

stomach oils is to store energy and water during their first week at sea.

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Thermal Relations of Nestling Red-winged Blackbirds in Southeastern Michigan

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Low ambient temperatures or abnormal rainfall may reduce the nesting success of birds by lowering the body temperatures, and therefore the growth rates, of the nestlings (Case 1978), reducing clutch sizes (see Klomp 1970), or increasing the incidences of starvation or nest abandonment because of an inability of

the parents to feed their young (e.g. Brenner 1966, 1968). The neonates and young of many altricial passerines may be especially vulnerable to adverse weather conditions if left alone in the nest because they are relatively small and lack thermoregulatory capabilities. For example, young Red-winged Blackbirds (*Agelaius phoeniceus*) weigh approximately 3-4 g at hatching, and they are largely naked and incapable of effective thermoregulation for roughly the first half of the 10-day nestling period (Holcomb and Twiest 1971, Hill and Beaver 1982, Olson in prep.) By day 4,

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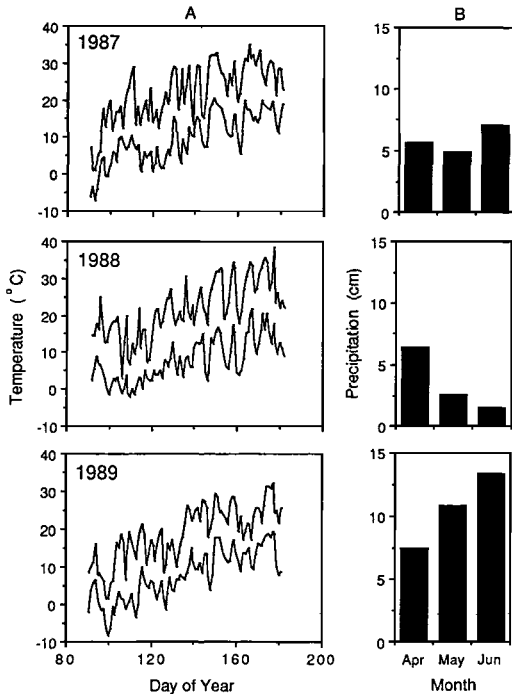


Fig. 1. Daily maximal and minimal temperatures ($^{\circ}\text{C}$) and total precipitation (cm) for April, May, and June 1987-1989.

nestlings are unattended for up to 96% of the daylight hours (Hill and Beaver 1982). The female parent must spend an increasing amount of time foraging to provide enough food to support their eight- to elevenfold increase in body mass during the nestling period (Williams 1940, Case and Hewitt 1963, Brenner 1964, Holcomb and Twiest 1970, Olson in prep.), thereby precluding extensive brooding.

Very little is known about the thermal relations of passerine nestlings in general or Red-winged Blackbird nestlings in particular. Brenner (1964, 1968) reported nest and body temperatures of nestlings at several ages. However, only mean values representing measurements over a fairly narrow range of ambient temperatures were presented, which precludes extensive analysis of the relationships among nest temperature, ambient temperature, and nestling body temperature. Therefore, I determined the thermal relations of Red-winged Blackbird nestlings in their nests in light of the variable environmental conditions and cool temperatures typical during their breeding season in Michigan (i.e. ambient temperatures well below the incubation temperature [37°C] for this species; Holcomb 1974) and the profound increases in body mass and thermoregulatory capabilities of the nestlings during the postnatal period.

This study was conducted between early May and late June (1987-1989), the peak of the breeding season

in southeastern Michigan (Fiala 1981b), in three marshes near Ann Arbor, southeastern Michigan: (1) "Doyle" site, located on Doyle Road in Livingston County, 27.2 km northwest of Ann Arbor near the E. S. George Reserve of the University of Michigan; (2) "Gosline" site, a marsh located on the property of William and Alice Gosline, ca. 16 km north of Ann Arbor, Washtenaw County; and (3) "Fosdick" site, located on the corner of State Highway 12 and Fosdick Road ca. 9.6 km directly south of Ann Arbor, Washtenaw County (1988 and 1989 only). The vegetation at all sites was similar, and included common and narrow-leaf cattails (*Typha latifolia* and *T. angustifolia*, resp.), bulrushes (*Scirpus acutus*), sedges (*Carex* spp.), pond lilies (*Nuphar* sp. and *Nymphaea* sp.), willows (*Salix* spp.), and several species of grasses. Deciduous and evergreen trees bordered the three marshes.

