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TEMPERATURE RESPONSES OF THE DESERT CICADA, DICEROPROCTA APACHE (HOMOPTERA, CICADIDAE)[1]

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Many insects exhibit an array of behavioral responses directed toward reaching and maintaining a body temperature above air temperature. These usually depend upon locating positions directly exposed to the sun and adopting postures to maximize incident radiation. If the body warms too much, the insect moves to the shade. In temperate climates the thermal load upon the insect usually permits sufficient warming for full activity, and only at midday are insects forced into shade (Heath 1967). On the warmest days shade temperatures approach the level of shade-seeking in the insect. Under these conditions activity is restricted to shaded locations.

The desert cicada, *Diceroprocta apache,* faces a different situation. Midday temperatures in the shade may approach the lethal level, and, except in early morning, elevated body temperatures are reached rapidly upon direct exposure to the sun. *Diceroprocta apache* has adapted to this situation by high thermal tolerance and behavior which emphasizes thermal loss and inhibits heat gain. These features permit *D. apache* to exploit the midday period for activity when predators must retreat to shelter. Consequently, *D. apache* escapes excessive predation, although it is a conspicuous insect living in dense, localized populations.

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MATERIAL AND METHODS

Diceroprocta apache were studied near Phoenix, Arizona, during June 1968 and June 1969. Much of the field work was performed in a mesquite thicket about 10 km northeast of the city. Some experimental work was performed on insects collected within the city and from a location about 25 km southeast.

Temperature measurements were made with a specially designed thermistor probe described by Heath and Adams (1969). This probe has a time constant of 0.2 sec and a heat capacity less than 1% of that of this insect. Temperature measurements are accurate to 0.2 C. The probe was calibrated against a calibrated U.S. Bureau of Standards mercury thermometer and was connected to a commercially made (Yellow Springs Tele-thermometer) bridge circuit.

Several precautions were taken to assure meaningful measurements. In the field insects were captured in an insect net. The net was tightened about the animal to immobilize it. The probe was introduced through the mesh and pushed to a depth of 4 mm into the mid-dorsal thorax. Care was taken to shelter the animal from the direct rays of the sun. The experimenter's fingers were kept at least 10 cm from the animal. If the period from capture to measurement exceeded 5 sec, the animal was discarded. Air temperature was obtained with the same probe at the height of the insect's perch (about 2 m). In the laboratory, temperatures were obtained with the same probe and with the same restrictions of 5 sec between an event and measurement. However, the experimenter, using his thumb and forefinger, grasped the insect by its wing tips and oriented it for insertion of the probe. If his fingers came in contact with the body, the insect was released without measurement.

RESULTS (FIELD STUDIES)

DAILY ACTIVITY

About sunrise, *Diceroprocta apache* move from feeding sites along the large branches of mesquite to exposed twigs and leaves. There they take up positions strongly oriented to present the maximal surface to the sun. They remain in this position, motionless, throughout the early morning hours. Though warm enough to fly or sing, they can be approached closely. When touched they give a warning call and fly off for distances of up to 100 m. During the morning period, birds, a primary predator on the cicadas, are active in the mesquite thickets. We recorded numerous encounters between cicadas and birds, since the male cicadas call out when seized. Large cicada wasps are also active in this period. By the number of encounters heard between cicadas and the wasps, we judge these probably account for a third of the predation on adult cicadas.

By midmorning the air temperature rises into the mid- to upper 30s C. Both the birds and wasps retire to shelter until dusk. The male cicadas begin singing from exposed perches. As the day advances and temperatures continue to rise, the cicadas shift their activity to the shade.

At midday *D. apache* reaches its maximum intensity of activity. There are no other animals active at this time. We frequently encountered cicada wasps near the ground in the deep shade of the mesquite trunk. We also came across birds panting deeply and with their wings outstretched. Indeed, we were also forced periodically to replenish our water loss and retreat to deep shade. If a cicada is approached at this time, it flies readily, but only very short distances, no more than 10 m and often less than 1 m.

