HOW FAST CAN A COCKROACH RUN?[1, 2]

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The rate of progression of walking or running insects has been determined in only a few instances. One of the reasons for this is that few insects will move at a constant rate for a sufficient distance to be timed by ordinary stop watch methods. As part of a larger study on the effects of temperature on various activities of the american cockroach, we have measured its speed of locomotion and found, as we had expected, that it is fast for so small an animal.

Previous data on running speeds of insects in relation to temperature have been on various ants which do indeed make excellent subjects for such determinations. Ants, however, are relatively slow, approximately 25–50 × slower. German cockroaches are much faster but only about half as fast as the american cockroach.

Species	Temp. °C.	Cm./sec.	Miles/hr.	Authority
Lasius niger	24.0	1.6	0.036	Barnes + Kohn
Tapinoma sessile	25.2	1.67	0.037	Shapley
Iridomyrmex humilis	25.2	2.62	0.06	Shapely
Blattella germanica				
adult male	22.	29.3	0.65	Wille
adult female	22.	18.2	0.41	Wille
first instar nymph	22.	2.7	0.06	Wille
Periplaneta americana				
adult male	22.0	66.	1.47	herein
adult female	22.0	57.	1.27	herein
male + female, av.	25.0	74.	1.65	herein

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At higher temperatures the ants run more rapidly. Thus, *T. sessile* reaches a maximum rate of 3.22 cm. per second at 35.8° C. (0.072 m.p.h.), and *I. humilis* reaches 4.22 cm. per second at 33.5° C. (0.095 m.p.h.). But the american cockroach also runs somewhat faster at higher temperatures; it attains on the average a speed of 91 cm. per second at 30–35° C. (2.0 m.p.h.), with our fastest racer at top speed attaining 130 cm. per second (2.9 m.p.h.).

Wille (1920) measured the speed of german cockroaches on various surfaces (all at 22° C.). The values copied in the above table were for rates on rough paper. Adults run 20–50% slower on linoleum or planed wood, and 50–80% slower on glass. However, the first instar nymphs were 50% faster on glass than on rough paper. Presumably the early nymphs rely less on setae and claws and more on adhesiveness for traction.

The top speed of slightly less than three miles per hour for american cockroaches may seem slow in an age adjusted to automobiles and aeroplanes. But, recall that a man can easily overtake a cockroach by walking even though the insect is fleeing headlong across the floor. To be sure, grabbing a cockroach calls for agility but this is due to the cockroach's rapid darting in various directions rather than to its velocity. Gray (1953) in his delightful little book points out, among other things, that this darting off for short distances in unexpected directions gives the illusion that small animals (e.g. minnows) progress at a considerably greater speed than they actually do. It is a good man who can walk much more than twice this speed (i.e. over six miles per hour) or run more than five times it; and no human has ever managed to run more than about eight times as fast as the cockroach's top speed.

Materials and Methods

Adult american cockroaches (*Periplaneta americana*) were obtained from our laboratory cultures by segregation of last instar nymphs. These were used as test insects over the period of about one week to three months after molting to the adult stage. During this period no significant change in speed was observed. Probably they are slower shortly after the molt. A single male tested the day after molting was relatively slow; it ran about 50% faster during the period 1–4 weeks later. Males weighed 1.0–1.2 grams, females 1.0–1.5 grams.

For reasonably short distances american cockroaches run too rapidly for accurate determination by a hand operated stopwatch. Accordingly a special race track was constructed. This consisted simply of a grooved runway down which the cockroach ran, interrupting first one then another beam of light as it passed over narrow slits in the floor of the runway (Fig. 1). Interruption of the beams was detected by two photocells which were wired to activate a signal magnet writing on the drum of a precision synchronous-motor kymograph. Since the motor and gear-train of the kymograph were immersed in oil, the viscosity of which changed with temperature, a second writing lever for simultaneously recording time was added. The entire apparatus and animal cages were kept in a constant temperature room where the air temperature could be varied and yet, despite apparatus and operator, maintained to better than ± 1° C.

