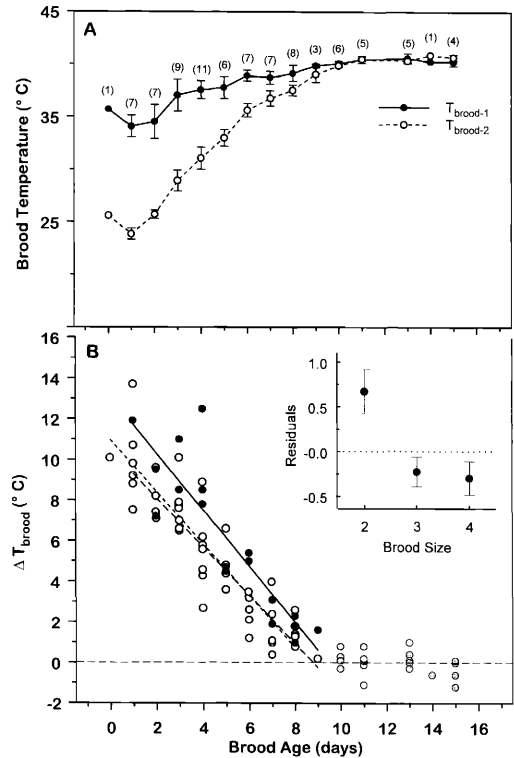*Relationship between brood size and thermolysis.*—Because the number of nest mates should

FIG. 5. Brood temperature before ($T_{brood-1}$) and after ($T_{brood-2}$) 10 min of exposure to ambient temperatures between -3 and 5°C (A) as a function of brood age. Numbers in parentheses indicate the number of broods used to compute each mean ± 2 SE (capped vertical lines). Distribution of temperature changes for individual broods as a function of brood age and brood size is shown in (B) (black circles = two-chick nests; open circles = three and four chick nests). Regression lines fit to each brood size are calculated on data to age 9 (solid line = two-chick nests; short-dash = three chick nests; long dash = four chick nests). Residuals for overall regression are shown with respect to brood size in inset. Dark gray circles (broods of all sizes after age 9) were not included in regressions.

affect the total surface-to-volume relationship of the brood, and thus the dynamics of heating and cooling, mean ΔT_{brood} were compared between chicks tested individually, and those for broods of two, three, and four chicks. Group size (from 1 to 4), exerted a significant effect throughout the nestling period (two-way ANOVA, effect of group size on ΔT_{brood}: $F = 361.89$, df $= 15$ and 180, $P < 0.0001$). For nestlings of all ages, broods showed significantly smaller drops in temperature as compared with indi-

viduals in the absence of brood mates (Tukey's HSD, $P < 0.05$). Whereas ΔT_{brood} averaged 10.2°C for broods of age 0–1, the mean drop in single chicks on day 1 was approximately twice that (23.5 ± 1.3°C). Those differences persisted throughout the nestling period, although the disparity between broods and single chicks decreased with advancing age. By age 8, broods averaged a ΔT_{brood} of 1.6°C as compared with a 14.5°C drop in solitary chicks. Effect of brood mates on heat loss during cold exposure was substantial enough that by age 5, broods of nestlings easily maintained homeothermy at levels comparable to or better than isolated day 14 nestlings.

In addition to differences in temperature stability between nestlings in broods and those alone, there were significant differences among broods of different sizes (two-way ANOVA: $F = 15.574$, df = 26 and 37, $P < 0.0001$). Mean ΔT_{brood} was significantly affected by both brood age ($F = 27.161$, df = 14 and 46, $P < 0.0001$) and brood size ($F = 4.459$, df = 2 and 46, $P = 0.017$). Temperature differences between the start and end of cold exposure were significantly larger in broods of two than those of either three or four nestlings (Tukey's HSD, $P < 0.05$), and although the regression coefficients calculated for those data did not differ significantly (brood age × brood size effect: $F = 1.024$, df = 22 and 46, $P > 0.1$), the y-intercept for the two-chick nests was about 4°C higher (Fig. 5B). Despite these differences, the age of onset for effective endothermy was only about a day different between two-chick nests and three- or four-chick nests. An analysis of the residuals obtained by regressing ΔT_{brood} on brood age, and then examining the variance with respect to brood size, corroborated that (ANOVA, $F = 6.817$, df = 2 and 63, $P = 0.002$; Fig. 5B, inset); residuals for temperature changes in broods of two were significantly greater than those for broods of either three or four chicks (Tukey's HSD, $P < 0.01$), but there were no significant differences between broods of three and four.