If the day is only moderately hot (40 C), the cicadas sing through early afternoon. On extremely hot days (48 C) they sit quietly from 1:00 until 3:00 P.M. and resume their activity when the temperature begins to drop.

In late afternoon *D. apache* retreats from its high singing perches to the trunks of the mesquite to feed. Nevertheless, some singing continues until dark. Although birds are abroad in the

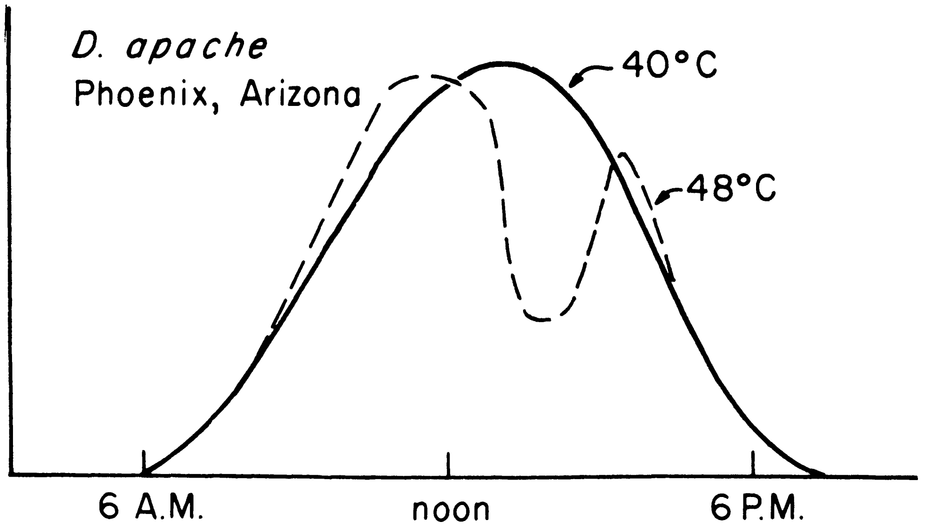

FIG. 1.—Effect of temperature on subjectively determined intensity of chorusing of *Diceroprocta apache*. The maximum air temperature at 2 m for 2 days is indicated. On very hot days the cicadas quiet down and become inactive during the hottest hours of the day. Maximum activity in either case occurs through the middle of the day.

late afternoon, we heard no encounters with cicadas. In the city *D. apache* sings in the early evening on hot nights if its perch is near artificial illumination.

In figure 1, we have indicated the subjective intensity of singing through the day. This summarizes the overall activity on a moderately hot and on an extremely hot day.

BODY TEMPERATURE OF ACTIVE CICADAS

Cicadas were captured in the field during the basking and active periods of their day. The body temperature at these times is related to air temperature in figure 2.

During the basking period body temperature rises well above air temperature. But it exceeds 40 C during basking only rarely because the insects move to shade when their body temperature approaches that level. The insects collected at air temperatures below 35 C were not singing. Later in the day the insects retreat to shade and begin to sing. At this time their body temperature is less than the general air temperature. The exception shown in figure 2 was a male singing from a "shaded" perch high on an isolated stem of a creosote bush (*Larrea divaricata*). His body was slightly larger than the stem and was exposed to the sun. The other insects occupied perches on the shaded side of large branches of mesquite. These animals had temperatures well below the general air temperature. They apparently utilized local patches of cool air adhering to the cool surface of the shaded trunks of the trees (fig. 3).

RESULTS (LABORATORY EXPERIMENTAL STUDIES)

RESPONSE TO COLD

Cicadas placed in a beaker in an ice bath rapidly lose motor control. Below about 15 C they are unable to move. As they warm, movement returns. A

