

GROWTH RATE AND ONTOGENY OF THERMOREGULATION IN NESTLING GREAT-TAILED GRACKLES, *CASSIDIX MEXICANUS PROSOPIDICOLA* (ICTERIDAE)

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The ontogeny of birds is often characterized by initial periods of poikilothermy followed by acquisition and maintenance of homeothermy (Baldwin and Kendeigh 1932; Kendeigh 1939; Dawson and Evans 1957). In altricial species, early periods of poikilothermy tend to restrict energy expenditures by young birds to those related to maintenance and development of organ systems (Dawson 1962). Furthermore, avian evolution has proceeded toward the altricial state, smaller adult body size, and diversification and elaboration of parental behavior (Kendeigh 1952; Dawson 1962). According to Huxley (1927), the altricial condition permits a reduction in time between fertilization, egg deposition, and subsequent hatching, thereby reducing energy expenditures per egg produced by the female. Hence, reduced incubation periods are associated with the production of smaller eggs, reduced energy content per egg, and immature hatchlings (Huxley 1927; Witschi 1956).

Ontogeny of thermoregulation was studied in precocial species by Bartholomew and Dawson (1952, 1954), Ryser and Morrison (1954), Farner and Serventy (1959), Howell and Bartholomew (1961), and Bartholomew (1966); and, in altricial species by Baldwin and Kendeigh (1932), Kendeigh (1939), Dawson and Evans (1957, 1960), Ricklefs and Hainsworth (1968), and others.

There are few studies that relate growth rates and body temperatures in altricial species (Baldwin and Kendeigh 1932; Dawson and Evans 1957, 1960), and these involve a limited number of species and families. Our study was initiated to clarify the ontogenetic relationships of thermoregulation in nestling Great-tailed Grackles (*Cassidix mexicanus prosopidicola*). This species is abundant in the southern United States and it is considered a major economic pest (Besser et al. 1968). Since *C. m. prosopidicola* has expanded its range northward within the past decade

(Selander and Giller 1961) and is considered to be an economic liability (Besser et al. 1968), this species requires further study.

SUBJECT AND METHODS

Great-tailed Grackles occur as far north as Kansas, east to Louisiana, south to northern South America, and west to Arizona (Bent 1958; Kincaid 1958; Selander and Giller 1961; Kolb 1966). According to Selander and Giller (1961) and Tutor (1962), it is both a summer and winter resident throughout east-central Texas, nesting from early April to late July. The incubation period varies from 11–13 days (Selander and Giller 1961; Tutor 1962).

During the period 27 June through 30 July 1971, nestlings were removed periodically from nests (located on the Texas A&M University campus), brought into the laboratory, and tested for thermoregulatory capabilities. Methods were those of Ricklefs and Hainsworth (1968), with the following modifications. Nestlings were confined within a natural nest, and whenever two or more individuals were tested simultaneously, they were separated by a plexiglass partition. We found that plexiglass was a good insulator, and did not conduct heat. All tests were conducted with a single nest to eliminate possible differences in nest insulation. Thermoregulation at low-temperature regimes was studied by inserting quick-registering, tele-thermometer thermistor probes (Yellow Springs Inst. Co.) equal distances into the rectum (probes were passed through the cloacal cavity and into the rectum), and placing the birds in the nest in a controlled cold temperature cabinet at 5°C ($\pm 0.5^\circ\text{C}$). Thermistor probes were held in place with a small tape harness to assure uniform insertion of the probe. Air, nest, and body temperatures were recorded at 5-min intervals for 1 hr. Birds held at temperature regimes of 22 and 40°C in a modified drying oven were studied as above.

Responses of nestlings to decreasing and increasing temperatures were studied by methods similar to those in Baldwin and Kendeigh (1932). Nestlings were placed initially in the cold temperature cabinet at 22°C, maintained at this temperature for 1 hr, and then subjected to progressive cooling (22–0°C) at 1°C/min. Air, nest, and body temperatures were taken at 1-min intervals throughout the tests. Similar tests, involving high-temperature gradients (22–45°C), were conducted using the modified drying oven. Experiments at 5°C, 22°C, and 45°C were conducted at 70%, 70%, and 40% relative humidities, respectively. Body weights, tarsal lengths, body tempera-



FIGURE 1. A Great-tailed Grackle nest. The nest is important in insulating the young birds.

tures, and lengths of second primaries were taken immediately before each test.

In order to complement information obtained in the laboratory, we monitored body temperatures of nestlings under natural conditions. Tele-thermometer thermistor probes were inserted rectally and body temperatures recorded at 12-min intervals by a six-stage sequential compiler which had been modified from a Rustrak recorder (Gulton Ind., Inc.). Tests were conducted over 24-hr periods during which air and internal nest-cup temperatures were recorded simultaneously. Electrodes did not appear to interfere with normal nestling behavior. Using a Wilson-Goodlet multiple regression analysis we tested for correlation and regression of body weight vs. age, body weight vs. body temperature, body temperature vs. age, and body weight vs. tarsal length. Calculations pertaining to instantaneous growth rates were obtained by the formula