Effect of brood size on temperature profiles in natural nests.—Thermoregulatory performance under natural conditions tended to confirm the results of the cooling experiments presented above. Tracings of continuously recorded nest temperatures for broods of one, two, and three chicks were obtained from eggs implanted

with thermocouples during incubation and left in the nest for the duration of the nestling period (T_{egg}). Due to movements of the nestlings and consequent changes in egg position, T_{egg} was not necessarily identical to the actual T_{b} of the chicks. However, depending upon their T_{b} and extent to which they filled the nest, nestlings were expected to influence the cooling rate of the implanted egg, enabling a thermal profile to be determined for each nest. Because nestling T_{b} were assumed to be at, or slightly higher than the egg temperature, T_{egg} was considered to be at least representative of the lowest temperature in the brood (see also earlier analysis of $T_{\text{brood-1}}$). Attentiveness patterns were determined by inspecting the regular pattern of temperature increases and decreases on each record; large, regular deviations indicated arrivals and departures of the female, whereas smaller fluctuations were due to the movements of chicks within the nest.

Records from three nests comparing the cooling curves of different sized broods at brood age 4 and 5 are shown in Figure 6 (no examples of four-chick nests were present because the implanted egg always precluded the hatching of a chick, and no nestlings were transplanted). Chicks of days 0 to 2 had little effect on cooling patterns and brood temperatures were essentially the same as for eggs alone (data not shown), but by days 4 and 5, nestlings exerted a visible effect. The presence of even one chick in the nest helped ameliorate the temperature differential between the implanted egg and the air temperature inside the nest, an effect that was enhanced as chicks increased in size. Compared with the relatively stable profiles when chicks were present, the pattern of T_{egg} without the influence of nestlings showed a sharp decline (see arrow indicating removal of chicks for weighing in Fig. 6). When replaced, they acted to rewarm the implanted egg even though the female was not on the nest. By day 8, in parallel with the increased resistance shown by chicks this size and age to experimental cooling, the attentiveness patterns of each female became difficult to discern. At day 9 and beyond, nest temperatures were too stable to detect female attentiveness and prolonged maternal absences had little direct effect on the implanted egg. For all ages up to age 9, the amplitude of temperature changes was smaller in the three-chick nest than in the
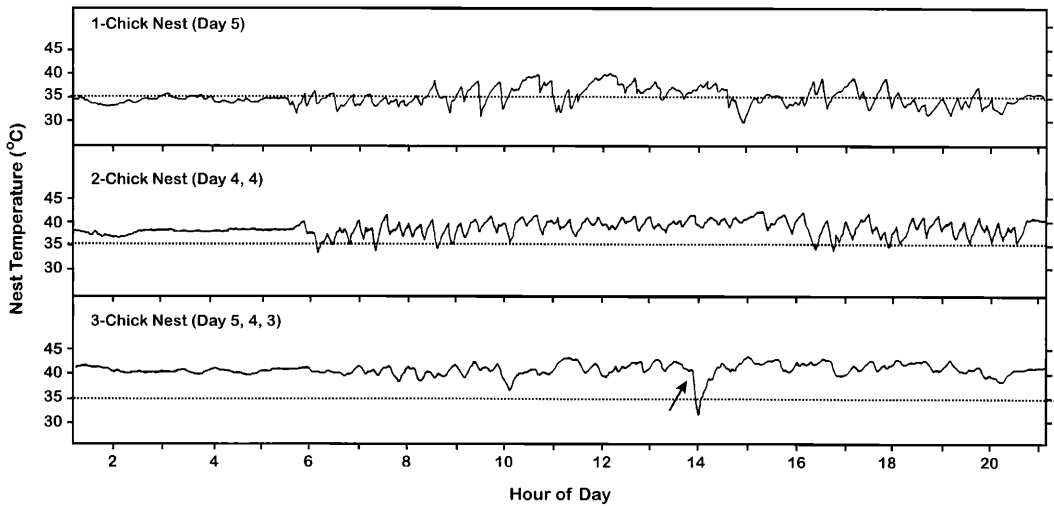
FIG. 6. Temperature profiles, obtained from implanted eggs, for three different sized broods (one, two, and three chicks) at age 5 days. Dashed line at 35°C denotes roughly 83% of adult body temperature. Arrow indicates removal of nestlings for weighing.

one- or two-chick nests, and overall mean temperature appeared to be about 5°C higher than in the one-chick nest (Fig. 6).

