

## TEMPERATURE, CONTACT RATES, AND INTERINDIVIDUAL DISTANCE IN WHIRLIGIG BEETLES (COLEOPTERA: GYRINIDAE)

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*Abstract.*—Contact rates between individual stream-dwelling gyrids increased with increasing temperature, while those for pond-dwelling gyrids remained fairly constant. In aggregated pond beetles, interindividual distance increased with increasing temperature up to 21°C, and then declined. These observations may be explained by the different constraints of the two habitats, and the function of whirligig beetle aggregations.

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Beetles of the family Gyrinidae are known for their conspicuous aggregations on the water surface of both ponds and streams. We examined the influence of temperature on the aggregating and contact behavior of whirligig beetles in the two habitats.

Pond- and stream-dwelling *Dineutes* were observed in Iowa County, Wisconsin, in a pond and on a part of the Wisconsin River; both sites were near the town of Arena. The stream gyrids were located in an eddy behind a fallen tree that was half submerged in the river. Observations of pond and stream gyrids were carried out on calm summer days to avoid the complications of choppy waves. Physical contacts that could be identified as part of sexual behavior (Kolmes, 1983a, 1985) are excluded from this data set. Observations were carried out during late morning through early afternoon hours.

In order to measure the rate at which pond- or stream-dwelling gyrids briefly contacted one another, an observer sat motionless approximately 2 to 3 meters from a gyrid swarm. Binoculars (7 × 35 mm) and a stopwatch were used to count and time contacts within the swarm. Small numbers of focal beetles were observed when counting contacts. Water temperature (approximately 1 cm below the surface) was measured immediately after each observation period was terminated. Focal beetles were randomly selected in the swarms. Observation periods were generally of 30 min duration each, occasionally of somewhat more or less time.

In the stream habitat, gyrids maintained a very consistent position within the swarm swimming into the current, aside from the brief “dashes” that resulted in each contact. Because of this spatial stability it was a simple matter to observe contacts as they occurred within a swarm, and to subsequently calculate a contact rate (number of contacts/(number of beetles × number of hours observed)). It is important to realize that these stream-dwelling *D. discolor* were limited to a constrained surface

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Table 1. Contact rates and water temperatures for *Dineutes discolor* located on the Wisconsin River. Every contact rate is the mean value for a separate observation period.

Water temp °C	Contact rate
25.0	10.8
25.5	5.4
25.5	7.7
26.0	32.5
26.0	13.3
26.0	40.0
26.0	50.0
26.5	33.3
27.0	18.6
27.0	47.6
28.0	80.0
28.0	99.2

area; they were aggregated in the area of relatively weak current provided by a fallen log near the bank.

The pond gyrimids (a mixture of *Dineutes* spp. other than *D. discolor*—*D. assimilis*, *D. hornii*, and *D. nigrior* all occurred in that area) had no fixed spatial limits to their aggregations; beetles that began to feed actively generally moved to the periphery of the aggregation and swam about in a region of emergent vegetation at the pond margin. Beetles selected for focal observations on the pond were not part of the motionless central clump of individuals that sometimes formed and floated in constant contact with their clump-neighbors. For information about the feeding behavior of pond-dwelling gyrimids, see Heinrich and Vogt (1980).

The water temperatures and contact rates are shown for stream-dwelling *Dineutes* in Table 1, and for pond-dwelling *Dineutes* in Table 2. Two things are immediately apparent in comparing these tables: 1) The contact rates for stream-dwelling gyrimids are generally higher at higher temperatures, while pond-dwelling gyrimids contact one another at a much more consistent rate regardless of ambient temperature. 2) The pond beetle contact rates are all within the contact rate range for river beetles when the river was cool. The pond beetles never achieved the elevated contact rates typical of stream-dwelling beetles at the higher temperatures, despite the fact that for some observation periods water temperatures in the pond exceeded those measured for river water.

If a least squares regression of water temperature and contact rate is calculated, it can be used to produce a coefficient of determination ( $r^2$ ) that expresses the percentage of the variation in contact rates that can be attributed to water temperature (Milton and Tsokos, 1983). The coefficient of determination for water temperature vs. contact rate for stream-dwelling *Dineutes* is 0.706, indicating that 70.6% of the variation in contact rate is accounted for by water temperature variability. For pond-dwelling *Dineutes*, the  $r^2$  value is 0.001, so that only 0.1% of the variation in contact rate is accounted for by water temperature variability. Stream-dwelling *Dineutes* exhibit a linear relationship between temperature and spacing behavior that does not appear to exist among their pond-dwelling congeners.



