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Temperature Selection and Activity in the Crayfish, *Orconectes immunis*

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Summary. Selected temperature and activity were continuously monitored from crayfish (*Orconectes immunis*) placed in a thermal gradient exposed to the natural photoperiod. The crayfish avoided temperature extremes in the gradient, but did not prefer a particular temperature (Fig. 2). During the night the crayfish were active, and selected a mean water temperature of about 22° C. During the day the crayfish were inactive, and selected a mean water temperature of about 18° C (Figs. 3, 4).

Introduction

Nearly all motile animals will actively select certain temperatures when given a choice of thermal environments (Fraenkel and Gunn, 1961; Whittow, 1970; Hammel, Crawshaw, and H. P. Cabanac, 1973). The mechanisms by which different animals select suitable thermal microhabitats are quite varied. Among the vertebrates, central and peripheral temperatures are integrated to produce behavioral responses which typically maintain internal temperature within rather narrow limits (Hammel, Crawshaw, and H. P. Cabanac, 1973). Many invertebrate species tend not to actively select a particular temperature, but rather to avoid temperature extremes (Fraenkel and Gunn, 1961).

In the present experiment crayfish were placed in a thermal gradient for extended periods; selected temperature and activity were continuously recorded. Thus, it was possible to assess the mode of active temperature regulation as well as interactions between time of day, activity, and selected temperature in an invertebrate species.

Methods

Crayfish (*Orconectes immunis*) were collected from a local pond and placed in a holding tank exposed to natural variations in light and temperature. The crayfish were fed at two to three day intervals. These experiments were conducted during the month of October, 1973. The carapace lengths of the crayfish ranged from 30 to 35 mm.

The temperature gradient apparatus, shown in Fig. 1, allowed the crayfish to select temperatures between 6 and 36° C. Each of the 11 chambers was 23 cm long and 20 cm wide. Water depth was 8 cm, and the openings between the chambers were 9 cm wide. Since the water flow in the coldest chamber was relatively slow ($>1.0\ l \cdot min^{-1}$), and the crayfish were rarely seen there, the flow probably had little effect on the behavior of the crayfish. The gradient chamber was exposed to the natural photoperiod, but was shielded from direct sunlight and surrounded by translucent plastic. The daytime illumination was, therefore, reasonably uniform throughout.

The temperature of the dorsal carapace surface (subsequently referred to as the selected temperature) was recorded via an attached 36 gauge copper-constantan thermocouple. The emf produced by the active thermocouple junction was continuously recorded on a Honeywell

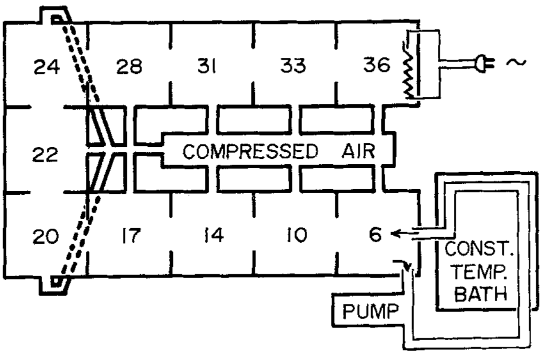

Fig. 1. The temperature gradient apparatus. The numbers depict the temperature (°C) of the middle of each chamber at a depth of 4 cm. The chamber is described more completely elsewhere (Crawshaw, 1974)

stripchart recorder. The thermocouple wire was suspended 2 m above the tank, and did not impede the motion of the crayfish as long as there was adequate footing. This was provided by rough gravel which was placed on the bottom of the gradient.

The study consisted of three parts. First, a number of crayfish were placed in the chamber with no temperature gradient present and their behavior observed at different times of day. Secondly, the heating and cooling units were activated and the same group crayfish observed at different times of day in the temperature gradient. Finally, single crayfish were placed in the gradient with an attached thermocouple wire, and left undisturbed for 7–10 days.

Results

Eight crayfish were placed in the chamber with no gradient present. During the night most of the crayfish actively wandered about, with no particular location preferred. Those not active preferred the ends of the gradient, where the heaters and cold water intake provided some degree of cover. During the day the crayfish were inactive, and were found in the corners provided by the baffles or the ends of the gradient with appendages and abdomen drawn tightly up to the cephalothorax.