Effect of storms on temperature profiles in natural nests.—Because inclement weather is frequent at high elevation, nests for which temperature profiles were obtained during storms were of special interest with regard to nestling survival. Three consecutive days of data for a nest containing two day 3 chicks and the recording egg during a storm are shown in Figure 7. Heavy rainfall began around 1300 on 9 August, continued through the afternoon, and was intermittent during the night and into the next morning. Despite increased attentiveness on the part of the female (two trips off for 1–2 min between 1300 and 1400 PDT on 9 August, as compared with four or five times on a normal day), temperatures in the nest declined substantially over the next few hours. By the onset of nighttime brooding between 2000 to 2200 PDT, T_{egg} was still only 31 or 32°C, as compared with 40 to 42°C on a normal night.

During the next 24 h, maximum T_{egg} ranged from 1 to 25°C below normal brooding temperatures, because cooling was exacerbated by intermittent rainfall, wind, and low T_a during the night and subsequent morning. The female's first off-bout around 0600 PDT on the morning of 10 August roughly coincided with the onset of further heavy rains, and marked the start of

the longest continuous decline in this nest's temperature profile, reaching lows between 15 and 17°C. Successive on-bouts only succeeded in rewarming the implanted egg, and presumably the day 4 nestlings, 2 to 4°C each time. Because the temperature of the implanted egg can be assumed to be at most a few degrees cooler than the chicks, the thermal profile of 10 August indicates that temperatures being experienced by chicks were probably at or below 35°C for a total of about 6 or 7 h. Direct measurements of low body temperatures in chicks from other nests during the same storm support that. In one brood of three day 8 chicks on 10 August, $T_{brood-1}$ was only 37.6°C at the start of testing, and water could be squeezed from the nest walls. Those data suggest that thermal profiles reported here are probably not unusual in this population. By 11 August, the storm had cleared and normal temperatures were again measured.

Although storm-induced nestling mortality was occasionally observed in *E. oberholseri*, and the rains from that storm were known to have killed nestlings of other species nesting nearby, no effect of that or less-severe storms was discernible on the nest whose profiles are reported here. That may have been due, in part, to a heavy aspen canopy above the shrub in which the nest was located, and during subsequent events, to the increasing age and thermoregu-
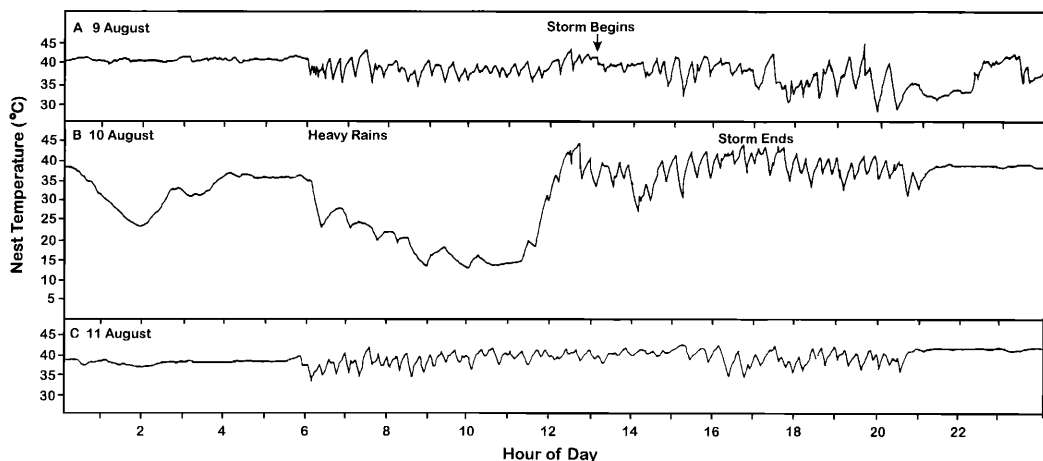
FIG. 7. Temperature profiles (derived from implanted egg) showing the effects of inclement weather on nest temperature in a nest containing two day 3 *Empidonax oberholseri* chicks. Temperatures shown here are from three consecutive days. In panel A, the storm began around 1300 PDT. (B) shows the effects of heavy rains on nest temperature; (C) shows the return of normal nest temperatures as the weather cleared and the nest dried out.