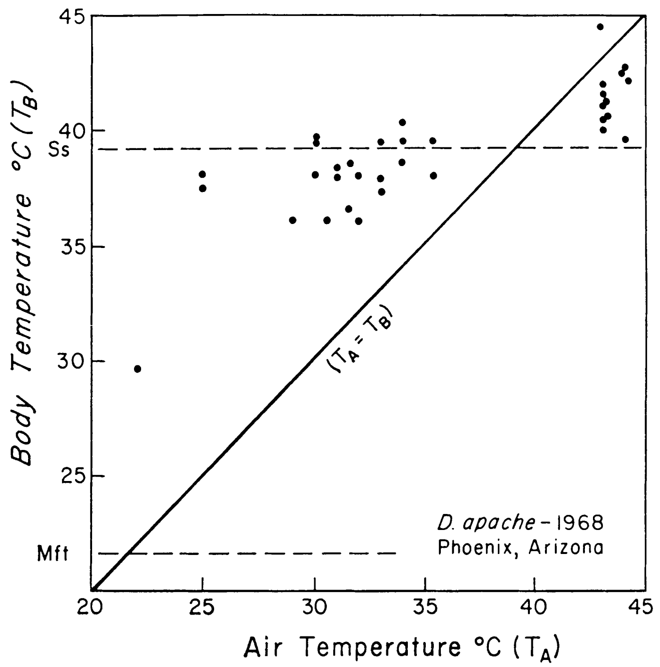

FIG. 2.—Field determinations of the body temperature of *Diceroprocta apache* is plotted against the air temperature (at 2 m height in shade). Ss = shade-seeking temperature (see text). Mft = minimum temperature for flight (see text).

critical level for a flying animal is the temperature at which neuromuscular coordination is adequate for directed flight. This can be approached crudely by throwing the insect into the air as it warms. Eventually, it is able to correct its position and make a controlled landing, instead of falling clumsily to the ground. In *Diceroprocta apache* the minimum temperature for flight is 21.92 C (table 1). Above this mean level the quality of flight improves steadily.

TABLE 1

TEMPERATURE RESPONSES OF "DICEROPROCTA APACHE" FROM PHOENIX, ARIZONA

Behavior	Mean (±SD)	Range	*N*
Minimum controlled flight	21.9 (1.8)	20.0–27	18
Shade-seeking	39.2 (2.5)	34.2–45	23
Loss of motor control	45.6 (1.0)	43.5–47.5	14

RESPONSE TO HEAT

Cicadas placed in pasteboard containers and held beneath a 250-w heat lamp warm rapidly. Eventually, their body temperature rises to a level where they are inactivated. At this point their body temperature is quickly obtained by the experimenter. *Diceroprocta apache* loses motor control at 45.6 C (table 1). Upon cooling, all 14 studied regained activity. If cicadas in the field reached this temperature while exposed to the sun, they would either continue heating or fall to the ground. The surface temperature of the ground during the day may be 70 C. In either case the animal would be unable to prevent further heating. For these reasons the temperature of motor loss represents an ecological lethal level.