Nests were built at variable heights above water predominantly in cattails, but were located in a variety of habitats with differing amounts of cover near the nest. Nests were found usually during oviposition or the 11- to 12-day incubation period, and were monitored every day in the morning or early afternoon to determine the hatching sequence, age, and status of all nestlings. Nestlings were assigned an age of 0 days on the day of hatching. Fledglings were collected in the marshes while they perched in the cattails. Birds were handled and measured only once to minimize disruption of the nests and nestlings.

After noting the age and number of the nestlings, I measured (1) ambient temperature (T_a) within 10 cm of and in the same conditions (shade, broken sun, or direct sun) as the nest cup at the time of measurement; (2) temperature in the nest adjacent to an interior wall but not near any nestlings (T_{nest}); and (3) body temperature of the nestling(s) ($T_{\text{b-field}}$), taken within 5 min of approaching the nest, using a YSI tele-thermometer with the tip of the probe inserted 1-2 cm (depending on nestling size) into the cloaca. Because fledglings were not closely associated with a nest, only T_a and their $T_{\text{b-field}}$ were taken at the time of collection. All measurements were made between 0800 and 1700 EDT.

Daily maximal and minimal temperatures (midnight to midnight, EST) and precipitation (1700-1700 EDT) were compiled at the University of Michigan. All three measures increased significantly between April and June in all three years of the study (Fig. 1). Comparisons of the monthly mean temperatures and total precipitation revealed that the conditions between April and June, 1989, were cooler (ANOVA; $P < 0.005$) and much wetter than the corresponding months in 1987 and 1988 (Fig. 1). In addition, the mean maximal temperatures during both May and June (but not April) in the first 2 yr of the study were significantly higher than the averages for each of these months during the previous 100 yr (1889-1989) ($P < 0.05$, t -test), whereas those in June 1989 were cooler than normal ($P < 0.05$, t -test). Precipitation also deviated significantly from the 100-yr averages. The

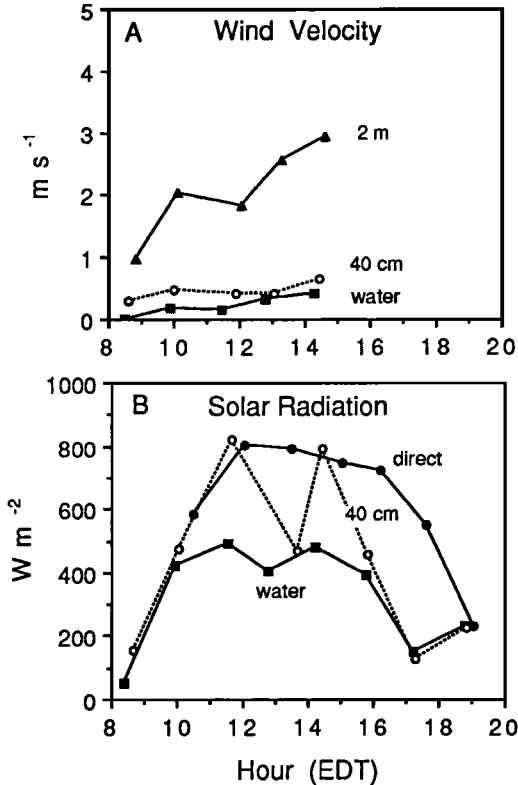


Fig. 2. Microclimatological data at Gosline marsh on 26 May 1989. (A) Wind velocity ($m \cdot s^{-1}$) at water level (—■—), and at 40 cm ($\cdot \cdot \circ \cdot \cdot$) and 2 m above the water (ca. 1 m above the top of the cattails) (—▲—) in the cattail marsh. (B) Solar radiation ($W \cdot m^{-2}$) in direct sunlight on a landing (—●—), and at water level (—■—), and 40 cm ($\cdot \cdot \circ \cdot \cdot$) above the water in the cattail marsh.

breeding seasons in 1987 and 1988 were much drier, and in 1989 much wetter, than normal. Total precipitation over the 3 months (April to June) was 6.6 cm below (1987), 13.1 cm below (1988), and 7.5 cm above (1989) the 24.2-cm normal level for this period.