When the temperature gradient was established in the chamber, the crayfish vacated the temperature extremes of the end chambers and were thereafter rarely seen there. At about three hour intervals the temperature selected by each of the eight crayfish was recorded for a twenty-four hour period. At any particular time, the crayfish occupied a relatively wide range of temperatures. During the night the crayfish were active, and the mean ($\pm$ S.E.M.) selected temperature was 22.5 $\pm$ 0.5° C. During the day, the crayfish were inactive, and the mean selected temperature was 18.0 $\pm$ 1.0° C. The difference between the temperatures selected during the day and night was statistically significant ($t = 4.2$, $df = 86$, $p < 0.001$).

Three crayfish, one at a time, were fitted with a thermocouple and placed in the gradient for periods of 7–10 days. Fig. 2 shows several representative recordings of the temperatures selected by these crayfish during periods of activity.

The continuous recordings of selected temperature were integrated over 30 min periods to produce 48 mean selected temperatures for each day as shown in Figs. 3 and 4. The activity numbers (also seen in Figs. 3 and 4) were obtained by assigning

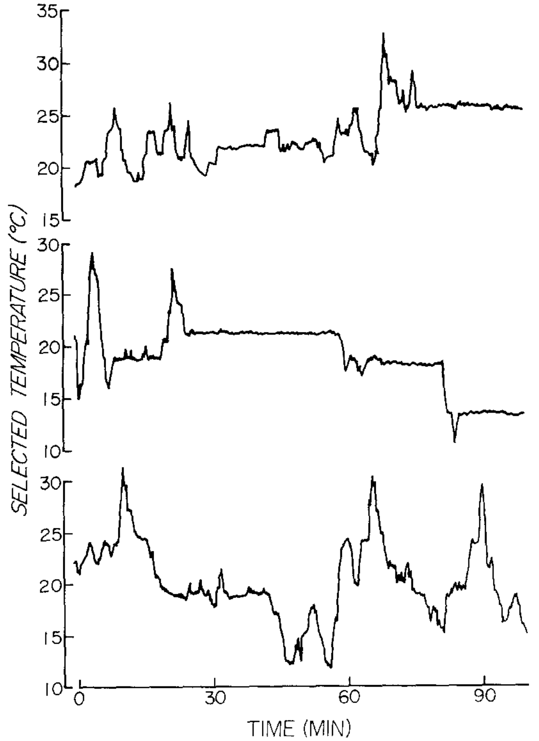

Fig. 2. Continuous records of selected temperature in different crayfish during the evening period of activity

one activity unit for each 1.25° C change in selected temperature. Such an assignment was possible because any movement within the gradient placed the crayfish in water of a different temperature and therefore altered the body temperature. Increased activity was not necessarily associated with a change in mean selected temperature, since during a 30 min period an active crayfish might balance its forays into warm and cold water. Fig. 3 depicts the 24 hour records of selected temperature and activity in one crayfish for one twenty-four hour period. In Fig. 4, each point represents the mean of all runs on the 3 crayfish. During active periods (activity ≥ 12) the mean temperature (in $°C \pm$ S.E.M.) selected by the three crayfish was 24.2 ± 0.2; 21.0 ± 0.2; 20.7 ± 0.2, while during inactivity (≤ 4) the mean temperature selected was 22.5 ± 0.4; 18.1 ± 0.2; 17.2 ± 0.3. In all three cases the mean temperature selected during inactivity was significantly lower ($p < 0.001$) than that selected during activity. However, as is the case with temperature selection during activity, the temperature selected for a period of inactivity varied greatly even for the same crayfish on different days. For example, one crayfish selected temperatures of 14°, 16°, 23°, 13°, 13°, 18°, 19°, 19°, and 13° for periods of daytime inactivity. During the entire period in the gradient, the duration and intensity of activity and the temperatures selected did not appear to undergo any systematic change.

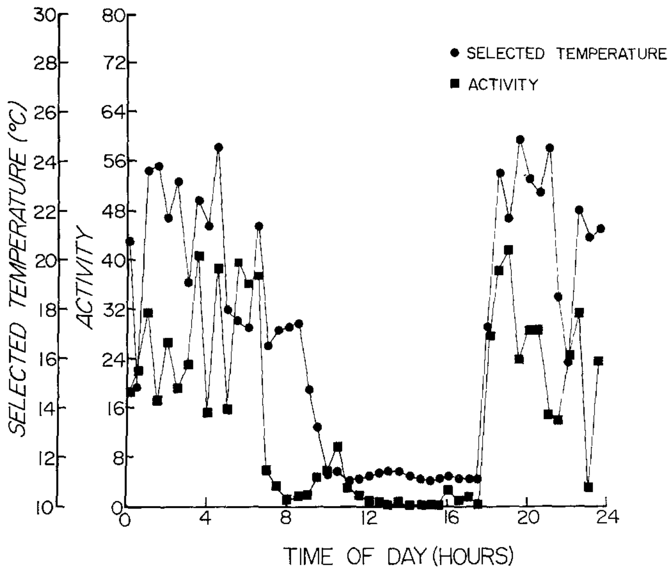

Fig. 3. Selected temperature and activity as a function of time of day for one 24 hr period of one crayfish. Each point represents the mean value of a 30 min period