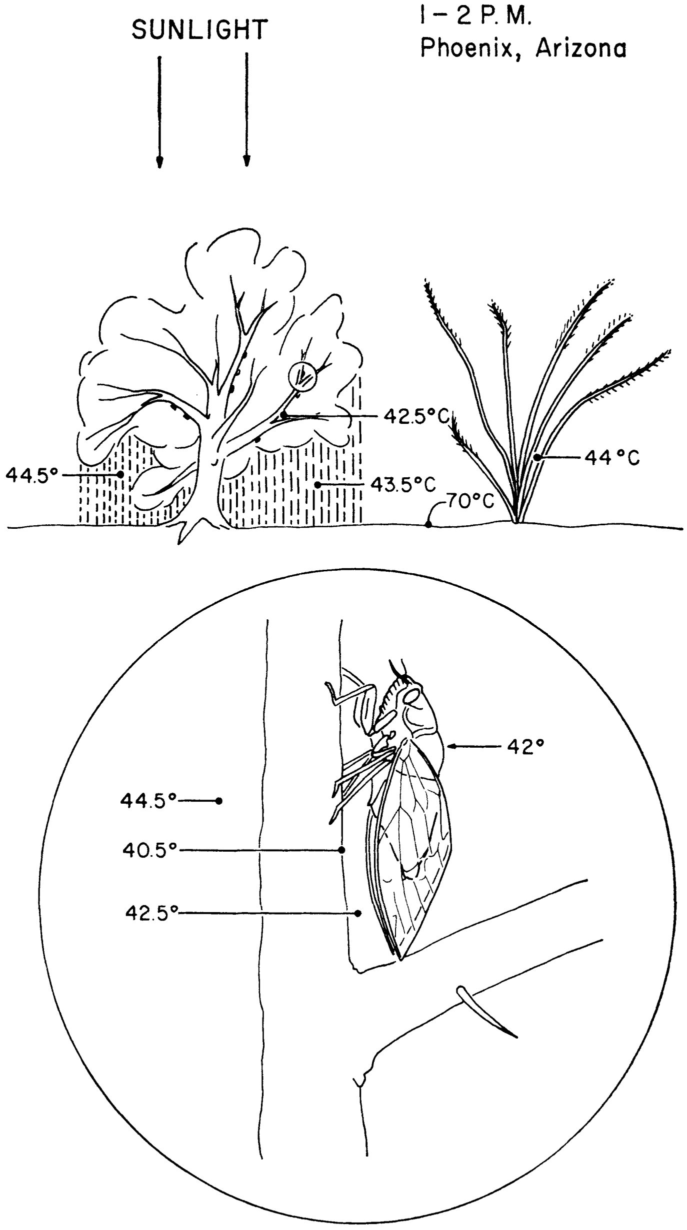

FIG. 3.—*Upper*, Temperatures in the environment of *Diceroprocta apache*. On the right is a creosote bush; on the left, a mesquite plant. Temperature in the shade is higher on the south and east sides of the mesquite than on the north and west sides. Air temperature is lowest in the layer of air next to the north side of large boughs. *Lower*, *Diceroprocta apache* selects these places as singing perches and avoids exposure to higher temperatures. The temperature at 2m in the shade was 43C.

TEMPERATURE REGULATION

Diceroprocta apache basks readily in the field and in the laboratory. This behavior consists of gross movements toward a source of heat, orientation of the body to maximize exposure to radiant heat, and quiescence during the warming period. When the body temperature reaches 39.2 C (table 1), *D. apache* either adopts a posture which minimizes exposure to the sun or retreats to shade. Since the latter is easier to observe and quantitate, this behavior is called "shade-seeking."

In the laboratory, the cicada's body temperature drops rapidly when it moves to the shade. Subsequently, the animal returns to an exposed position and resumes basking. Among some cicadas in milder climates, shuttling between sun and shade occurs throughout the day and is a major determinant in selection of singing perches (Heath 1967). The desert cicada may shuttle during a short interval in the morning, but shortly the air temperatures rise so high that occupation of shaded perches becomes permanent for much of the day. *Diceroprocta apache* shows some shuttling activity, but, unlike other cicadas, it does not sing until it has adopted more permanent shaded perches. During the period when shuttling occurs, birds and wasps are still abroad. Singing at that time could alert these predators of cicadas to the location of prey.

Four animals collected while active and singing had body temperatures above the shade-seeking level and averaged 41.9 C. When the body temperatures exceed 43 C, *D. apache* diminishes its singing activity.

HEAT PRODUCTION IN FLIGHT

Diceroprocta apache is a strong flying cicada. When warm, its movements are so rapid that it resembles a bee. When it is between its minimum temperature for flight and the shade-seeking temperature, it is capable of long flights. At higher temperatures its flight time diminishes. At temperatures above 39 C, it is unlikely to fly for more than 3 seconds. Other cicadas, *Magicicada septendecem,* may raise the thoracic temperature 2–4 C above the rest of the body during intermittant flight (Heath 1968). The migratory locust reaches an excess of body temperature of 6 C during long flights (Weis-Fogh 1952). Neither of these animals depends on this heat production for activity, but both will cease flying if the thoracic temperature becomes too high.

Diceroprocta apache does not fly at high temperatures, unless forced. However, it restricts flight time as temperature rises. If it produces heat in flight and is forced to fly from a shaded perch at midday, it may be well below general air temperature as it leaves its perch. Even a short flight may cause the thoracic temperature to rise above the temperature of heat inactivation.