On 26 May 1989, I measured solar radiation and wind velocity over several hours in the vicinity of the nests at the Gosline site to characterize the temporal and spatial heterogeneity of a cattail marsh. The daily fluctuations of ambient temperatures were typical of a clear day in late May, although the wind was more intense than usual. Significant temporal and spatial variation in the microclimatological conditions of the nest sites existed within the cattail marsh (Fig. 2). Wind velocity increased markedly with time of day and height above the ground; the latter trend generally conformed to the well-known logarithmic attenuation of this variable with decreasing height. In addition, solar radiation at sites in direct sun in-

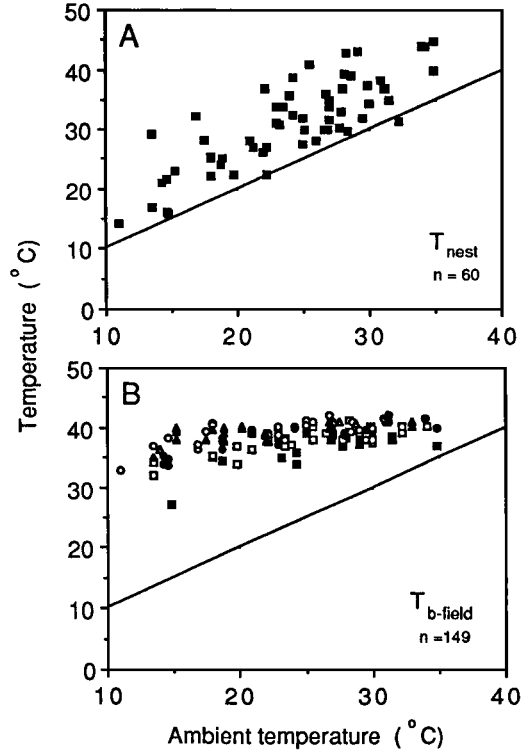


Fig. 3. Temperatures in the nest (A) and of nestlings in several age classes (B) as a function of ambient temperature. Age classes: 0- to 2-day olds (■); 3- to 4-day olds (□); 5- to 6-day olds (●); 7- to 8-day olds (○); 9- to 10-day olds (▲); fledglings (△). The solid line illustrates the isothermal line for ambient temperature. The relationships were best described as follows: $T_{nest} = 1.01 (T_a) + 6.68$ ($n = 60$; $P < 0.0001$; $r^2 = 0.69$), and $T_{b-field} = 0.23 (T_a) + 33.03$ ($n = 149$; $P < 0.0001$; $r^2 = 0.34$).

creased twentyfold throughout the day. At midday it was double that measured in partially shaded sites near the ground (Fig. 2).

The length of both the daily and seasonal observation periods and the variable weather conditions during the 3 yr of this study (Fig. 1) provided a fairly wide range of ambient temperatures (11–35°C at time of measurement) to examine the thermal relations of the nest and nestlings. Generally, T_{nest} tracked T_a (Fig. 3A), and the slope of this relationship (1.01) did not differ significantly from that of the isothermal line ($P = 0.88$, t -test). However, T_{nest} averaged 6.7°C higher than T_a , probably because of the effects of solar radiation and protection of the inside of the nest cup from wind. In contrast, $T_{b-field}$ was generally independent of both ambient temperature (Fig. 3B) and nest temperature (Fig. 4). Nearly all $T_{b-field}$ values fell between 35°C and 41°C, a range only slightly below the average body temperature of adults (mean $[\pm 1 \text{ SEM}]$

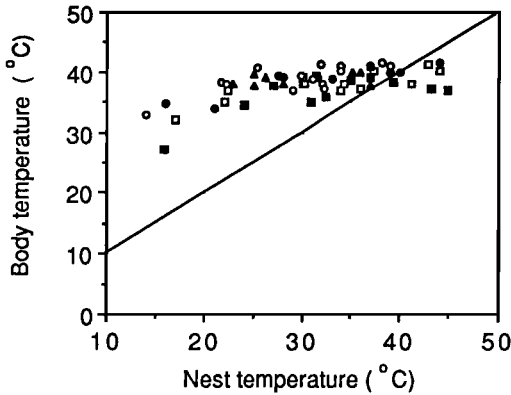


Fig. 4. Nestling body temperature as a function of nest temperature. Symbols as in Fig. 3. The solid line illustrates the isothermal line for nest temperature. The two variables are related as, $T_{b\text{-field}} = 0.22(T_{\text{nest}}) + 31.44$ ($n = 58$; $P < 0.0001$; $r^2 = 0.40$).

