THE TIMING OF ENDOTHERMY IN THE DEVELOPMENT OF ALTRICAL BIRDS

ERICA H. DUNN[1]

Museum of Zoology
University of Michigan
Ann Arbor, Michigan 48104

Nestlings of altricial birds are unable to maintain homeothermic body temperatures at hatching, and their abilities to thermoregulate improve gradually during growth. Numerous studies have indicated the ages at which various species become essentially homeothermic (the "age of endothermy," e.g., Dawson and Evans 1957, 1960, Maher 1964, Ricklefs and Hainsworth 1969). However, little is known of the degree of flexibility of that age with respect to other growth processes, or of the adaptive significance of its timing.

Dawson and Evans (1957) noted a correlation between the age of endothermy and the length of the nestling period for several species of altricial birds. Contrary results were found by Maher (1964) who demonstrated nearly identical ages of endothermy in the Snow Bunting (*Plectrophenax nivalis*) and the Lapland Longspur (*Calcarius lapponicus*) in spite of the former's markedly longer nestling period. On the other hand, Morton and Carey (1971) stated that rapid acquisition of endothermy is a primitive characteristic of the Fringillidae and that the Snow Bunting has more recently acquired a protected nest site and a longer nestling period. Ricklefs and Hainsworth (1968) were able to show that the age of endothermy does not occur at the same stage of growth in all species. Thus, the age of endothermy normally may be flexible with respect to growth and most directly dependent on the length of the nestling period.

This paper examines the correlations among various growth parameters, nestling period, and the age of endothermy for a variety of altricial species to determine which factors best predict that age.

METHODS

The data analyzed are listed in table 1 or can be calculated from data therein (see table 2 for complete list of variables). I define age of endothermy arbitrarily as that age at which individual nestlings can keep their body temperatures at least 75% as high above an ambient temperature of 20°C as can an adult, after some period of exposure. Some species were measured only at temperatures other than 20°C; these are noted in table 1. For birds which were studied over a wide range of ambient temperatures, age of endothermy calculated as 75% of adult regulation at ambient temperatures from 15° to 25°C did not differ by more than 0–1 day from that calculated at 20°C (Dawson and Evans 1957, 1960, Maher 1964, Ricklefs and Hainsworth 1968). Those measured at lower ambient temperatures generally were exposed for a much shorter period than those at 20°C (10 min vs. 1–2 hr), and probably are not less accurate (Irving and Krog 1956, Morton and Carey 1971). Those measured at or above 30°C, however, may be listed as thermoregulating 1–2 days too early.

Three measures of growth rate were used in the analysis: K, $t_{10\text{-}90}$, and "maximum growth rate." K is a constant relating to the growth curve and represents the rate at which asymptotic weight is achieved; $t_{10\text{-}90}$ is the time in days between attainment of 10% and 90% of asymptotic weight. This is a better measure of growth rate than K for comparing weight gain among species with growth curves fitted to different equations because it is independent of those equations (Ricklefs 1968). Because K and $t_{10\text{-}90}$ depend on asymptotic weight, which can be difficult to determine accurately, "maximum growth rate" also was included. This is the maximum instantaneous growth rate (as a percentage of adult weight) and occurs at the inflection point of a growth curve (Hussell 1972). For growth data best fitted to the logistic curve, the appropriate formula is $KR(100)/4$, and for the Gompertz curve, $KR(100)/e$, where K is the growth constant mentioned earlier, R is the ratio of asymptotic to adult weight, and e is $\ln^{-1}$.

Adult and asymptotic weight also were considered in the analysis to test whether the age of endothermy and size are correlated. Information on weight at the age of endothermy was included to test whether there is a critical weight or stage of growth at which homeothermy can be maintained.

Simple correlation coefficients were calculated between all possible pairs of variables. Multiple correlations were then calculated for selected groups of variables to determine the best predictors of the age of endothermy. Correlations were used instead of other analyses because they describe co-relations of variables jointly affected by external influences, as most of the variables in table 2 clearly are. The object was to determine which easily observed characters vary in parallel with the age of endothermy and have predictive value, even if not causally related (Steel and Torrie 1960).