$$Kg = \frac{\log_e Y_1 - \log_e Y_0}{t_1 - t_0}$$

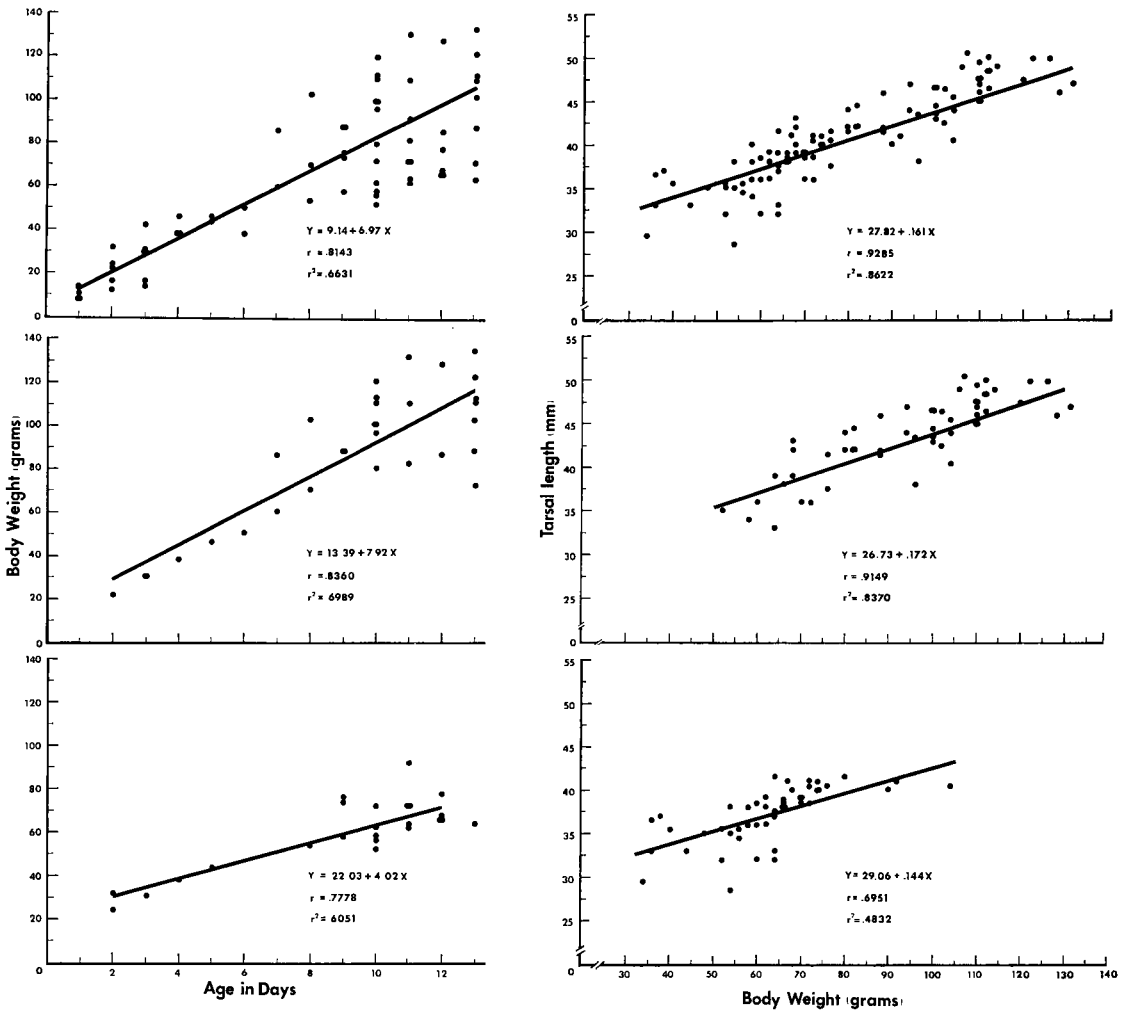


FIGURE 2. Multiple regression analyses of data pertaining to growth rates of nestling Great-tailed Grackles. Left: relationships between body weights and ages in males and females (top); males (middle); females (bottom). Right: relationships between tarsal lengths and body weights in males and females (top); males (middle); females (bottom). Lines were fitted by the Wilson-Goodlet multiple correlation test.

TABLE 1. Growth rates of Great-tailed Grackle nestlings expressed as changes in body weights (grams).

Age in days	Mean body weight (g)	Log _e Y	K _e	Mean growth rate (g day ⁻¹)	% Growth per day
1	10.0(4) ^a	2.302	—	—	—
2	21.2(5)	3.054	0.752	11.2	53%
3	27.2(6)	3.303	0.249	6.0	22%
4	40.7(3)	3.706	0.403	13.5	33%
5	45.0(3)	3.807	0.101	4.3	10%
6	44.0(3)	3.784	0.023	-1.0	-2%
7	73.0(3)	4.290	0.506	29.0	40%
8	75.7(3)	4.327	0.037	2.7	4%
9	76.8(5)	4.341	0.014	1.1	1%
10	84.8(12)	4.440	0.099	8.0	9%
11	85.6(9)	4.560	0.120	0.8	1%
12	79.9(7)	4.381	0.179	-5.7	-7%
13	100.5(8)	4.610	0.229	20.6	20%

^a Sample sizes are given within parentheses.