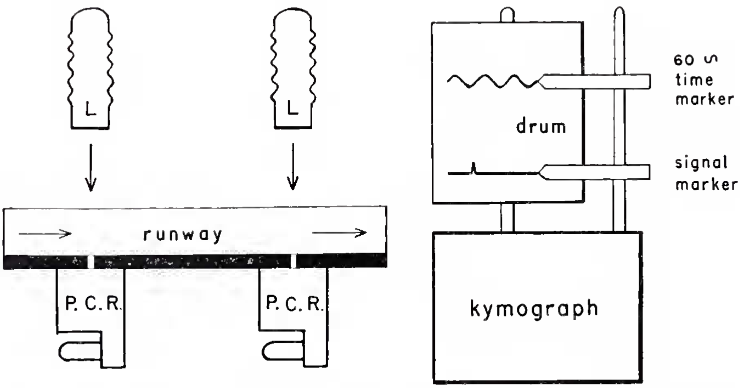

Fig. 1. Diagram (not drawn to scale) of the essential elements of the apparatus used for measuring running speed of cockroaches. Clamps and electrical wiring omitted. *L* = microscope lamps; *P.C.R.* = photocell-relay units ("Photobell," ES-1, Eby Sales Co.).

The runway was a board overlain with two steel strips (because at one stage we tried electrical shocking to stimulate the insects to run at full speed) and made flush with plastic wood. The surface had been leveled by rubbing with heavy emery paper and felt slightly rough (probably equal to Wille's "rough paper" rather than his smooth boards, linoleum or glass surfaces). The runway was 1 × 28 inches with slits for the light beams at 25 and 50 cm. intervals. Sides were vertical glass strips about 1½ inches high. Less difficulty with cockroaches attempting to climb the side walls was found when these glass side walls were covered with aluminum foil.

Our only serious difficulty was in learning how to handle the cockroaches. Various methods of mechanical and electrical stimulations were tried and discarded. Finally, cockroaches were placed in small envelopes (about 1 × 2 inches) or other suitable containers, to keep them readily available and quiescent until run. They were then grasped by the wings with forceps, placed on the track, released and simultaneously the cerci flipped with a finger. Being released near one end of the track they attained full speed before interrupting the first light beam, and hence recorded speeds are always full speed without any complication as to how long it may take the insect to attain this speed. After considerable experience, individual cockroaches can be handled to give consistently reproducible results.

Most individual cockroaches behaved consistently and reproducibly but a few had to be discarded because they either ran hesitantly or tried to climb over the sides rather than run in a straight line down the groove.

At 13.5° C. a running distance of 25 cm. was used. At the other temperatures a distance of 25 or 50 cm. was used.

Results

Average values for a population of cockroach adults were obtained by recording the times for 51 runs at 13.5° C., 58 runs at 20°, 170 runs at 25°, 60 runs at 30° and 47 runs at 35° C. The frequencies of various times at the different temperatures are plotted in Figure 3. The peak of the curves obtained is taken as the average value for that particular temperature. The breadth of these curves is not an index of the experimental error or of range in values for an individual. Single individuals do, of course, show a certain amount of variation from one run to another run, but most of the spread in the curves drawn in Figure 3 is due to the presence of fast and slow individuals. One set of 4 ♂ and 5 ♀ that were run repeatedly over a period of several months consistently showed one particular male as the fastest racer (averaging 10% faster than the next fastest), and several females tied for slowest. The fastest individual was consistently about 50% faster than the slowest ones.

In general, males were found to average 15–20% faster than females but the fastest females outran the slowest males. A larger sex difference (about 50%) is reported for german cockroaches by Wille (1920). This sex difference is paralleled by a 3–4x difference reported by several laboratories for muscle enzyme activity in american cockroaches. But a 300–400% difference in muscle enzyme activity does not make a good correlation with a mere 15–20%

difference in speed. There is no obvious correlation between weight and speed in our data.