RESULTS

Table 2 shows the results of calculations of simple correlation coefficients among all pairs of variables. Growth rate K is the best single

[1] Present address: Long Point Bird Observatory, Box 160, Port Rowan, Ontario NOE 1MO, Canada.

 The Condor 77:288–293, 1975

TABLE 1. Age of endothermy, nestling period, and growth data for various altricial birds.[a]

Species	Age of endothermy[b]	Nestling period	K[c]	t_{10-90}	Adult weight	Asymptotic weight	Weight at age of endothermy	Sources
Tree Sparrow *Spizella arborea*	4.5 (10)	9.5	0.589*	7.5	18.4	17.2	9.8	Heydweiller 1935, Baumgartner 1938,* Irving and Krog 1956, Bent and collaborators 1968.
Red-winged Blackbird (male only) *Agelaius phoeniceus*	4.5 (32)	10.0	0.536	8.2	63.0	42.0	17.0	Brenner 1964, R. B. Payne, pers. comm.
Field Sparrow *Spizella pusilla*	5.5	8.1	0.648	6.8	12.0	11.0	9.2	Dawson and Evans 1957
Vesper Sparrow *Pooecetes gramineus*	5.5	9.6	0.624	7.0	24.3	19.5	14.0	Dawson and Evans 1960
Snow Bunting *Plectrophenax nivalis*	5.5	13.1	0.576	7.6	33.7	31.0	21.4	Maher 1964
Lapland Longspur *Calcarius lapponicus*	5.5	7.4	0.520	8.5	27.0	23.0	15.6	Maher 1964
Chipping Sparrow *Spizella passerina*	6.0	9.9	0.546	8.1	12.2	11.0	8.8	Dawson and Evans 1957
White-crowned Sparrow *Zonotrichia leucophrys*	6.5	9.5	0.512	8.6	26.6	20.5	16.5	Morton and Carey 1971
Great-tailed Grackle (female only) *Cassidix mexicanus*	6.5 (22)	21.0	0.385*	8.0	121.6	90.0	55.0	Bent 1958, Selander and Giller 1961, Gotie and Kroll 1973*
Red-backed Shrike *Lanius collurio*	7.5	14.5	0.446*	9.8	33.3	27.5	19.9	Böni 1942, Diehl and Myrcha 1973*
Brown-headed Cowbird *Molothrus ater*	8.5	8.7	0.576	7.6	43.5	30.0	29.0	Norris 1947, Neal 1973
Barn Swallow *Hirundo rustica*	8.5 (33)	20.0	0.456	9.7	17.8	20.5	18.1	Stoner 1935
Cliff Swallow *Petrochelidon pyrrhonota*	8.5 (33)	26.0	0.428	10.3	20.1	27.0	20.5	Stoner 1945
House Wren *Troglodytes aedon*	9.0	15.0	0.464	9.5	10.8	11.2	9.9	Kendeigh and Baldwin 1928, Bent 1948
Rosy Finch *Leucosticte tephrocotis*	9.0 (9)	12.0	0.406*	10.8	49.5	42.0	31.5	Bent and collaborators 1968, Yarbrough 1970*
House Sparrow *Passer domesticus*	9.5 (15)	14.0	0.393*	11.2	28.0	25.0	20.4	Weaver 1942,* Summers-Smith 1963, Seel 1969
Tree Swallow *Iridoprocne bicolor*	10.0	18.0	0.428*	10.3	21.1	21.5	18.8	R. L. Marsh, pers. comm.*
Cattle Egret *Bubulcus ibis*	11.0	30.0	0.231*	19.0	320.0	267.0	135.0	Palmer 1962, Hudson et al. 1974*
Domestic Pigeon *Columba livia*	10.5	36.0	0.206*	21.3	290.0	250.0	125.0	Ginglinger and Kayser 1929*
Cactus Wren *Campylorhynchus brunneicapillus*	12.0	20.0	0.394	11.1	38.7	31.4	29.0	Ricklefs and Hainsworth 1968
Double-crested Cormorant *Phalacrocorax auritus*	12.0	45.0	0.215*	20.2	2050.0	1900.0	498.0	Dunn 1975*
Masked Booby *Sula dactylatra*	18.0 (28)	118.0	0.095	46.4	1600.0	1700.0	300.0	Bartholomew 1966