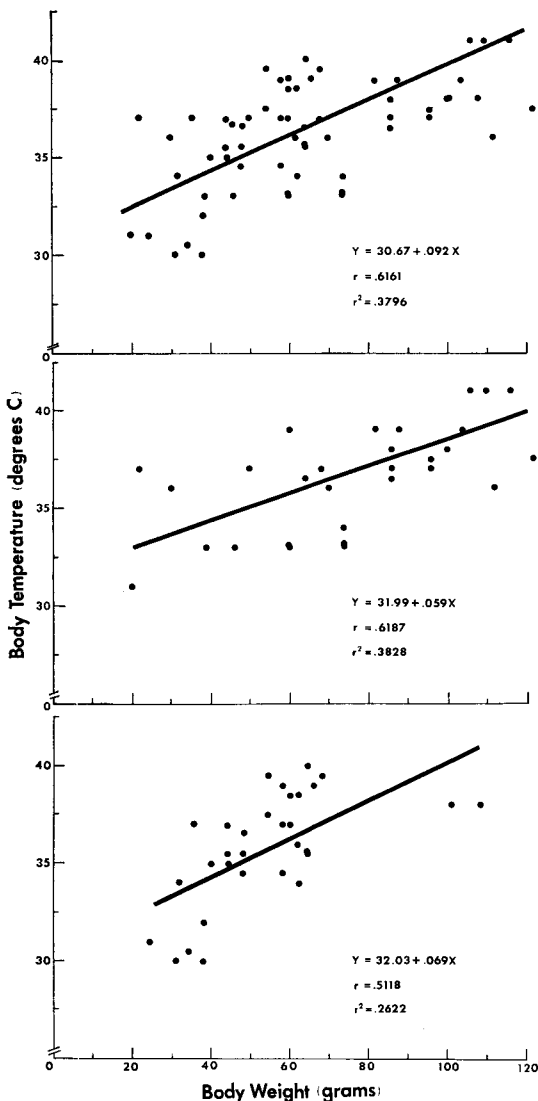


FIGURE 3. Multiple regression analyses on body temperatures vs. body weights. Males and females (top); males (middle); females (bottom). Lines were fitted by the Wilson-Goodlet multiple correlation test.

where K_g represents the geometric rate of increase; Y_0 is the initial value; and Y_1 is the value after the time interval $t_1 - t_0$. Other statistical tests and calculations are discussed below.

RESULTS

Nests and nestlings. Great-tailed Grackle nests (fig. 1) are cup-shaped structures built of long strips of grass, vines, twigs, and, in some cases, paper or cloth which are woven around supporting branches. The cup is usually lined with mud and grass, although in some cases paper is used. Bailey and Griffin (1969) reported the following dimensions: nest depth 10–33 cm; cup depth 5–10 cm; and longest dimensions of cup 13–21 cm. In our study, nests were located in live oak trees (*Quercus virginianus*), 4.5–18 m above the ground. Nest dimensions and construction were within the limits described by Bailey and Griffin (1969).

On hatching, nestlings are blind and naked and, in our study, they weighed an average of 10 g (range, 8.0–14 g) (table 1, fig. 2). Growth rates for males and females collectively averaged 7.54 g/day. During the 13+ day nestling period (individuals were sexed by gross examination of leg joint and tarsal length; Arnold, unpubl. data). Males averaged 11.96 g/day and females averaged 7.18 g/day. These data agree with the observations of Selander and Giller (1961) on the dimorphic nature of this species. However, a Z-statistic test (Ostle 1963) on the null hypothesis, $\rho_{\delta} = \rho_{\text{f}}$, indicated that the slopes of these data were not significantly different ($P < 0.05$). Multiple regression analysis (fig. 2) suggests significant rectilinear relationships ($P < 0.01$) between body weight and age in males ($r = 0.8360$; mult. $r^2 = 0.6989$), females ($r = 0.7778$; mult. $r^2 = 0.6051$), and males and females collectively ($r = 0.8143$; mult. r^2

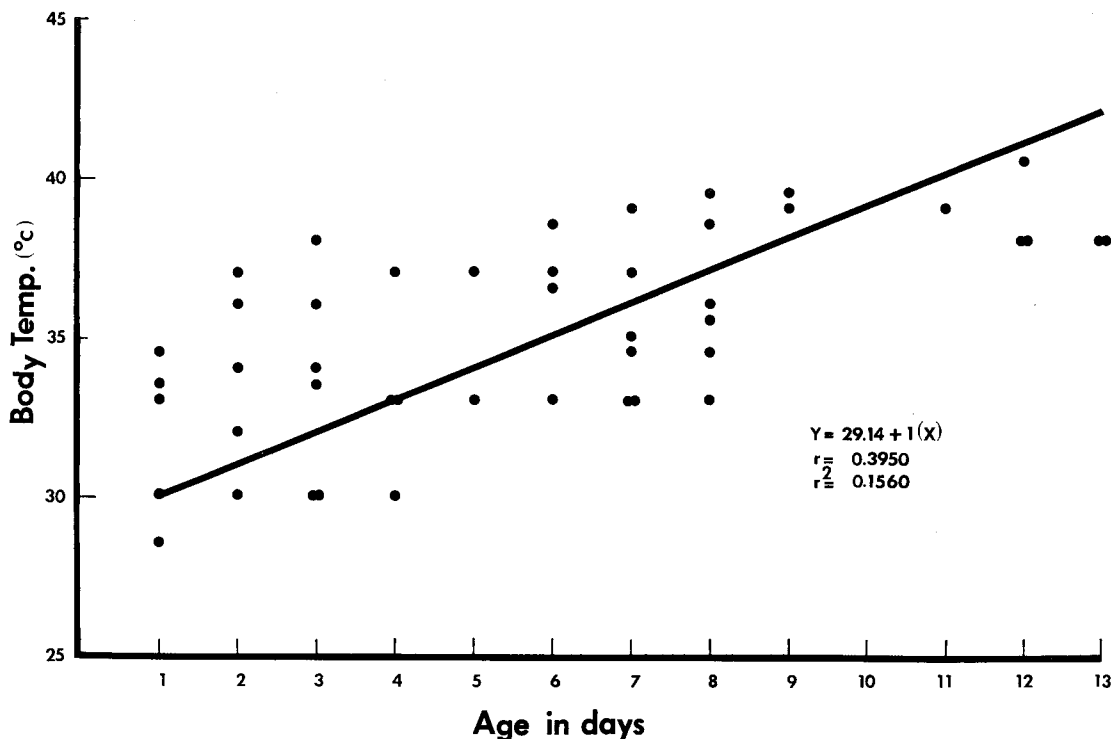


FIGURE 4. Multiple regression analyses on body temperatures vs. age for males and females collectively. Regression line was fitted by the Wilson-Goodlet multiple correlation test.