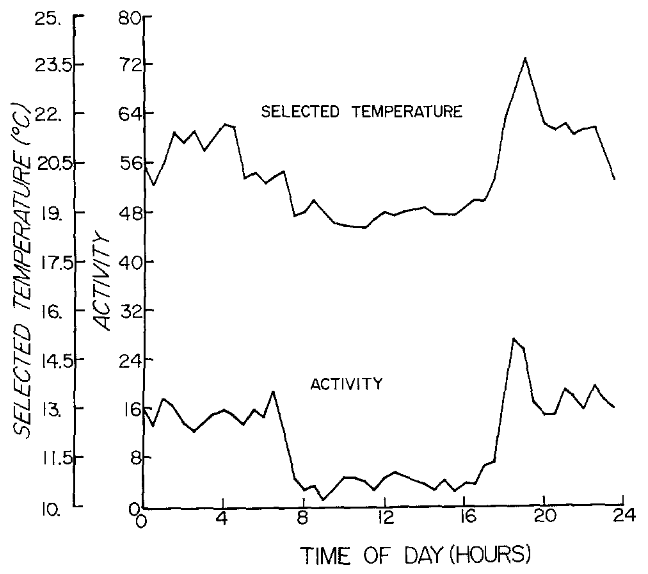

Fig. 4. Selected temperature and activity as a function of time of day for all runs on all three crayfish. Each point represents the mean value of a 30 min period

In a previous study (Crawshaw, 1974), brown bullheads (*Ictalurus nebulosus*) and bluegill sunfish (*Lepomis macrochirus*) were placed in the gradient chamber used in the present study. Fig. 5 illustrates representative records of temperature selection by these fish, and is included to allow comparisons between temperature

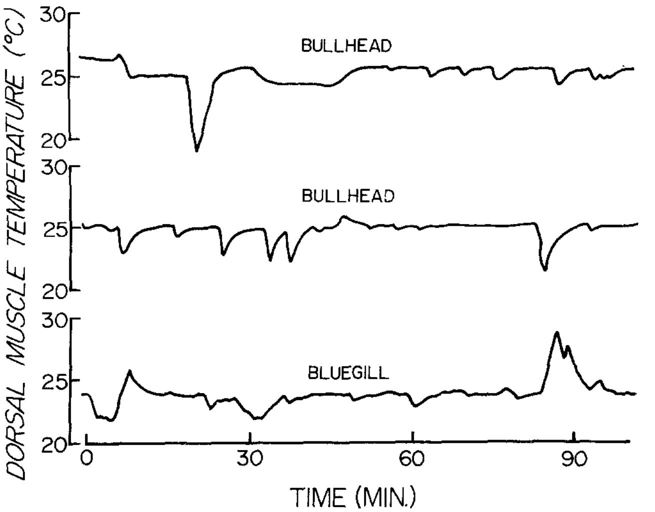

Fig. 5. Continuous records of selected temperature in the brown bullhead (*Ictalurus nebulosus*) and bluegill sunfish (*Lepomis macrochirus*) during periods of activity. These records are a part of the data which were tabulated in an earlier paper (Crawshaw, 1974)

selection in teleost fish and crayfish. Note that although the fish are often active (depicted by a changing temperature), there is a rather definite temperature that is being selected. The crayfish (Fig. 2), on the other hand, wander rather freely throughout a wide band of temperatures, actively avoiding only the extremes.

Discussion

Orconectes immunis inhabits slowly moving or stagnant waters with muddy bottoms and abundant vegetation (Tack, 1941). Observing *O. immunis* in outdoor ponds, Tack (1941) noted that most individuals are hidden under stones or in burrows during the day. At dusk large numbers of individuals appear and "apparently are active all night" (p. 422). Crocker and Barr (1968) made the general observation that during the summer crayfish occur in deeper water during the daylight hours, migrating into shallower water to forage at night. The nocturnal nature of various members of the crayfish family (Astacidae) has been documented for some time (Girard, 1852; Ortmann, 1906; Chidester, 1908, 1912); Huxley (1880) classifies this information as "common knowledge".