[a] Ages are in days, weights in grams. Definitions of variables given in text.
[b] Figures in parentheses are temperatures (°C) at which measurements were made, if not at 20°C.
[c] Starred values were calculated from the starred sources; others are from Ricklefs (1968). Underlined values are fitted to the Gompertz equation, the rest to the logistic.

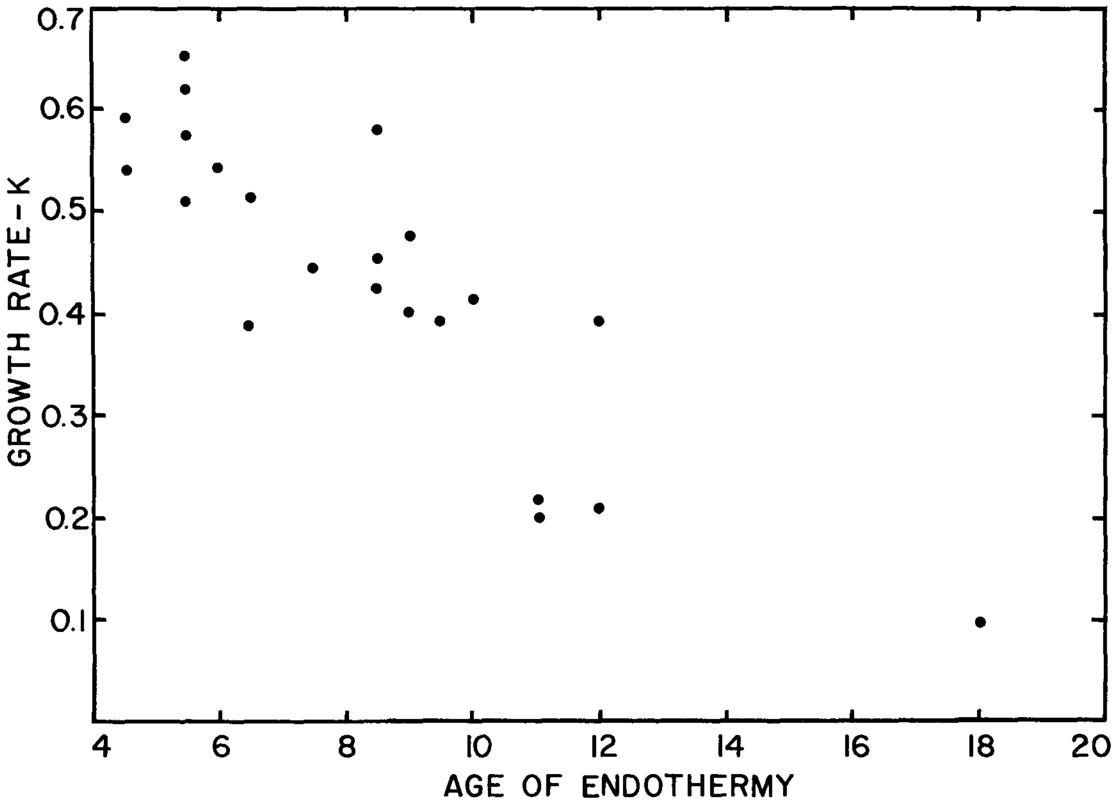

FIGURE 1. The relationship between growth rate K and age of endothermy in nestlings of various altricial species. See text for definitions, table 1 for sources of data, and table 2 for significance of the correlation.

predictor of the age of endothermy (fig. 1), accounting for 75% of the variation in the age of endothermy. Although nestling period is also a good predictor, this results largely from the close correlation between nestling period and growth rate t_{10-90} (table 2) indicating again the close relationship between age of endothermy and overall growth rate. There is no evidence that birds thermoregulate upon reaching a certain weight.