= 0.6631). Other regression analyses (fig. 2) reflected significant rectilinear relationships ($P < 0.05$) between tarsal length and body weight in males ($r = 0.9148$; mult. $r^2 = 0.8370$), females ($r = 0.6951$; mult. $r^2 = 0.4831$), and males and females collectively ($r = 0.9285$; mult. $r^2 = 0.8621$). A Z-statistic test (null hypothesis, $\rho \delta = \rho \varphi$) gave a significant difference ($P < 0.05$) between rates of tarsal development in males and females. We must note here, however, that these data (viz., age vs. body weight, and tarsal length vs. body weight) probably represent curvilinear relationships when adults and nestlings are considered in toto. But, in this case, the data truly fit ($P < 0.05$) rectilinear models within our class limits. Correlations between age and tarsal lengths give extremely low r -values (viz., males, $r = 0.2210$; females, $r = 0.4114$; males and females, $r = 0.2781$) and do not fit rectilinear or curvilinear models ($P > 0.30$).

Ontogeny of thermoregulation. We divided nestlings into three developmental classes representing featherless stages, feather eruption stages, and pre fledgling stages. These classes had weights of 0–40 g, 40–80 g, and 80–120+ g (individuals weighting exactly 40 or 80 g were included in the preceding weight class). Mean body temperatures (taken in (the nest) for these weight classes were:

29.0°C (24–32.5°C, N = 12); 33.6°C (33.5–40°C, N = 16); and 37.4°C (33.5–40°C, N = 12), respectively. Hence, body temperatures maintained by nestlings increased with body weight to a point where they approach normal, adult body temperatures (approximately 40°C). Regression analyses for males, females, and both sexes indicate a significant ($P < 0.01$) rectilinear relationship between both weight and body temperature (fig. 3). Other regression analyses on body temperatures vs. age indicate a rectilinear relationship ($P < 0.05$; fig. 4). However, the correlation coefficient for these data was very low (i.e., $r = 0.3950$; mult. $r^2 = 0.1560$). Therefore, thermoregulatory capabilities increase with body weight and age, but are more closely related to body weight than age.

In order to demonstrate development of thermogenic mechanisms in hatchlings, we subjected them to low temperature regimes. Twenty-nine nestlings of different weights and ages were observed in a static test at 5°C and at cold gradients of 24–0°C ($\Delta T = 1^\circ\text{C}/\text{min}$). In both experiments, individuals in the 0–40 g class behaved as poikilotherms, while some of those in the 40–80 g and those in the 80–120+ g classes showed progress toward homeothermy (figs. 5 and 6). Losses in body temperatures by 0–40 g nestlings during cold

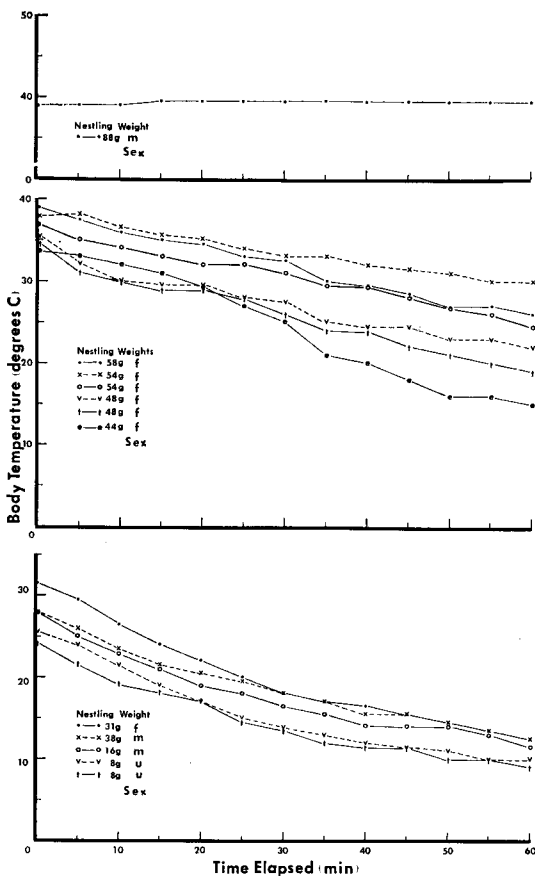


FIGURE 5. Thermal behavior of 12 nestlings of different weights in static 5°C tests. Note that thermoregulatory capabilities increase with weight.

gradient tests averaged 7.72°C, and were significantly greater ($P < 0.01$) than those of birds in the other two weight classes ($t = 3.67$ and 5.28, respectively). Thermogenic abilities increased with weight to fledging (80–120+ g), at which time the birds were able to fly and forage among adults.