Observations made in the controlled temperature gradient of the present study agree with the foregoing field observations. Activity occurred almost entirely at night. At dawn, the crayfish selected cooler water in which to become inactive. In a natural environment, this would of necessity lead them into deeper water. Advantages accruing to animals utilizing such behavior patterns would include lower metabolic expenditures and increased predator avoidance during inactive periods (Regal, 1967; Brett, 1971).

When temperature selection and activity patterns exhibited by the invertebrate ectotherm *O. immunis* are compared to those of the vertebrate ectotherms

I. nebulosus (the brown bullhead) and *L. macrochirus* (the bluegill sunfish) a number of differences are apparent even though these animals occupy similar habitats. The crayfish wanders about through a relatively wide range of temperatures, avoiding only the extremes. This type of orientation has been termed klino-kinesis by Fraenkel and Gunn (1961) and is apparently the method by which many insect species remain within reasonable thermal limits (Fraenkel and Gunn, 1961). Although a mean thermal preference can be computed for any animal species, in many situations the animals are quite spread out in the temperature gradient, and a computed mean thermal preference may misrepresent the actual state of affairs (Deal, 1941; Frankel and Gunn, 1961; Cloudsley-Thompson, 1970). Nevertheless, certain insect species do appear capable of responding to small temperature changes (Heran, 1952; Herter, 1953).

Brown bullheads and bluegill sunfish, like many vertebrates, select a rather specific temperature, from which they periodically deviate for various reasons (Crawshaw, 1974). If the fish are agitated, or offered food or shelter at a specific location, the preferred temperature will not be readily apparent. Also, some species may find it difficult to navigate in an experimental temperature gradient (Crawshaw and Hammel, 1973), thus giving a false impression of their thermoregulatory capabilities. Under conditions where crayfish, bullheads, and bluegill remain undisturbed for long periods of time, it is clear that bullheads and bluegill maintain body temperature within much narrower limits than crayfish.

Daily activity periods of crayfish are quite regular, and are determined primarily by the light cycle. The overall activity level in the temperature gradient did not change from day to day. As reported earlier (Crawshaw, 1974), the active periods of bullheads and bluegill sunfish are less rigidly determined by the light cycle, and tend to decrease in number and intensity on successive days. It is possible that the high levels of nocturnal activity sustained by the crayfish preclude the maintenance of a relatively constant body temperature in an artificial temperature gradient. In a pond the crayfish could wander relatively large distances under isothermal conditions. However, the fact that quite diverse temperatures are selected for inactive periods (both for short periods at night and the long inactive period during the day) suggests that at any given time crayfish may not have a definite preferred temperature, as do many vertebrates.

Both Prosser (1936) and Kerkut and Taylor (1958) found temperature sensitive neurons in isolated abdominal ganglia of crayfish. The firing rates of these neurons were proportional to temperature throughout the range of 10–30° C. Kerkut and Taylor observed that rapid temperature increases served to transiently inhibit the ongoing firing rate, while rapid temperature decreases had the opposite effect. These authors also observed that blinded crayfish (*Astacus fluviatilis*) became active when cooled from 17° to 3° C. Upon rewarming, the activity ceased. They concluded that crayfish use this mechanism to keep within the range of optimum temperatures. Thus, by being more active in excessively cold (or hot) environments, and quiescent in a neutral environment, the animals would thereby usually be found within a certain band of temperatures. This type of orientation is termed orthokinesis by Fraenkel and Gunn (1961), and is probably important in temperature preference orientation in certain insects (Fraenkel and Gunn, 1961). The crayfish *O. immunis*, however, does not appear to utilize this kind of orientation during periods of high activity in the temperature gradient. As seen in Fig. 2, during such periods the crayfish are active at many different temperatures, and simply change their direction of movement when an extreme temperature is encountered. An orthokinetic response to cool water might be activated by light. If such a response occurs, then crayfish encountering cool water during the day would remain there. It could also be that there is a continuous circadian shift in the zone of acceptable temperatures. This zone would be lowest during the day, rising to a peak in the early evening, gradually falling during the night, with an abrupt fall in the early morning (Fig. 4).

In conclusion, crayfish show highly regular nocturnal activity patterns. During these active periods the crayfish select warmer temperatures than during inactivity, and in all cases a range of temperatures, rather than a particular temperature, is preferred.

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