latory ability of the chicks themselves. They remained robust and healthy looking up until day 10, when the equipment was removed. Fledgling calls and adult alarm notes in the vicinity of the nest two weeks later suggest that they had successfully left the nest. The effects that that weather might have had on development were not known as those chicks were not weighed. However, in other *E. oberholseri* nests that were active during that period, none showed any obvious effects on either nestling development or fledging success.

DISCUSSION

GROWTH RATES

Although rapid growth and early endothermy should be advantageous in subalpine environments, there was little evidence of accelerated physiological development in *E. oberholseri*. The growth rate calculated for that species was 0.425, ranging from 0.387 to 0.448 during the four years of the study. That is similar to growth rates reported for other tyrannids, and many tropical and subtropical groups reported in Ricklefs (1968, 1976), Dunn (1975), and Starck and Ricklefs (1998). The overall mean growth rate (±SD) calculated for 21 tropical and temperate tyrannid species was 0.380 ± 0.062. Because variation in body weight

does not appear to account for variation in growth rates within this family ($r^2 = 0.01$, df = 19, $P > 0.1$), the available tyrannid species were divided into tropical- and temperate-zone breeders. Although mean growth rates differed between tyrannid species breeding in temperate North America (0.414 ± 0.053, $n = 10$ species), as compared with those breeding in the Neotropics (0.349 ± 0.050, $n = 11$ species; t-test, $t = 2.7$, df = 19, $P = 0.013$), the growth rate for *E. oberholseri* did not fall into the higher end of the temperate tyrannid range, as would be expected if selection has increased the rate of development in that environment. Instead, its growth rate fell within 0.207 SD units of the temperate tyrannid mean (95% confidence intervals for the mean: 0.378, 0.450), and slightly below the mean of 0.444 calculated for three other species of *Empidonax* (*E. difficilis*, Davis et al. 1963; *E. traillii*, King 1955; *E. virescens*, Mumford 1964). In all, growth rates in 6 of the 10 species of temperate flycatcher (none of which are high-altitude breeders) were higher than those calculated for *E. oberholseri*.

The time taken for *E. oberholseri* to progress from 10 to 90% of their asymptotic weight was approximately 10.4 days, with most chicks achieving their asymptotic mass by day 12, and a few as early as day 10. Asymptotic weights were close to adult masses (ratio of asymptotic

to adult mass, 1.02), which suggests that growth of locomotory appendages and associated musculature was essentially complete by day 12; despite this, fledging did not usually occur for another 5 or 6 days.

THERMOREGULATORY DEVELOPMENT IN INDIVIDUALS

The ontogeny of endothermy depends, in large part, on the acquisition of sufficient mass to generate and retain heat economically. Its development, in most species, coincides closely with improvements in the physical features enabling heat retention, most notably mass and associated decreases in ratio of surface-to-volume (e.g. Great-tailed Grackle, *Quiscalus mexicanus*, Gotie and Kroll 1973; Bank Swallow, *Riparia riparia*, Marsh 1979; Tree Swallow, *Iridoprocne bicolor*, Marsh 1980; Great Tit, *Parus major*, Mertens 1977). In *E. oberholseri*, T_b and ΔT_b were both strongly correlated with increases in body mass, an effect that appeared to be largely passive, with slightly higher T_b in heavier nestlings. Deviations from a largely mass-dependent relationship, indicating that other developmental features were taking precedence, did not occur until after day 8 or 9. At that age, post-cold-exposure T_b between older and younger chicks of equivalent weights began to diverge, coinciding with age-related maturational differences in both physical and physiological features.