Previous studies (cf. Baldwin and Kendeigh 1932; Ricklefs and Hainsworth 1968) dealt primarily with abilities of altricial nestlings to thermoregulate at extremes of temperature. Therefore, we subjected nestlings to a constant temperature of 22°C. Thermoregulatory capabilities appeared at lower body weights and ages (fig. 7) than observed in the previous low-temperature tests. Nestlings in the 40–80 g class maintained body temperatures well above ambient, whereas individuals in this class failed to maintain stable body temperatures at 5°C (fig. 5). Individuals in the 0–40 g class were unable to thermoregulate at 5°C or 22°C.

Thermolysis. To study thermolytic capabilities of nestlings at high temperatures, we

tested 14 individuals at a constant 40°C (fig. 8) and 29 individuals in a high-temperature gradient of 22–45°C. Individuals in all three classes exhibited hyperthermia during the static test. Certain thermolytic behaviors (i.e., panting with the mouth open, spreading of the wings, and escape reactions) were more apparent in older birds, and presumably facilitated dissipation of body heat by these individuals. Panting appeared first at weights of 40–80 g (approximately 6 days of age) and continued through fledging. Panting was not observed in birds weighing 0–40 g. Completely feathered birds seemed at a disadvantage when confined within the nest (fig. 8) and often exhibited signs of heat stress (i.e., calling, trying to escape). The presence of feathers plus the thermal properties of the nest probably contributed to this situation. However, one individual (116 g) periodically lowered its body temperature by panting (fig. 8).

Mean changes in body temperatures shown by birds of three weight classes at static tests of 5°C, 22°C, and 40°C are presented in figure 6. Nestlings in all weight classes exhibited greater fluctuations in body temperatures during cold (5°C) tests than during moderate (22°C) or high-temperature (40°C) tests. Fluctuations in body temperatures at 22°C were much less than those at temperature extremes. In all cases, however, a general decline in body-temperature fluctuations occurred with increased body weight.

Field observations. In order to complement data from laboratory experiments, we conducted 24-hr temperature studies on three nestlings under field conditions. A typical 24-hr recording of body, air, and nest temperatures is presented in figure 9. The test on a 6-day nestling weighing 48 g began at 18:00 (CDT) on 14 July 1971 and continued through 20:00 (15 July). The female returned to the nest shortly after the electrodes were implanted. She continued to brood the young (section A, fig. 9) through 08:00. During this time, the nestling's body temperature approximated air temperature and dropped to a minimum of 26°C. The nestling was inactive during this period and was not fed by the female. The nest maintained a high temperature, which was probably due to the female's presence. At 08:00, the female left the nest (section B, fig. 9), and a corresponding drop in nest temperature was recorded. The female returned at 08:30 and fed the young. The presence of the female plus nestling activity caused a rapid increase in nest and nestling

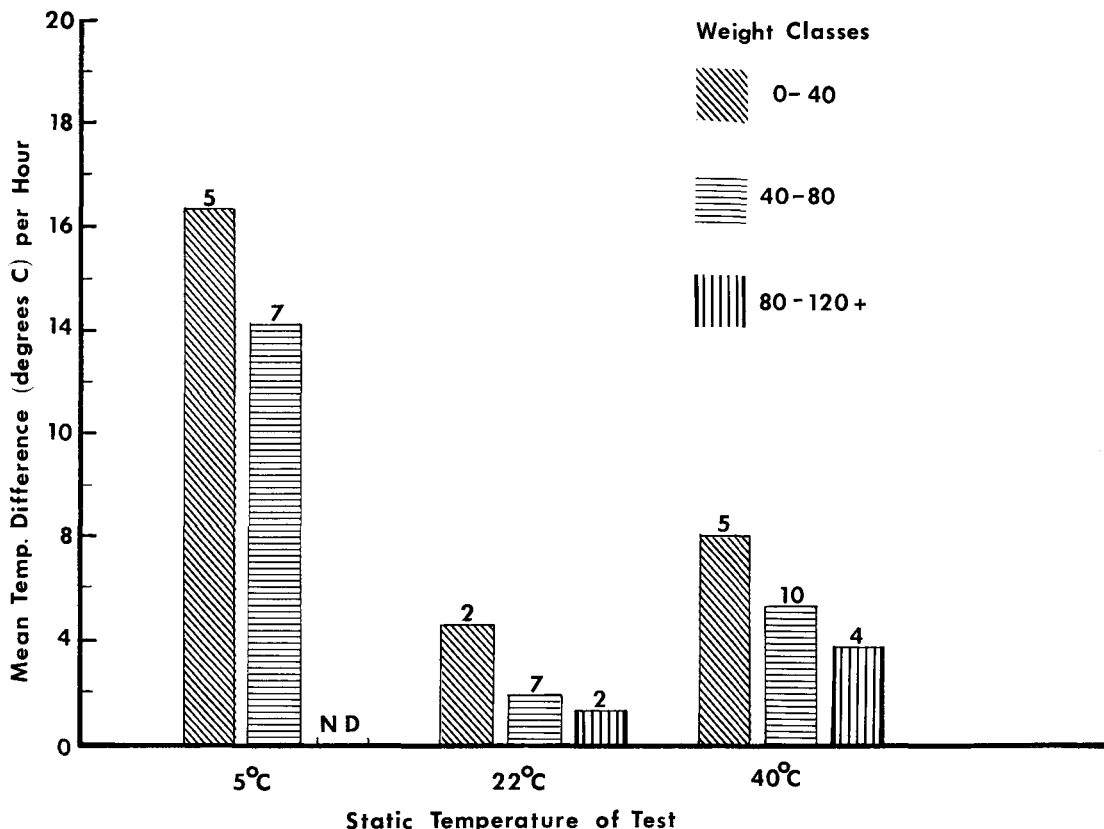


FIGURE 6. Mean differences in body temperature between start (0 min) and finish (60 min) of static tests. Sample sizes are given above each bar.

body temperature (section C, fig 9). Nestling body temperature continued to climb throughout the day and closely approximated that of the nest (section D, fig. 9). Another feeding period occurred between 14:00 and 18:00, resulting in a second rapid rise in nestling body temperature (section E, fig. 9).