In temperature studies in biology one commonly makes an Arrhenius plot of the natural logarithm of the rate of whatever is being measured against the reciprocal of the absolute temperature. This is done in Figure 2. As for many biological processes, a straight line is obtained or approximated in the lower part of the temperature range. To be sure, few points are available for this curve but each of the points in the average curve (*B*) is based on a significant number of determinations (47–170) and further supported by nu-

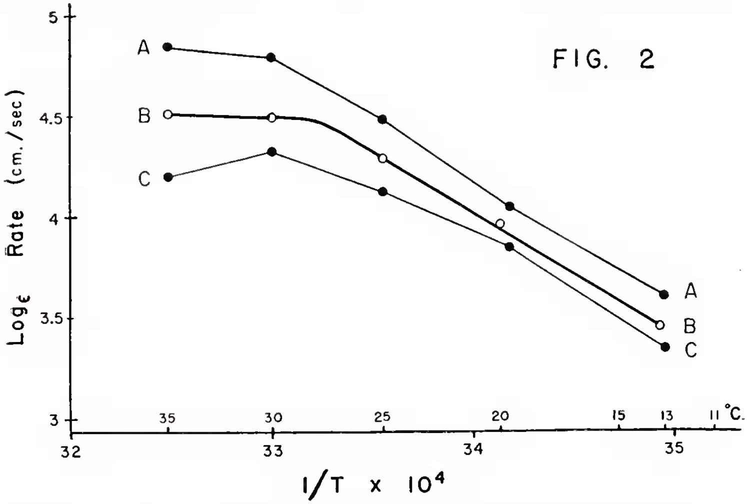

Fig. 2. An Arrhenius type plot of the natural logarithm of the running speed against the reciprocal of temperature. For convenience the corresponding centigrade temperatures are given above the abscissa. Curve *B* is based on peaks of curves of Fig. 3; curves *A* and *C* are corresponding determinations for respectively a single fast and a single slow individual.

merous additional values on individual cockroaches, values from two such individuals being plotted as curves *A* and *C*.

Unusual and unexpected in this curve is that it levels off to an approximately constant maximum rate in the upper portion of the normal temperature range. It is common for rates to level off and even decrease near the upper thermal limit but the highest temperature used here is well within the normal viable range for american cockroaches. This species has been kept in the laboratory here at 35° C. for months without apparent harmful effects. It seems that the running machinery can operate just so fast, and that this maximum rate is reached at 27–28° C. We have found only one other such record in the arthropod literature and that as an individual rather than a specific trait. Crozier (1924) recorded that some specimens of a millipede (*Parajulus pennsylvanicus*) were incapable of crawling faster than they go at 15° C. though others (presumably most) increased in rate regularly over the range 8–30° C.

Average values for the american cockroach at 35° C. were similar to those at 30° C. However, individual values were erratic above 30°. Of 7 cockroaches run individually and repeatedly at these

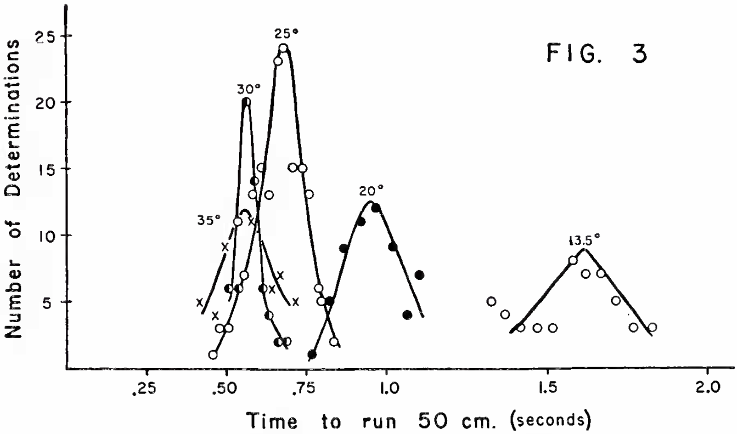

Fig. 3. Frequency of running speed determinations at the indicated temperatures (C.) for various individuals of a population. Determinations made at various times over a period of several months.

temperatures, 4 ran faster at 35° and 3 ran faster at 30° C. We can only ascribe this to erratic behavior near the extreme end of the temperature scale.