Heat production in flight was measured to gain estimates of the rate of temperature rise during flight. If cicadas are held by one wing, they execute very active flight movements. After two and one-half minutes of this treatment, their body temperature rises 4.5–8.5 C. Further activity only maintains this differential between air and body temperature. Temperature measurements of the thorax at intermediate intervals permit an estimate of the rate of rise of temperature. This method, though crude, has advantages over continuous measurement of a permanently tethered insect. Tethered animals frequently fly sluggishly, in part because the tether interferes with wing movement and in part because a temperature sensor in the thorax damages and interferes with the muscles. We found that tethered cicadas warm only 3–4 C, while animals forced to fly warm as much as 8.5 C. Tethered animals do not fly continuously or for extended periods. The flow of air over the surface of the body is faster than with tethered animals and thus approaches conditions of true flight more closely.

An object, such as an insect, with a uniform heat input will rise in temperature depending upon the balance between the heat input and the rate of heat loss to the environment.

$$\frac{dT_b}{dt} = \frac{1}{WS}\left[\frac{dH_p}{dt} - \frac{dH_l}{dt}\right], \quad (1)$$

where dT_b/dt = rate of change of temperature (degrees per second), W = mass of object (grams), S = specific heat of object (cal/g deg), dH_p/dt = rate of heat input (calories per second), and dH_l/dt = date of heat loss.

Where heat loss is due to conductive loss from the surface, heat loss is described by Newton's law of cooling.

$$\frac{dH_l}{dt} = AC(T_b - T_a), \quad (2)$$

where A = surface area of the object (square centimeters), C = thermal conductance of the surface (cal/deg sec cm^2), T_b = object temperature, and T_a = environmental temperature.

If equations (1) and (2) are combined, then the log of increasing temperature is linear with time. If the initial temperature, the asymptote, and an intermediate value are known, the entire warming curve can be reconstructed. Figure 4 presents this graphically. The body temperature at any interval after flight begins can be read from the graph. The individual whose warming curve is presented warmed 1 C after only 6–7 sec of flight. After 20 sec it had reached 2.7 C gradient. In other words, a *D. apache* beginning flight at 43 C body temperature would lose motor control after only 20 sec of flight.

Diceroprocta apache maintains a constant gradient to the environment during a long flight. Since heat production must equal heat loss, the heat

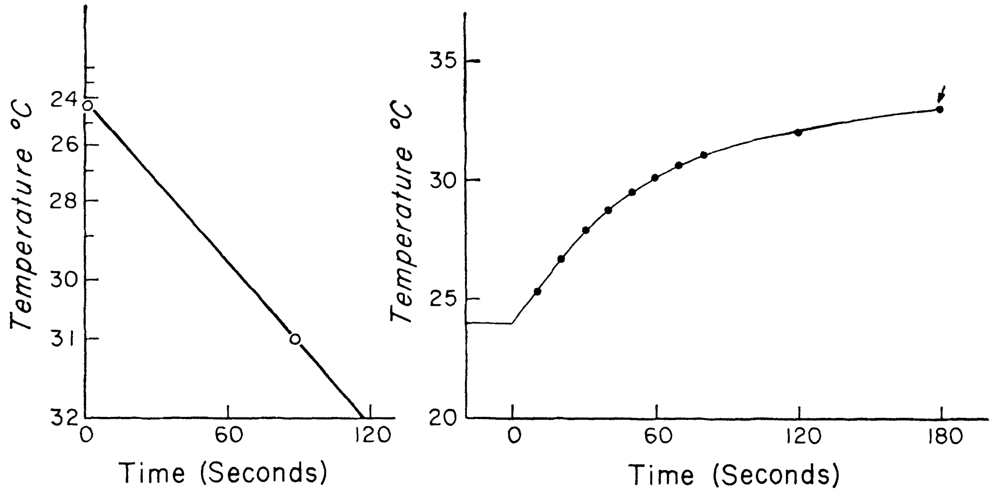

FIG. 4.—Change in body temperature with flight in *D. apache*. *Left*, The insect began flight at air temperature (24.5 C); after 1½ min it reached 31 C. After several minutes it reached 33 C. The final temperature was used to construct the ordinate. Since heat production is assumed constant, the rate of heating depends upon the rate of cooling and is logarithmically related to time. ***Right***, A straight line drawn through the initial and intermediate values was used to reconstruct the warming curve. The initial temperature, the point at 31 C, and the point at the arrow are real values. The insect warms 1 C in only 6–7 sec.