DISCUSSION

The initial poikilothermy in nestlings of certain altricial species may be evolutionarily significant in that this condition restricts energy expenditures by nestlings to those involving development and maintenance of organ systems, thereby hastening fledging. Huxley (1927) and others have suggested that the altricial condition permits reduction in incubation periods and energy expenditures per egg. We suggest further that such conservation of energy may be offset by increased energy expenditures by adult birds during brooding, reflecting a higher degree of behavioral development than among precocial species. Hence, energy conservation occurs only at the nestling level, as more energy is required to go from food → adult → egg material → young than from food → young. The

brooding behavior of adults probably protects the nestlings from temperature extremes, allowing the young to develop at economical growth rates.

In Great-tailed Grackles, development of thermoregulation takes place gradually over the nestling period (13+ days) and probably involves differential maturation of neural, hormonal, muscular, and integumental systems. However, there is no evidence about the relative contributions of the above in the acquisition of thermoregulatory capabilities in this species. The nestling period is probably characterized by three periods of rapid growth (i.e., at 1, 6, and 12 days), which are reflected in body-weight increases (table 1). The first 5 days of growth involve rapid increases in body weight and concomitant development of organ systems (Dawson and Evans 1960). Feather eruption occurs at 5 days and, at this time, there is a rapid decline in growth rate. This probably results from tremendous energy expenditures for feather development. The eruption of feathers is followed (at ca. 6-7 days) by another rapid growth period. At this time, certain heat-retaining and thermolytic abilities are first

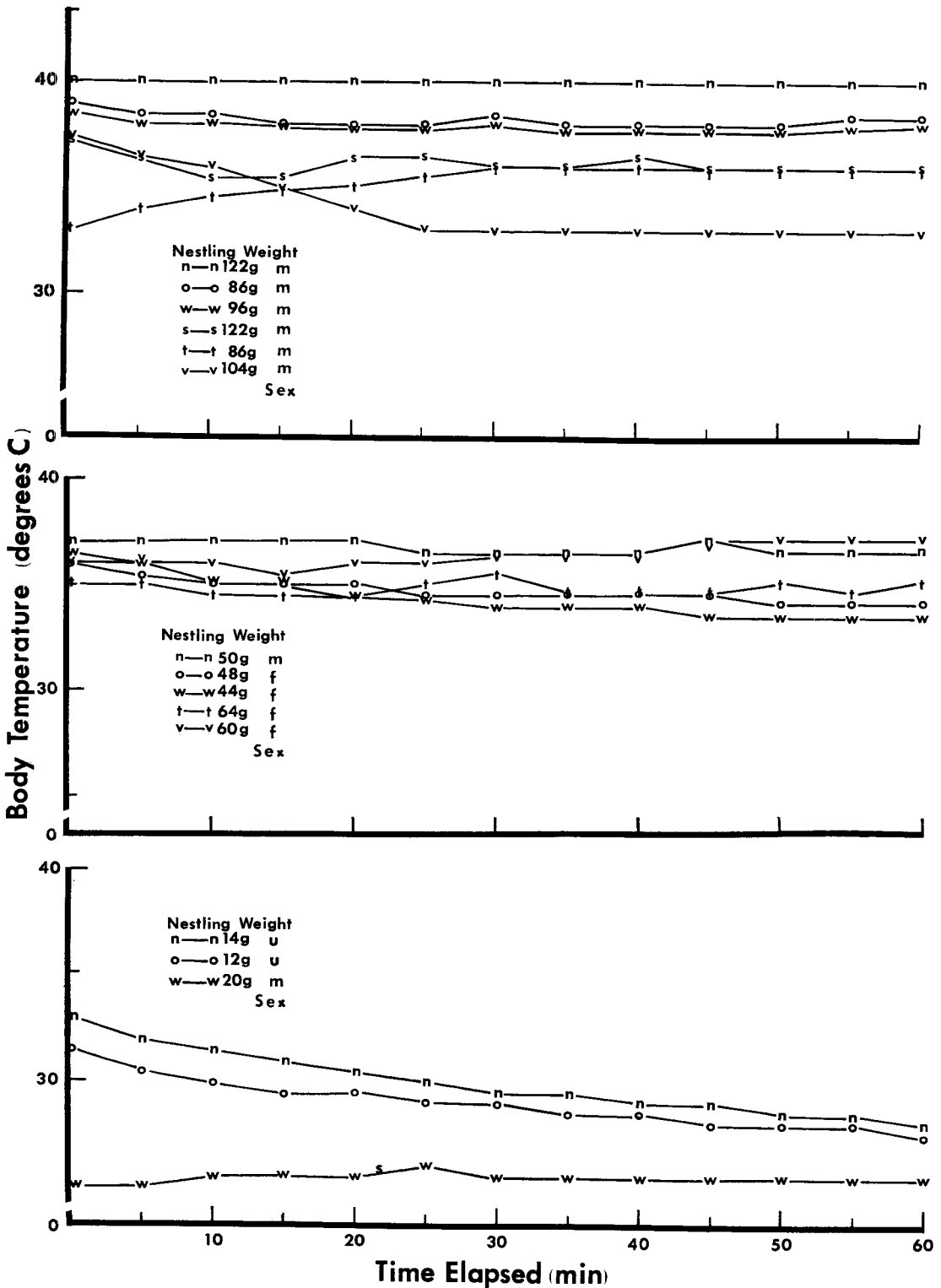


FIGURE 7. Thermal behavior of 14 nestlings of different weights in static 22°C tests. Note that thermoregulatory capabilities occur at lower weights than at high-temperature (40°C) or low-temperature (5°C) tests.