One can use the Arrhenius equation to calculate the heat of activation of chemical systems. Substituting values from Figure 2 in the equation:

$$\frac{\text{Rate at } T_2}{\text{Rate at } T_1} = e^{\frac{\mu}{2}\left(\frac{1}{T_1} - \frac{1}{T_2}\right)}$$

we obtain a μ value of about 12000 calories for the slope from 13–25°. This is closely similar to the value obtained for portions of the curves for diplopod (Crozier, 1924) and ant locomotion (Shapley, 1924; Barnes & Kohn, 1932) and various other processes which

Crozier & Stier (1925) suggest may be controlled by discharges from the central nervous system in arthropods. For a favorable review of Crozier's ideas see Barnes (1937); for an unfavorable review see the discussion following Hoagland's symposium paper (1936). Whatever validity one may assign to Crozier's ideas, ants differ from cockroaches in showing a much higher μ value for a portion of the curve (usually the lower temperature range).

Clearly, there is no direct correlation between the μ value of 12000 for running and the μ value of 20000 reported for the energy-releasing muscle apyrase (ATP-ase) enzyme system of the same species (Davison + Richards, 1954).

Barnes and Kohn (1932) found with ants that the change in speed with temperature is complicated by being partly related to frequency of leg movement and partly due to leg position and hence length of stride. Differences in stride as a function of walking speed have also been recorded for oriental cockroaches (Hughes, 1952) but that study was not comparable to the present one since it dealt only with submaximal velocities (and does not even state the temperature).[3] We did not study this point in detail but with measurements of footprints made on smoked paper (few dozen sets) we found that the width of stride remained constant irrespective of temperature but that the length of stride was sometimes the same and sometimes shorter at lower temperatures (up to 25% shorter). Individual differences seem to be involved; at least some individuals consistently maintained the same stride while others consistently shortened the stride at lower temperatures. Theoretically the situation is further complicated by some individuals dragging the body on the runway at lower temperatures. With so many known

[3] Hughes' paper is quite interesting to the general reader. It is based on analysis of successive frames of motion pictures. He discusses concepts of running and walking, points out that insects unlike mammals do not run in a dynamic balance such as has been termed a "braked fall" since insects can stop at any point in the walking pattern because the center of gravity is always within the support area provided by the legs, that no distinction can be made between walking and running in insects since both the velocity and change in stride are continuous over the range from zero to maximum speed, that six is the minimum number of legs which will permit the arthropod type of walking, that the pattern of leg movement shows more variation and plasticity than is generally thought, and that the only rules are (1) no pro- or mesothoracic leg is moved forward unless the next posterior leg is on the floor, and (2) opposite legs of the same segment always alternate

complications we do not care to attempt assessing the μ value obtained other than to remark that it is similar to the value recorded for certain portions of the curves for ants and that a straight line plot is not inconsistent with a complicated controlling mechanism.

Finally, we might mention than a check with thermocouples inserted into the muscles of the mesothorax showed that the temperature of the room was an adequate index of the temperature of the cockroach. Using a thermocouple sensitive to about 0.1° C. we found that a quiescent insect equilibrated to room temperature. At 20–35° C. some cockroaches taken at random were 1–2° lower than the air temperature, presumably due to hyperventilation. Single runs equal to that of a run down the race track did not detectably alter the intrathoracic temperature. Repeated runs totalling 100–200 cm. elevated the intrathoracic temperature less than 1° C. Incidentally, although not strictly relevant, intrathoracic temperature was raised only about 2.5° C. by several minutes of continuous flying and, presumably due to ventilation, returned to room temperature in 3 to 4 minutes.

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