$= 41.1 \pm 0.2^\circ\text{C}$, $n = 15$; Olson 1990). The slopes of both the overall regressions (0.23 and 0.22, respectively) and of the lines for each of the 6 age classes (Fig. 3: legend) were all significantly lower than that of the isothermal line ($P < 0.0001$; t -test) and not significantly different from 0 ($P < 0.1$; t -test). Although the $T_{b\text{-field}}$ of nestlings in the youngest age class (0- to 2-day olds) fluctuated with ambient temperature slightly more than those in the oldest age class during the nestling period (9- and 10-day-olds) ($P < 0.005$; ANCOVA), the body temperatures of nestlings in these two disparate age classes did not differ at any nest temperature ($P < 0.60$; ANCOVA). Furthermore, all nestlings monitored under conditions where T_{nest} was higher than the euthermic adult body temperatures demonstrated an effective thermolytic response (Fig. 4). This relative uniformity of body temperature existed despite striking variation in both the biotic (e.g. age, number, thermoregulatory capabilities, and condition of insulating plumage of nestlings) and abiotic (e.g. location and corresponding microclimate) characteristics of the nest and nestlings.

Although data on the body temperatures of passerine nestlings in their nests are rare, Red-winged Blackbirds are apparently remarkable in the uniformity of their body temperatures (cf. the diurnally variable body temperatures of the closely related Great-tailed Grackle *Quiscalus mexicanus*; Gotie and Kroll 1973). The mechanisms responsible for this uniformity probably change with age. Early in the nestling period, a combination of brooding by the female parent and huddling of the nestlings is primarily responsible (Dunn 1976, 1979; Hill and Beaver, 1982; Webb and King 1983). The importance of huddling throughout the nestling period is underscored by the observations that the proportion of the daylight hours that the nestlings are brooded is fairly low throughout the nestling period, decreasing to only 4% by day 4 (Hill and Beaver 1982), and the ambient temperatures in this study were sufficiently low to elicit a thermogenic response in Red-winged Blackbirds tested either individually or in broods assigned an age of 5 days and older (Hill and Beaver 1982, Olson in prep.) Later in the nestling period, the increasing thermal inertia of the brood and, during the second half of the 10-day nestling period, the heat produced by the endothermic nestlings and the improved insulation feathers provide, all contribute to homeothermy. The microclimate of the nest itself apparently offered relatively little benefit, though some thermal advantage was gained from the effects of solar radiation and protection from wind. The T_{nest} was slightly higher than but directly related to T_a (Fig. 3A). Red-winged Blackbird nestlings demonstrated a well-developed thermolytic response very early in the post-natal period (Fig. 4).

The variable weather conditions had relatively little impact on the clutch size of Red-winged Blackbirds. Clutch size did not vary over the breeding season, despite considerable variation in both ambient temperature and precipitation, nor did it vary significantly among the 3 yr of my study at any of the three sites (Table 1). The modal clutch size was 4, but nests of 3 eggs were almost as common. Nests with 1-2 eggs were very rare, and I found no nests with 5 or more eggs. The mean clutch size of the pooled sample was 3.75 ± 0.58 eggs (± 1 SD; $n = 133$ nests), which approximates the following means of other populations of Red-winged Blackbirds: 3.7, $n = 153$ (Beer and Tibbitts 1950); 3.5, $n = 926$ (Case and Hewitt 1963); 3.4, $n = 243$ (Goddard and Board 1967); and 3.4, $n = 72$ (Cronmiller and Thompson 1980). Despite the apparent insensitivity of clutch size to variable envi-

ment

TABLE 1. Clutch size by site and year.^a

| Year | Doyle | Gosline | Fosdick |
|------|----------------------|----------------------|----------------------------------|
| 1987 | 3.62 \pm 0.50 (21) | 3.35 \pm 0.71 (23) | — |
| 1988 | 3.89 \pm 0.32 (18) | 3.56 \pm 0.62 (18) | 3.86 \pm 0.38 (7) |
| 1989 | 3.64 \pm 1.29 (11) | 3.50 \pm 0.38 (26) | 3.78 \pm 0.83 (9) ^b |

^a Values are means ± 1 SD. Number in parentheses is number of nests used in calculation. Only active nests where clutch size was stable for at least 5 days were used in calculations.

^b An unusually large number of nests in this sample were not used by the birds; of the 22 nests built and actively defended at this site, only 12 ever contained eggs and/or nestlings.

ronmental conditions, weather conditions over the 3 yr may have contributed to the lower overall nestling success at the Doyle site in 1989, where I found significantly fewer active nests in 1989 ($n = 9$) than in 1987 (22) and 1988 (21) (Table 1). Because Red-winged Blackbirds prefer to nest in old-growth cat-tails (Brenner 1966, 1968; Robertson 1972; this study), the lower primary productivity at Doyle in 1988, possibly due to the dry conditions in 1987 and the first half of 1988 (Olson 1990), may have reduced the number of preferred nesting sites in 1989.