The rapid onset of feather brushing was one of the most visible changes in physical appearance coinciding with that divergence. Although not a prerequisite of physiological endothermy, feather development is a strong correlate of thermoregulatory competence, and the major integumentary factor regulating heat loss (Dawson and Evans 1957, 1960; Breitenbach and Baskett 1967, Jehl 1968, Morton and Carey 1971), providing the insulation necessary for economical temperature control. However, during early stages of feather development, growing feathers might also function as a significant route for heat loss (Breitenbach and Baskett 1967, Morton and Carey 1971, Ricklefs 1983), a particularly disadvantageous situation at high altitude, where low T_a are commonplace.

Although we expected that variability in T_b should correlate with the extent of pin-feathering, when the total feather length, age, and body mass were controlled, that expectation was only marginally supported, and only briefly for feathers having the largest cross-sectional area. During eruption of primaries, roughly 8% of the variation in T_b was explained by primary pin length, and although negative correlations between T_b and erupting body tracts were also present, they were not statistically significant. That suggested that the potential for radiative heat loss through the growing pin feathers may be restricted to the period during and immediately after eruption, when the blood supply to growing feathers is closest to the surface, and their termini have not yet matured. Interestingly, as the pin-feathers continued to elongate, there was evidence that instead of enhancing thermolysis, they may actually increase resistance to heat loss.

The positive correlation between T_b and primary pin length during phase II is consistent with the decreased heat loss observed in pin-feathered chicks of some small precocial species prior to brushing (Spiers et al. 1974, McNabb and McNabb 1977, Webb and King 1983). Changes in the physical structure of the pin feather during growth may be the most likely explanation for the increased resistance to heat loss in both groups of birds. Because the area of active feather growth is located primarily beneath the skin, at the base and center of the pin (Lucas and Stettenheim 1972, Stettenheim 1972), continued growth of the feather does not necessarily result in comparable levels of exposure for the vascular supply. That is because the terminal portions of the feather above the skin surface mature well in advance of the growth of new feather segments at the base. With maturation of each new segment, a cap forms, with resorption of pulp beneath it and the formation of an overlying air pocket (Lucas and Stettenheim 1972). The series of air pockets, formed as the feather elongates, may act as a thermal barrier to heat loss by minimizing exposure of the basal blood supply to the environment.

Accelerated rates of feather growth and brushing would be one way to ameliorate effects of exposure during the long nestling period. However, feather growth in *E. oberholseri* occurred on the same schedule and at roughly the same rates as for other tyrannids, irrespective of species or geographic origin (e.g. *E. trail-*

lii, King 1955; *E. virescens*, Mumford 1964; *Sayornis phoebe*, Mahan 1964, Murphy 1981; *Tyrannus tyrannus* Murphy 1981; *Contopus sordidulus*, M. Pereyra unpubl. data). The similarity in feather growth rates among tyrannids extends to other avian species, as well. Absolute feather growth rates, which are independent of total length, appear to be remarkably consistent among birds from a wide variety of families (Starck 1998), which suggests that overall rates of feather growth may not be particularly amenable to selective modification. However, the fact that young passerines vary widely in plumage appearance and rates of progression through the different stages of feather growth indicates that adaptive variation in those schedules could still occur, even if limited to differences in eruption and brushing schedules.

Although feathers on exposed surfaces such as the dorsum might be expected to erupt earlier, all tracts in *E. oberholseri* were on roughly the same schedule and grew at nearly the same absolute rates. Only the femoral feathers, which emerged slightly earlier, and the rectrices, which erupted slightly later, appeared to deviate from the other tracts. In contrast to the uniformity observed in eruption schedules, brushing did appear to vary with tract and degree of exposure. The first evidence of brushing on both dorsal and ventral surfaces began on day 6, only two days after eruption, becoming widespread on day 7. Brushing progressed at a slightly faster rate in the ventral tracts—as expected on the basis of the potential vulnerability of that area to heat loss. Due to differences in shapes of the two surfaces, however, complete coverage of the dorsal surface by brushing was actually attained earlier. From days 7 to 9, when the shift toward physiological endothermy was occurring, coverage of the dorsal apteria increased from 75 to 95%. During that same period, coverage of the ventral surface amounted to <50%, mainly due to the continued protrusion of the abdomen. The potential for heat loss through the abdomen was probably largely ameliorated by the nest lining, brood mates, and the tendency for nestlings to face one another with heads and necks intertwined and abdomens pressed together. The importance of posture was most evident during the first few days of postnatal development, and when T_a were low. The asymmetry between coverage on dorsal and ventral surfaces declined in magnitude with expansion of the pectoral muscles and relative reduction in the size of the abdomen.