Table 2. Contact rates and water temperatures for *Dineutes* spp. that inhabit a pond habitat. Every contact rate is the mean value for a separate observation period.

Water temp °C	Contact rate
23.0	22.7
23.0	12.7
23.0	17.0
23.0	18.0
23.5	21.3
23.5	13.0
23.5	18.0
30.5	15.0
31.0	20.4

To examine the effect of temperature on interindividual distance in pond beetle aggregations (*D. hornii*), a series of photographs was taken of beetle aggregations located in small ponds in southwestern Ohio. These photographs were taken over water temperatures ranging from 11° to 28°C. The photographs were made into slides, projected on a screen to actual size, and the distance between individual beetles was measured as nearest neighbor distance.

Figure 1 shows that with an increase in temperature, there is a corresponding increase in nearest neighbor distance, up to 21°C, after which the nearest neighbor distance decreases.

It seems probable that an increased temperature produces both an increased metabolic rate and an increased energetic demand in stream-dwelling *Dineutes*, and that under such conditions they contact one another more often as part of their social spacing system. The maintenance of an individual distance around a beetle in a swarm is crucial to stream-dwelling *Dineutes* because each feeds at its location in the swarm, and competes for space within a circumscribed area (Kolmes, 1983b). The interindividual distances between the *D. discolor* on the river were not free to vary appreciably, as whatever number of beetles made up the swarm was limited to the small surface area of weak current behind the fallen log. This is typical of the eddy habitat of stream-dwelling gyrids (on rapidly flowing streams), and, as was true in this case, other suitable patches of habitat are often several kilometers or more distant.

The pond-dwelling *Dineutes*, in contrast, "rest" in tight aggregations but feed in a more dispersed fashion over a larger surface area that is not limited by the energetic advantages provided by a small protected area of weak current. There is therefore no advantage to these animals in defending a small individual area more intensively (by more contacts) as temperature increases, as they can merely spread further apart if greater distances between swarm members become adaptive.

Animals that aggregate must balance the benefits of aggregation against a tendency to increase individual space. As the water temperature increases, pond beetles do not increase their contact rates, but do increase their individual distance up to a point. A possible explanation of this spacing behavior relates to the primary function of these aggregations.

Gyrinid diurnal aggregations function in defense by allowing individual beetles to