apparent. Growth rates then decline until 12 days when there is a third and final rapid growth period. Declines in growth rates must result from energy expended in tissue main-

tenance and increased involvement of thermoregulatory mechanisms. At approximately 13 days, fledglings resemble adults but lack complete feather development and adult body

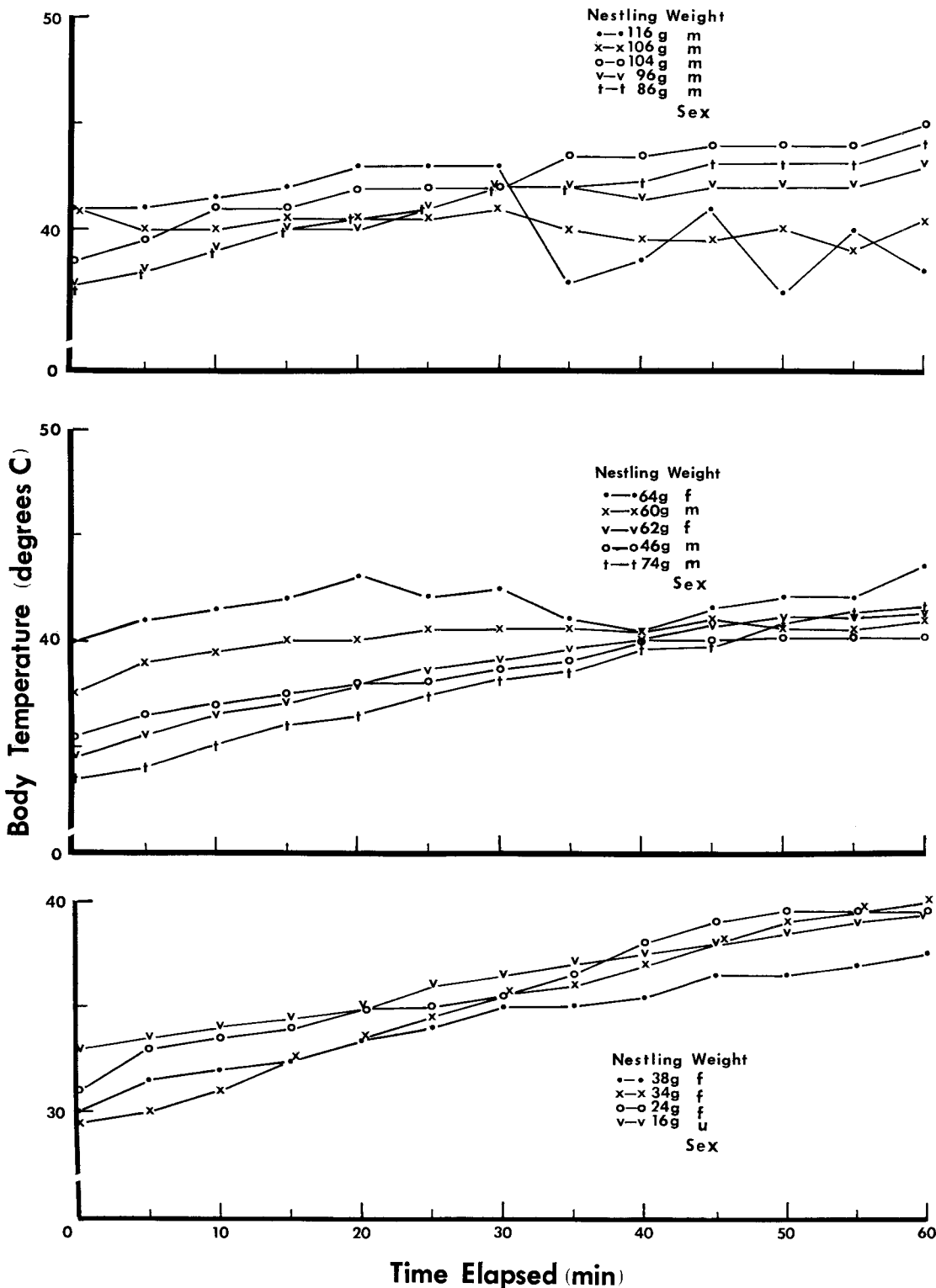


FIGURE 8. Thermal behavior of 14 nestlings of different weights at static 40°C tests. Fully feathered individuals (heavier birds) are at a disadvantage at high temperatures due to the insulatory nature of feathers.

size. According to Ricklefs and Hainsworth (1968), increases in growth rates at fledging probably involve the development of flight muscles and other flight-related mechanisms.

Although the above data may reflect random fluctuations due to sampling, they agree with observations by Arnold (pers. comm.) on this same species.