Early brushing was also observed in two other areas of potential thermal importance, the tracts covering the pectoral and femoral muscles, both of which play important roles in shivering thermogenesis (Aulie 1976a, b; Aulie and Steen 1976, Dawson et al. 1976). However, variance in brush length in these or other areas was not significantly correlated with improvements in T_b or ΔT_b, when effects of age and mass were controlled. As in other studies, importance of plumage development to attainment of homeothermy probably lies less in the initiation of control than the mitigation of thermoregulatory expenses (Shilov 1968, Seel 1969, Dawson and Hudson 1970, O'Connor 1984). In *E. oberholseri*, neither the emergence of high, stable T_b, nor their control appeared directly contingent upon increases in insulation, but rather followed other, potentially more important, physiological and morphological changes enabling better generation and regulation of heat flow.

The first, almost imperceptible evidence of shivering thermogenesis occurred around days 5 and 6, presumably coinciding with physiological changes known to occur during the first week of passerine postnatal development (Dawson and Allen 1960, Dawson and Evans 1960, Dyer 1968, Shilov 1968), but well before the attainment of much body size or insulation. The emerging capacity to shiver, along with the increased muscle mass on which it depends (Hohtola and Visser 1998), is an essential component of the temperature-control system (Dawson and Evans 1960, Morton and Carey 1971, Aulie and Steen 1976, Dawson et al. 1976, Marsh 1979, 1980). However, that energy expenditure occurs at the expense of growth and may have only transient thermal benefits if it occurs prior to the acquisition of sufficient size and insulation to preserve the heat generated. The altricial mode of development has been viewed by many as an evolutionary means through which growth rates could be accelerated by postponing thermoregulatory expenditures until other aspects of growth are mostly complete. Once sufficient size and insulation have been attained, energy can then be reallocated from growth to thermogenesis. Despite

the advantage of delaying that activity until most growth is complete, data from numerous studies indicate the appearance of shivering occurs relatively early in development (Hohtola and Visser 1998, Ricklefs and Starck 1998) and well before much demonstrable control over heat flow is achieved (Kendeigh 1939, Odum 1942, Morton and Carey 1971, Marsh 1980, Clark and Balda 1981).

What advantage might there be to early shivering? The first small improvements in ΔT_b occurred in E. oberholseri at the same time that visible shivering was first detected. However, compared with effects of body size alone, the overall effects on heat balance were probably small because the capacity for intense heat production is still limited when shivering begins (Hohtola and Visser 1998). Before day 6, T_b in nestling E. oberholseri after cold exposure were positively correlated with T_a between $-3°C$ and $10°C$ ($r = 0.48$, df $= 85$, $P < 0.0005$). After day 6, however, postexposure T_b were increasingly independent of T_a in this range, suggesting the existence of limited abilities to regulate temperature within the first week. Despite that, single nestlings exposed to low T_a, could not prevent deep hypothermia until after day 7 and were unable to maintain homeothermy at adult levels until after day 12, when more than 90% of asymptotic weight had been achieved. For a passerine with an asymptotic weight of 11.7 g, the predicted mass at which homeothermy should occur is 10.1 g (Visser 1998: equation 5.12), which was attained in E. oberholseri at day 10 (mean mass $\pm$ SD at day 10, 10.07 $\pm$ 0.84, n = 76 nestlings). In actuality, nestling E. oberholseri did not achieve homeothermy until two or three days later.

THERMOREGULATORY DEVELOPMENT IN GROUPS

Although physiological homeothermy at adult levels did not begin until after day 9 in isolated nestlings, cold-stress experiments with broods and the temperature profiles obtained from natural nests showed that even day 0 chicks could prevent considerable heat loss by being in a group. $T_{brood-2}$ for day old nestlings dropped about 10°C (to 24°C) after 10 min of cold stress, as compared to drops of 24°C (to around 10°C for individual nestlings). In a group setting, even chicks as young as age 5

were able to significantly reduce heat loss through their collective thermal inertia, aided perhaps, by low levels of shivering. At that age, when the first manifestations of active thermoregulation were beginning in individuals, broods were essentially homeothermic during the testing period and easily maintained T_b of 33°C, nearly 80% of adult values. Temperatures in some broods dropped less than 3°C, and by day 9, mean $T_{brood-2}$ remained at a level of around 40°C, where they remained until fledging.