Although many factors influence the evolution of clutch size in Red-winged Blackbirds, I believe the need to huddle to reduce the passive loss of heat probably contributes in part to setting the lower limit. The rarity of clutches smaller than 3 eggs or young may be due to the susceptibility of small clutches to adverse environmental conditions (Bryant and Gardiner 1979). Small clutches could be at a disadvantage during the cool and wet weather sometimes encountered during the breeding season in southeastern Michigan, especially when the female parent is off the nest. The potentially high rate of nest predation suffered by Red-winged Blackbirds (e.g. Case and Hewitt 1963, Goddard and Board 1967, Robertson 1972, Olson 1990) may serve as an ultimate factor in limiting clutch size at the other extreme (Fiala and Congdon 1983). In this connection, clutch size is apparently not limited by the ability to feed the young, as parents apparently can usually feed >4 young without any adverse effects on the survivability or growth of the nestlings (Cronmiller and Thompson 1980, Fiala 1981a). I found that mortality due to brood reduction, abandonment, and starvation was rare. Other studies of Red-winged Blackbirds in the central and eastern U.S. (e.g. Illinois, Smith 1943; Wisconsin, Young 1963; New York, Cronmiller and Thompson 1980) reported similar results. However, these causes of mortality are important in some conditions, for example, severe drought during critical periods (e.g. Robertson 1973, Brenner 1966, 1968).

The thermal stability of Red-winged Blackbird nestlings is undoubtedly important in support of the high growth rates (see Case 1978), which rank among the highest reported for altricial species (Olson in prep.; cf. rates for other altricial species in Dunn 1975, Ricklefs 1984). The facts that low ambient temperatures prevail during the peak of the breeding season in southeastern Michigan (mid-May to early June) and that $T_{b-field}$ is above T_a even before an effective insulation is developed suggest substantial expenditures of energy associated with the maintenance of thermal stability in the young. Determining how these expenditures are partitioned between the nestlings and their parents would be of interest.

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Nutritional and Energetic Implications for Raptors Consuming Starving Prey

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Starvation is often a factor that predisposes individuals to being killed by predators. Although starving individuals are weakened and easier to capture, they are also a less nutritious meal. The body of a starving animal has a greatly reduced lipid content and an increased water content and hence a lower overall caloric value than the body of a well-nourished individual.

When preying on starving individuals, predators should be forced to increase their food consumption to maintain body weight by killing more individuals than they would when preying on well-nourished individuals. This prediction is based on the fact that starving individuals provide fewer calories per gram of body weight than well-nourished individuals. We tested this prediction by feeding captive American Kestrels (*Falco sparverius*) diets that duplicated the energy and nutritional content of well-nourished and starving rodents.

General trends in the gross body composition of starving mammals include a severe reduction in lipid content and an increase in water content (Morgulis 1923). Based on fresh body weight, adult rodents fed *ad libitum* in the laboratory contain (mean \pm SE) 14.5 \pm 3.9% lipid, 61.9 \pm 3.5% water, 18.5 \pm 1.8% protein, and 3.6 \pm 0.3% ash (Morgulis 1923, Chanutin 1931, Elkington and Widdowson 1959, Bailey et al. 1960,

Hayward 1965, Fedyk 1974, Sawicka-Kapusta 1974). Rodents starved until death or a 40% loss of body weight contain 2.2 \pm 0.8% lipid, 71.1 \pm 3.9% water, 20.1 \pm 1.2% protein, and 3.6 \pm 0.9% ash (Terroine et al. 1922, Morgulis 1923, Elkington and Widdowson 1959, Rock and Williams 1979).

We created a low-lipid diet that approximated the composition of starving rodents using 1-day-old laboratory rats (*Rattus norvegicus*) as the basic ingredient. Neonatal rats are naturally as low in lipid and high in water as starving, adult rodents. A high-lipid diet that approximated the composition of well-nourished rodents consisted of chopped, adult laboratory mice (*Mus musculus*). The lower legs, tails, jaws, and skin of the mice were removed so that the diet would be as digestible as the low-lipid diet. A moderate-lipid diet, intermediate between the two previous diets, was a combination of skinned, chopped adult mice and neonatal rats. When we prepared batches of the three diets, beef fat, casein, and bone meal were sometimes added to adjust lipid, protein, and ash to constant levels.

We analyzed the lipid content, protein content, water content, ash content, and energy content of each diet. Samples of each diet were dried to a constant weight at 50°C and then ground into a homogenized powder. Samples were extracted in anhydrous diethyl