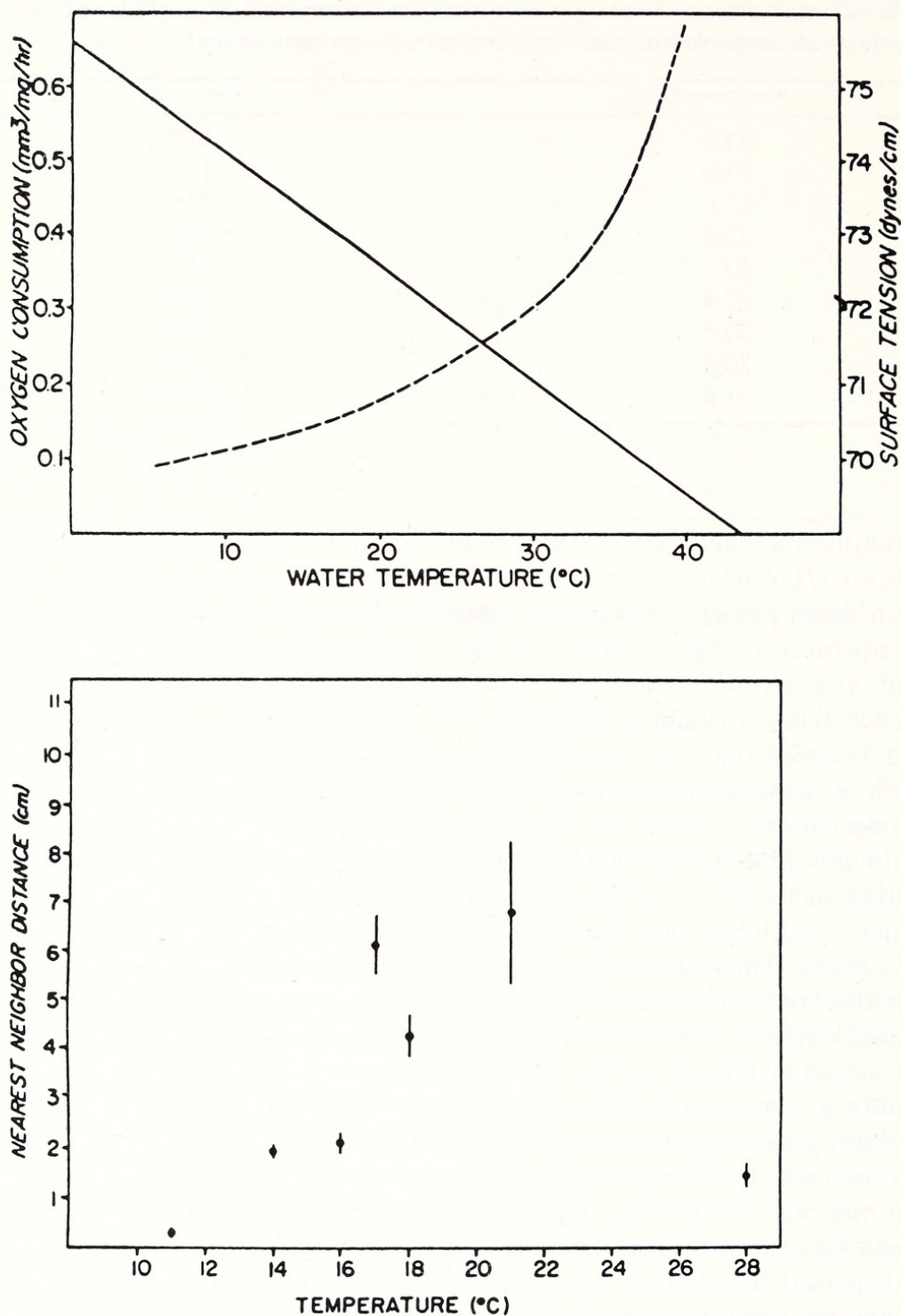


Fig. 1. LEFT. The nearest neighbor distance (cm) of gyrinids at different water temperatures (°C). Error bars are  $\pm 1$  standard error. N for each temperature: 11°C = 1,393; 14°C = 83; 16°C = 135; 17°C = 75; 18°C = 97; 21°C = 6; 28°C = 163. RIGHT. Relationship between metabolic rate of an insect as measured by oxygen consumption and temperature (°C) (dashed line). Relationship between surface tension (dynes/cm) and water temperature (°C) (solid line). The intersection of the lines would represent the theoretical maximum of nearest neighbor distance. (After Hutchinson, 1957; Keister and Buck, 1974.)



gain an early warning of approaching predators through perception of the waves generated by the swimming movements of other beetles (Vulinec, 1983). Their ability to respond quickly is related to their metabolic rate, which in turn is a function of ambient temperatures.

As the water temperature increases, the ability of the beetles to respond increases, so they can afford to be farther away from each other. However, surface waves in warm water attenuate sooner than waves in cold water. Therefore, whirligig beetles can only move a certain distance apart before they are no longer able to feel their neighbors' waves. At even warmer temperatures, wave attenuation forces the beetles to move closer together (Fig. 1).

There is some evidence that gyrid contact behavior may have some communicatory function (Freilich, 1986). Although beetles may be exchanging information during these encounters, this possibility does not account for the difference in contact rates between pond- and stream-dwelling gyrids.

The response of aggregating animals to environmental variables may be complex. Aggregations tend to confer on animals certain benefits—thermoregulation (Graves and Graves, 1978; Kavanaugh, 1977; Lee, 1980), exploitation of certain food sources (Tsubaki and Shiotsu, 1982), and, as in this case, protection from predators (Aldrich and Blum, 1978; Henry, 1972; Vulinec, 1983). In all cases, the overriding selection pressure appears to be the maintenance of the aggregation. Stream beetles are more constrained because of the limited eddy habitat. Aggregations may form in these beetles purely in response to this habitat. Pond beetles, however, do not need to form conspicuous aggregations in response to their habitat, and protection from predators is the primary function of these groups. With this one constraint, more flexibility is available to pond gyrids, and they can afford to increase their inter-individual distance as conditions permit.

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