TABLE 2. Matrix of correlation coefficients between age of endothermy and various growth parameters of altricial birds.[a]

Variable number and name[b]	1	2	3	4	5	6	7	8	9	10
1. Age of endothermy	1.0	–0.8642	0.8583	0.8391	–0.7751	0.6713	0.6519	0.6483	–0.3388	–0.3122
2. Growth rate K		1.0	–0.8353	–0.7905	0.8274	–0.6750	–0.6840	–0.7266	0.5808	0.5095*
3. Growth rate t_{10-90}			1.0	0.9759	–0.7452	0.7875	0.7579	0.7091	–0.6783	–0.5968
4. Nestling period				1.0	–0.6718	0.8089	0.7674	0.7048	–0.6675	–0.5386
5. Maximum growth rate					1.0	–0.6502	–0.6382	–0.6973	0.5612	0.6548
6. Asymptotic weight						1.0	0.9850	0.9583	–0.7690	–0.6717
7. Adult weight							1.0	0.9751	–0.7450	–0.6840
8. Weight at age of endothermy								1.0	–0.7331	–0.6830
9. Weight at age of endothermy as % asymptotic weight									1.0	0.8268
10. Weight at age of endothermy as % adult weight										1.0

[a] All correlation coefficients are significant at the 1% level except the starred value, which is significant at the 5% level; and the underlined values, which are not significant.
[b] See text for definitions.

The lack of correlation between age of endothermy and weight at age of endothermy as a percent of asymptotic or adult weight indicates that at a given age of endothermy, the stage of growth attained is highly variable. However, an overall trend (fig. 2) for endothermy to occur at an earlier stage of growth in larger birds is evident. This probably is related to the attainment of low surface area-volume ratios (reducing heat loss) earlier in growth than for small birds and to the larger bulk of tissue which can contribute to thermogenesis. Ricklefs and Hainsworth (1968) also demonstrated that the age of endothermy does not occur at the same stage of growth in all species but did not consider the dependence of its variation on body size.

In order to test whether prediction of age of endothermy from growth rate K could be improved by taking other factors into account, each other variable in table 2 was added separately to a multiple correlation calculation with K and the age of endothermy. The only important result was that nestling period adds significantly ($P < 0.01$) to prediction of the age of endothermy even after variation due to K has been accounted for (the two factors together account for 81% of the variation in age of endothermy). Thus, for birds with the same growth rate but different nestling periods, those with longer nestling periods will reach the age of endothermy somewhat later.

Adult and asymptotic weight do not add significantly to the prediction of age of endothermy once K and nestling period have been considered. This indicates that the trend in figure 2 for larger birds to thermoregulate relatively earlier in growth is already taken into account by consideration of growth rate K, which also declines with larger body size.

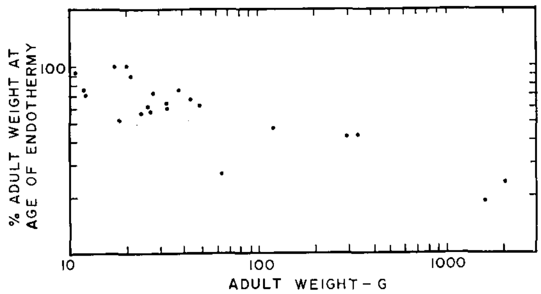

FIGURE 2. The relationship between adult weight and the weight at age of endothermy as a percent of adult weight for various altricial birds. See table 1 for sources and table 2 for significance of correlation.

DISCUSSION

Most of the diversity in age of endothermy is related to growth rate K, which in turn is closely related to body size (Ricklefs 1968; table 2). However, a significant amount of variation due to the length of the nestling period exists also, so that a change in the age of endothermy can occur independently of changes in body size. This probably occurs through differences in rates of feather growth, in nest insulation, or in other factors influencing rates of heat loss, rather than through changes in rates of metabolic development. Metabolic maturation probably is linked closely to overall body growth.