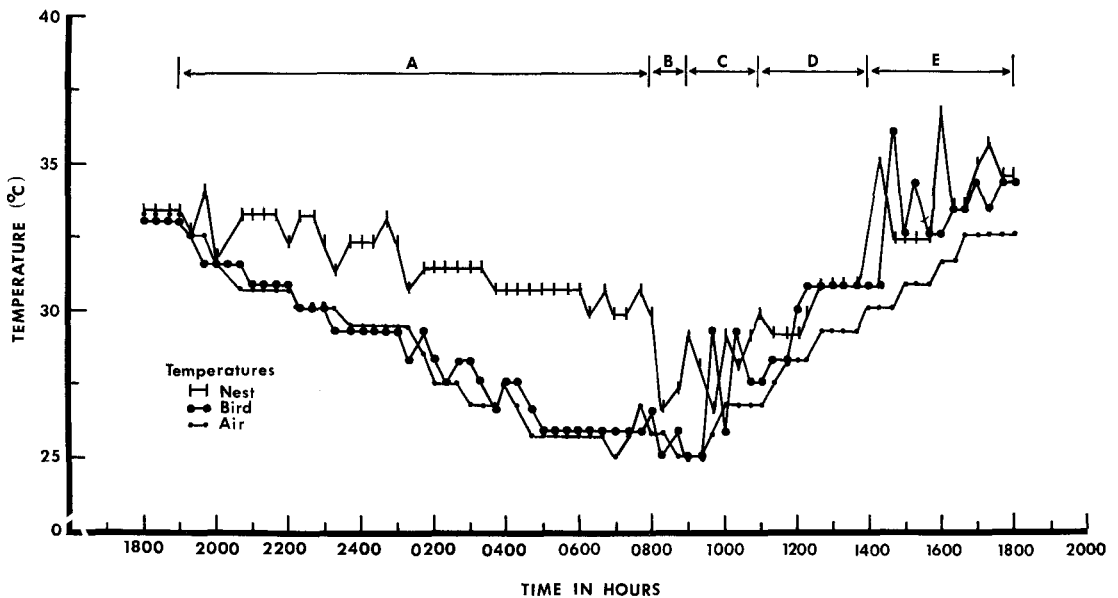


FIGURE 9. Twenty-four hour plots of nestling body, nest, and air temperatures for the period 14–15 July 1971. The bird weighed 48 g. See text for explanation of letters.

Observations on the thermal behavior of nestlings maintained at static temperatures of 5°C, 22°C, and 40°C suggest that thermolytic mechanisms develop prior to thermogenic mechanisms. At 6 days of age, certain physiological and behavioral phenomena (i.e., panting, spreading of wings, and escape responses) appear which serve to dissipate heat accumulated by the body. Nestlings less than 6 days of age (0–40 g) are unable to dissipate heat effectively, and their body temperatures often approached ambient values during static 40°C tests. Individuals in the 40–80 g class could maintain relatively constant body temperatures after 35-min exposure to 40°C, whereas body temperatures of those in the 80–120+ g class became constant after 20-min exposure. We must note here, however, that completely feathered birds, when confined to the nests, were at a disadvantage during these tests. Feathers became a liability as they served to hold heat within the body. Normally, a fully feathered bird could escape high-temperature regimes by moving within or leaving the nest. We have concluded from these data that thermolytic systems develop early (ca. 6th day) and continue to improve with age. Further, behavioral mechanisms enhance thermoregulatory capabilities. These facts may be significant in allowing the expansion of range by this species into primarily arid, hot climates.

Newly hatched Great-tailed Grackles are unable to maintain stable body temperatures, and during cold tests body temperatures often

dropped to 10°C. Sustained body temperatures appear much later in the nestling period (ca. 10th day) than thermolytic mechanisms. This species is tropical and semi-tropical in distribution and individuals are rarely subjected to environmental temperatures below 20°C during the nesting season. All nestlings (0–13+ days) tested at moderate temperatures (22°C) maintained relatively constant body temperatures.

Female Great-tailed Grackles remain at the nest and brood very young nestlings from sunset to sunrise. Although the temperature of the nest remains relatively stable during this period, nestling body temperatures continue to decline throughout the night in response to decreasing air temperatures. The young are not fed, their activity is minimal, and we feel that the decline results from decreases in digestive activity, muscular activity, and energy reserves. This hypothesis is supported by the observation that body temperatures increased rapidly during and after feeding periods. By 8–10 days, nestlings are able to maintain fairly stable body temperatures. As they mature, the female spends proportionately less time with them. Furthermore, females shade very young nestlings during extremely hot portions of the day, protecting them from lethal or near-lethal temperatures. Older nestlings have well-developed muscular coordination and are able to move to more favorable areas (supporting limbs and edge of nest) when environmental temperatures exceed their thermoregulatory capabilities.

SUMMARY

Growth rates and development of homeothermy in nestling Great-tailed Grackles were studied from 27 June through 30 July 1971. Thermolytic mechanisms develop at about the 6th day, whereas those related to thermogenesis develop at about the 10th day. Older nestlings dissipate body heat by panting and spreading of wings. When confined to the nest during 40°C tests, fully feathered individuals exhibited heat stress. All nestlings functioned well at temperatures within normal environmental limits (i.e., 22–30°C). Mechanisms for heat retention are less important than thermolytic mechanisms at those air temperatures which occur during the nesting season. The brooding behavior of females may be important during the first few days of life in protecting young from particularly high-temperature extremes. Females brood the young throughout the night and shade them during hot portions of the day. Growth of nestlings is characterized by three rapid growth periods. The first occurs shortly after hatching and reflects the greatest amount of weight increase. The second occurs shortly after feather eruption, and the third takes place just prior to fledging. The latter period probably involves development and maturation of flight muscles and related flight mechanisms.

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