production or metabolic rate can be estimated by measuring the rate the insect cools through a 6 C interval. At a 6 C gradient a cicada with a thorax of 0.35 g cools 2.4 C/minute. If we assume a specific heat of 0.8, it loses 0.42 cal/minute.

DISCUSSION

Diceroprocta apache shows remarkable tolerance to high temperature. It voluntarily exposes itself to direct insolation until it reaches 39 C and then retreats to shade. This tolerance is comparable with that of several desert lizards (Norris 1953; Heath 1965). Unlike the lizards its most intensive activity follows retreat to shade. It retains full activity to 45.6 C before it is inactivated. This value corresponds to the highest tolerance among desert reptiles and birds (Norris 1953; Dawson 1954; Schmidt-Nielson and Dawson 1964). Figure 5 relates the temperature response of *D. apache* to its daily activity.

Diceroprocta apache does not rely solely upon high thermal tolerance to exploit the desert. It possesses an exquisite ability to select perches minimizing its exposure to high temperature. Males tend to sing from locations on the north side of large branches of

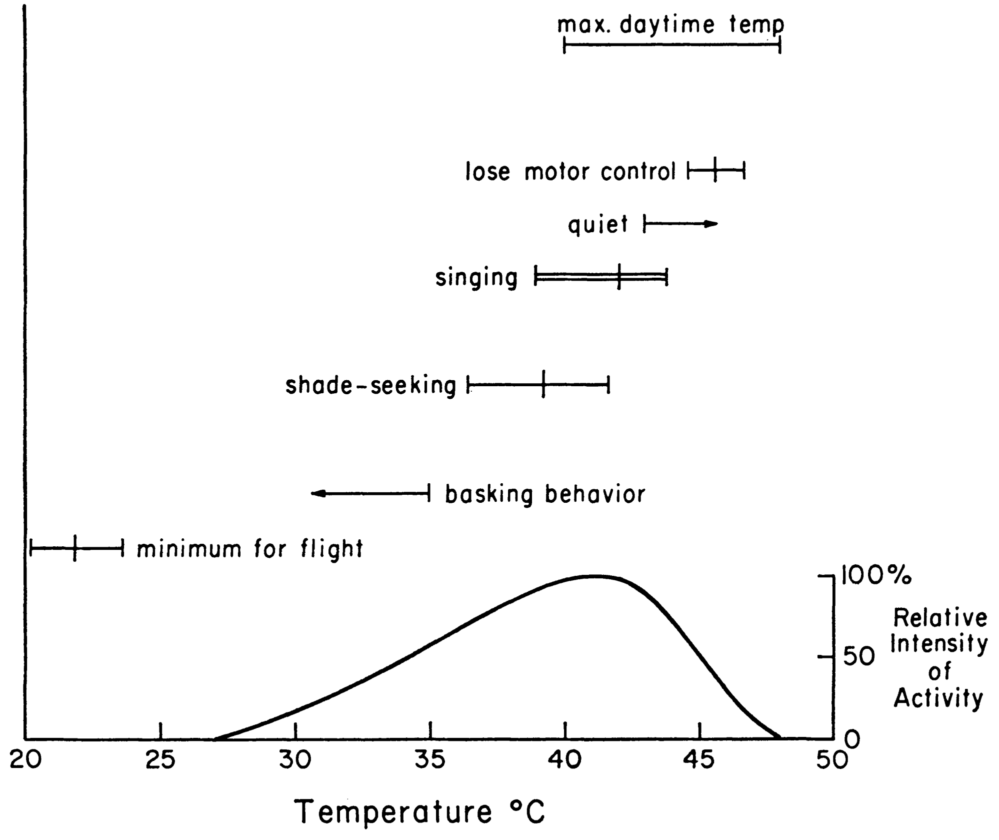

FIG. 5.—Summary of the responses to temperature by *Diceroprocta apache*. The mean (vertical line) body temperature and range (horizontal bar) are given for each activity. The curve (bottom) relates the subjective intensity of activity to ambient temperature.