The age of endothermy discussed thus far might best be termed the "physiological" age of endothermy, as it is determined from the capabilities of individual nestlings to stay warm after exposure for some time to moving air of various temperatures. This physiological age of endothermy may be unrelated to the age at which "effective" endothermy occurs under natural conditions. For example, Rosy Finch (*Leucosticte tephrocotis*) nestlings can thermoregulate as a brood in the nest 6 days before an individual attains physiological endothermy (Yarbrough 1970), and Red-backed Shrike (*Lanius collurio*) broods can thermoregulate 3 days earlier, even out of the nest (Diehl and Myrcha 1973). Great Tit (*Parus major*) young are substantially insulated by their siblings and nest hole and probably also thermoregulate effectively before the age of physiological endothermy (Royama 1966, Mertens 1969).

These examples show the influence of insulation on the effective age of endothermy, but other factors also could be important. For instance, some nests are known to be oriented to avoid or take advantage of prevailing winds (Ricklefs and Hainsworth 1969) or thermal radiation (Calder 1973). Reflective characteristics of plumage and nest lining may have an effect on absorption of solar radiation (Linsdale 1936). Also important is any behavior by which the young seek shelter or sun, moving into temperature zones in which they can thermoregulate effectively (Bartholomew et al. 1953, Bartholomew and Dawson 1954). Lastly, differences in climate between years or among parts of a species' range may lead to variation in the age at which homeothermy becomes effective.

The adaptive significance of the timing of homeothermy depends on when it occurs under natural conditions. Any parent which modifies the nest environment such that effective thermoregulation occurs earlier in nestling growth may benefit from being able to cease brooding sooner, thus freeing both parents at an earlier stage to provide food, or reducing the risk of the parent being taken by a predator. Of course, any advantage must be considered in terms of increased reproductive output in the long run which must override any disadvantages due to time, energy, or risk involved in making the modifications to the nest environment. Selection of thermoregulatory behavior in the young must be considered in the same way.

Unfortunately, essentially no data on the age of effective endothermy, its degree of variability, or the difference between it and the age of physiological endothermy exist for any species. The specific benefits of the occurrence of effective thermoregulation before the age of physiological homeothermy have not been discussed for any species and may differ among them depending on their particular ecological circumstances.

ACKNOWLEDGMENTS

I am grateful to D. J. T. Hussell for advice on the interpretation of correlations and for comments on the paper. W. R. Dawson also gave helpful suggestions, and R. L. Marsh kindly allowed me to quote unpublished data. J. C. Barlow gave me access to the collections in his care at the Royal Ontario Museum. This work was completed under tenure of an NSF Graduate Fellowship.

LITERATURE CITED

Bartholomew, G. A. 1966. The role of behavior in the temperature regulation of the Masked Booby. Condor 68:523–535.

Bartholomew, G. A., and W. R. Dawson. 1954. Temperature regulation in young pelicans, herons, and gulls. Ecology 35:466–472.

Bartholomew, G. A., W. R. Dawson, and E. J. O'Neill. 1953. A field study of temperature regulation in young White Pelicans, *Pelecanus erythrorhynchos*. Ecology 34:554–560.

Baumgartner, A. M. 1938. A study of the development of young Tree Sparrows at Churchill, Manitoba. Bird-Banding 9:69–79.

Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers and their allies. U.S. Natl. Mus. Bull. 195.

Bent, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211.

Bent, A. C., and collaborators. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and allies. U.S. Natl. Mus. Bull. 237 (1 and 2).

Böni, A. 1942. Über die Entwicklung der Temperaturregulation bei verschiedenen Nesthockern. Arch. Suisses Ornithol. 2:1–56.

Brenner, F. J. 1964. Growth, fat deposition and development of endothermy in nestling Red-winged Blackbirds. J. Sci. Lab. Denison Univ. 46:81–89.

Calder, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. Ecology 54:127–134.

Dawson, W. R., and F. C. Evans. 1957. Relation of growth and development to temperature regulation in nestling Field and Chipping Sparrows. Physiol. Zool. 30:315–327.