Those data suggest that whereas endothermy in individuals may be slow to develop, the physiological and physical changes that occur within the first week, along with improved surface-to-volume ratio created by a brood, were highly effective in protecting T_b inside the nest environment. That may help explain the early appearance of thermoregulatory responses so early in altricial development, and so far in advance of the development of effective mechanisms to control heat loss. Because E. oberholseri generally occur in broods of two or more, cost of early thermoregulation to each individual may be greatly exceeded by benefits of shared thermogenesis for two reasons. First, cost of thermoregulation at low T_a is reduced for each individual in a group context (Mertens 1969, O'Connor 1975, Hill and Beaver 1982, Sullivan and Weathers 1992); at T_a below the thermoneutral zone, oxygen consumption per individual is less in huddled groups of young endotherms than when each individual is isolated (Hill and Beaver 1982, Thomas et al. 1993). Second, if in the context of a more favorable collective surface-to-volume ratio, low levels of thermogenesis result in a more stable thermal environment, as suggested by the thermal profiles of natural nests, then a greater proportion of each chick's energy budget could theoretically be allocated toward growth, and on a more continuous basis. Studies showing increases in age-specific body mass with brood size (Royama 1966), despite fewer feedings per individual (Seel 1969, Johnson and Best 1982), appear to support that.

Although nestling cooling rates and temperature stability within nests were strongly affected by the presence of brood mates, as has been shown for a number of other species (Yarbrough 1970, Hamas 1981, Clark 1982, Verbeek 1988), effect of brood size did not change be-

yond three chicks. Similarly, the age at which homeothermy was attained was only mildly influenced by number of chicks in a brood, probably due to the packing characteristics observed in open-cup nests. Brood size appears to exert the greatest effect on the age at which homeothermy is attained in cavity-nesting species such as parids (Royama 1966), wrens (Dunn 1976), and starlings (Clark 1982). Dunn (1979) attributed that effect to larger brood sizes and the tendency for nestlings in those species to pack themselves into more than one layer, leading to greater reductions in cooling at earlier ages. In contrast, effects of brood size on cooling dynamics are much smaller in species whose nestlings sit alongside each other (Dunn 1979). In view of the limited range of clutch and brood sizes in *E. oberholseri*, the incremental improvements in insulation associated with adding each additional nestling, from two to four in a monolayer, may produce relatively small changes in brood volume relative to surface area as compared with the changes produced by adding extra layers of chicks. Because the size of the nest cup is limited, the thermal benefits that might accrue from packing more than one layer of nestlings are impractical in an open nest, in which each nestling must retain a grip on the nest interior to avoid falling out.

Although there was no evidence of accelerated growth or feather development to explain the success of *E. oberholseri* in the subalpine, there are several ways in which the observed pattern of development, coupled with clutch size characteristics, could contribute to its success at high elevation. Larger clutches early in the season, when T_a are lower, may enable early season broods to maintain thermal stability without a disproportionate increase in maternal attentiveness. For species that depend on limited energy sources, slow growth rates are one mechanism through which the daily energy requirements of the young can be reduced (Ricklefs 1968, Weathers 1996). The relatively slow growing *E. oberholseri*, as compared with other open-nesting subalpine passerines, may distribute their energy requirements more evenly across the nestling period, minimizing sibling competition. That may also contribute to the ability of nestlings to tolerate prolonged periods of light hypothermia and perhaps fewer feedings during periods of inclement weather.

The similarity between patterns of growth in *E. oberholseri* and those of its low elevation, tropical, and subtropical relatives suggests that most of those characteristics probably originated early in the evolutionary history of the Tyrannidae, and without much subsequent adaptive modulation from changing environments. Although the selective pressures that led to those patterns were undoubtedly different from those at high latitudes and altitudes, those characteristics, acting together, appear to function remarkably well in enabling this species to utilize high-altitude environments even in the absence of specific developmental adaptations for nesting there.

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