mesquite. These locations heat less rapidly than the surroundings because they do not receive direct insolation. Further, the heat capacity of the stem may be great enough to prevent it from heating much above a mean daily temperature. Consequently a cool layer of air adheres to the surface. *Diceroprocta apache* is small enough to immerse partially in this layer.

Diceroprocta apache warms up during flight; when cool it flies readily. Above the temperature of shade-seeking (39 C) it becomes reluctant to fly. If it is then forced, it will fly for only short intervals or very short distances. This behavior minimizes overheating due to internal heat production.

The desert cicada is most active during the warmest time of the summer, late June and July. During this period many desert animals aestivate or restrict their activities to nocturnal and early morning hours. The temperature tolerance and behavioral specializations of *D. apache* permit it to be active during the hot months. It further restricts its activities to those daylight hours when predators have retreated to cooler protected locations. During its most active singing and courting periods it is virtually alone. When its predators are abroad, *D. apache* spends its time quietly basking. Its disruptive coloration and immobility make it difficult to detect visually.

Cicadas commonly occur as widely separated individuals or in high concentrations over a wide geographic area. *Diceroprocta apache* is somewhat intermediate; it inhabits mesquite–palo verde thickets along dry stream courses. It reaches high population density in the thickets. In the study area the largest thickets covered only a few acres. Our best collecting was from a thicket covering less than two acres. Lloyd and Dybas (1966*a*, 1966*b*) have extensively considered the problem of cicada population density. They conclude that large concentrations of cicadas over a wide geographic area can saturate local predators. In periodical cicadas, the life cycle is long enough (13–17 years) and sufficiently synchronized that predator populations are unable to match their size against the potential food supply of cicadas. They argue that a shorter life cycle, smaller geographic distribution, or assynchronous life cycles would permit the predator populations to match the population of cicadas.

Diceroprocta apache violates most of the conditions that Lloyd and Dybas reason necessary for large concentrations of cicadas. *Diceroprocta apache* live in localized, high concentrations and emerge annually in large numbers. They have solved the problem of predation with a combination of special features. *Diceroprocta apache* emerge and are most active during midsummer. Birds are a major predator on cicadas, and birds place the heaviest energy demand on their environment during a nesting and brooding period in the spring. *Diceroprocta apache* is dissynchronous with that period. *Diceroprocta apache* are least active daily during early morning when birds are most active. When the birds must retreat to protected locations because of soaring environmental temperatures, *D. apache* begin chorusing and moving. They are able to exploit the hot midday period because of their high temperature tolerance and their ability to locate perches microclimatically milder than surroundings. These perches are too small for exploitation by larger animals such as birds. *Diceroprocta apache* is also dissynchronous with its other major predator, cicada wasps.

SUMMARY

1. The temperature responses of the desert cicada, *Diceroprocta apache,* were studied near Phoenix, Arizona, during June 1968.

2. Daily activity was temperature dependent. Maximum activity, as measured by intensity of chorusing, occurs during the middle of the day. On very hot days—above 45 C air temperature—there was a quiet period at midday.

3. *Diceroprocta apache* is unable to fly at body temperatures below 21.9 C. It moves to shade when it reaches 39.2 C. It loses motor control at 45.6 C.

4. The thoracic temperature of *D. apache* rises 4.5–8.5 C during extended flight. At high environmental temperature the thorax might warm above the temperature where motor control is lost within a few seconds. *Diceroprocta apache* restricts its flights to 1–3 sec intervals during these periods.

5. *Diceroprocta apache* is adapted to its environment through a high thermal tolerance and behavior which emphasizes thermal loss and inhibits heat gain. It is thus active in the midday period when its predators have retreated to shelter.

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