Dawson, W. R., and F. C. Evans. 1960. Relation of growth and development to temperature regulation in nestling Vesper Sparrows. Condor 62: 329–340.

Diehl, B., and A. Myrcha. 1973. Bioenergetics of nestling Red-backed Shrikes (*Lanius collurio*). Condor 75:259–264.

Dunn, E. H. 1975. Growth, body components and caloric value of nestling Double-crested Cormorants. Condor 77:in press.

Ginglinger, A., and C. Kayser. 1929. Établissement de la thermoregulation chez les homéothermes au cours du développement. Ann. Physiol. Physicochim. Biol. 5:710–758.

Gotie, R. F., and J. C. Kroll. 1973. Growth rate and ontogeny of thermoregulation in nestling Great-tailed Grackles, *Cassidix mexicanus prosopidicola* (Icteridae). Condor 75:190–199.

Heydweiller, A. M. 1935. A comparison of winter and summer territories and seasonal variations of the Tree Sparrow (*Spizella a. arborea*). Bird-Banding 6:1–11.

Hudson, J. W., W. R. Dawson, and R. W. Hill. 1974. Growth and development of temperature regulation in nestling Cattle Egrets. Comp. Biochem. Physiol. 49A:717–741.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42:317–364.

Irving, L., and J. Krog. 1956. Temperature during the development of birds in arctic nests. Physiol. Zool. 29:195–205.

Kendeigh, S. C., and S. P. Baldwin. 1928. Development of temperature control in nestling House Wrens. Am. Nat. 62:249–272.

Linsdale, J. M. 1936. Coloration of downy young birds and nest linings. Condor 38:111–117.

Maher, W. J. 1964. Growth rate and development of endothermy in the Snow Bunting (*Plectrophenax nivalis*) and Lapland Longspur (*Calcarius lapponicus*) at Barrow, Alaska. Ecology 45:520–528.

Mertens, J. A. L. 1969. The influence of brood size on the energy metabolism and water loss of nestling Great Tits *Parus major major*. Ibis 111:11–16.

Morton, M. L., and C. Carey. 1971. Growth and the development of endothermy in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*). Physiol. Zool. 44:177–189.

Neal, C. M. 1973. Cooling rates and development of homeothermy in the Brown-headed Cowbird (*Molothrus ater ater*). Condor 75:351–352.

Norris, R. T. 1947. The cowbirds of Preston Frith. Wilson Bull. 59:83–103.

Palmer, R. S. (ed.). 1962. Handbook of North American birds. Vol. 1. Loons through Flamingos. Yale Univ. Press, New Haven.

Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis 110:419–451.

Ricklefs, R. E., and F. R. Hainsworth. 1968. Temperature regulation in nestling Cactus Wrens: the development of homeothermy. Condor 70:121–127.

RICKLEFS, R. E., AND F. R. HAINSWORTH. 1969. Temperature regulation in nestling Cactus Wrens: the nest environment. Condor 71:32–37.

ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. Ibis 108:313–347.

SEEL, D. C. 1969. Food, feeding rates and body temperature in the nestling House Sparrow *Passer domesticus* at Oxford. Ibis 111:36–47.

SELANDER, R. K., AND D. R. GILLER. 1961. Analysis of sympatry of Great-tailed and Boat-tailed Grackles. Condor 63:29–86.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., New York.

STONER, D. 1935. Temperature and growth studies on the Barn Swallow. Auk 52:400–407.

STONER, D. 1945. Temperature and growth studies of the northern Cliff Swallow. Auk 62:207–216.

SUMMERS-SMITH, D. 1963. The House Sparrow. Collins, London.

WEAVER, R. L. 1942. Growth and development of English Sparrows. Wilson Bull. 54:183–191.

YARBROUGH, C. G. 1970. The development of endothermy in nestling Gray-crowned Rosy Finches, *Leucosticte tephrocotis griseonucha*. Comp. Biochem. Physiol. 34:917–925.

Accepted for publication 27 September 1974.