

in investigating. Finally, groups in which the functions $u(x)$ are discontinuous would seem to be worthy of consideration.

¹ G. Kowalewski, *Sitz. ber. Math. Akad. Wiss. Wien*, **120**, Abteilung IIa¹, IIa², 1911 (77-109, 1435-72).

² See writer's doctor's dissertation (Chicago, 1918).

³ *Trans. Amer. Math. Soc.*, **15**, 1914r (139).

⁴ In a paper by the writer soon to be published on Linear Partial Differential Equations with a Continuous Infinitude of Variables.

⁵ This formula has already been obtained by Volterra as the general solution of a functional differential equation in his paper, *Atte R. Accad. Lincei*, Ser. 6, **23**, 1914, 1st semester, (p. 393).

⁶ See paper by writer entitled, Integro-differential Equations with Constant Kernels, *Bull. Amer. Math. Soc.*, **26**, 1920 (193).

THERMOKINETICS OF *LIOMETOPUM APICULATUM* MAYR

BY HARLOW SHAPLEY

MOUNT WILSON OBSERVATORY, PASADENA, CALIFORNIA

Communicated by W. M. Wheeler, February 16, 1920

Variation in the activity of a cold-blooded animal is largely dependent on metabolic changes, which in turn probably depend mainly on the acceleration of oxidation and of other chemical reactions. The physical nature of the environment affects most of these chemical processes, and we should expect that the same physical properties would also directly influence the kinetic manifestations of animal life. While many observations record the qualitative relation of animal activity to such factors as humidity and external temperature, only a few give definitive numerical results.

An opportunity for precise quantitative measurement of the variation in the rate of expenditure of animal energy under the different natural stimuli arising from changing meteorological conditions, is afforded by the study of the foraging and patrolling activities of ants of the subfamily Dolichoderinae. Although some of my observations have been made on other genera of this group (*Tapinoma*, *Dorymyrmex*), I find the most suitable material to be the "Argentine ant," *Iridomyrmex humilis* Mayr, and two species of *Liometopum*. In briefly describing the activities of these ants and the observations based upon them, a number of reasons are proposed in the following paragraphs why members of the subfamily, and particularly the California *Liometopa*, are thought to be better adapted than nearly any other organism for the close quantitative investigation of kinetic response to changes in field conditions.

The trail-running habit, which is common to all genera of Dolichoderinae except *Leptomyrmex* of Australia,¹ is fundamental for the observations discussed below. It permits permanent observing stations to be set up along the trail so that the speed over fixed intervals of distance can be

measured under different conditions of light, air-temperature, relative humidity, wind-velocity, and barometric pressure, and at different times of the day and during all seasons of the year. The trails are maintained for long intervals of time, many of those of *Liometopum apiculatum* and *L. occidentale* on Mount Wilson have not changed during two years of observation. Colonies of the closely related *L. microcephalum* of Europe are also known to maintain constant trails for several years.² Ants running in these files, whether toward or away from the nest, are for the most part unburdened, their function apparently being mainly that of patrol.

Another characteristic of the *Liometopa*, which is very fortunate for this research, is that they are equally diurnal and nocturnal in habit—a characteristic that permits continuous series of observations as well as favorable opportunities for the investigation of natural phototactic reactions.

The conspicuous differences in stature of the workers of *Liometopum* allow the possible correlation of activity and hardihood with size. The average live weight of a worker maxima of *L. apiculatum* is, according to my measures, about five hundredths of a grain (140,000 to a pound); the average worker minor weighs half as much, but the extremes of weight for maxima and minima are probably in the ratio of four to one.

The wide range of temperature, humidity, wind, and light, throughout which these ants are active, enables a thorough testing of the extent to which the various meteorological factors are involved in kinetic reactions. The files are maintained with the relative humidity near its maximum of 100%, or when as low as 5%; the patrols are running when the temperature is 38° centigrade (over 100° Fahrenheit) and also when it is less than 8°. After a few warm days late in December thousands of ants of two species of *Liometopum*, on Mount Wilson, were out of their nests only a few feet from banks of snow.

There is a distinct advantage for thermokinetic studies in the comparative freedom of the patrolling *Liometopa* from the erratic motions which are characteristic of many kinds of insects, or which are in fact characteristic of most active animals of all the higher phyla. It is this common irregularity and discontinuity of action that usually prevents quantitative measurement of the kinetic responses of cold-blooded animals. A fixed patrol of Dolichoderines from a populous colony, however, is essentially a steady flow of animal energy; its quantity is governed largely by food and its speed by meteorological conditions. Except at low temperatures the normal speed of running appears to be very near the maximum speed possible under the prevailing conditions. For temperatures below 15° centigrade the excitation of battle or food temporarily increases activity.

The California *Liometopa* are carnivorous, granivorous, and aphidicolous. This catholicity of taste permits successful baiting for the purpose of main-

taining the density of a file, for the establishment of new trails over some special terrain, or for other experiments.

The large population of the nests makes possible the establishment of files of sufficient density for statistical treatment of the observations of speed. The population of colonies of *Liometopum* and of *Iridomyrmex humilis* is to be numbered by the tens of thousands. On an average patrol during the warmer months, 100 ants pass a given point in one minute (see table III, p. 209). From one nest on Mount Wilson, in the summer of 1919, four files issued, and every day, under favorable conditions of weather, 70,000 ants went out along each file and nearly 70,000 ants came in.

The observations tabulated below were made on Mount Wilson (altitude 5700 feet) on ants from a nest of *L. apiculatum*, located in the basal, slightly-decayed trunks of a group of *Quercus chrysolepis* Liebm. This species of *Liometopum* is not assigned to the state in Wheeler's "Mountain Ants of Western North America."³ The subspecies *luctuosum* Wheeler, however, has been taken on nearby mountains⁴ and probably occurs on Mount Wilson. In a discussion of California ants, Woodworth⁵ states that "*Liometopum* is a very rare insect," it is probably uncommon, therefore, in many parts of the state, but in the San Gabriel mountains it is by far the most numerous ant, with the species *occidentale* Emery predominating.⁶

Of the nine different "speed traps" set up for the study of the nest of *L. apiculatum*, Stations A and Y were principally used. The former is at the base of a concrete wall some 50 feet from the nest; the latter, on another trail, is on a plank surface about 2 feet from the main nest openings. These two pieces of trail are of comparable smoothness, and each is 30 centimeters in length. The time required for individuals to pass through the speed traps was recorded (with a stop watch for high temperatures), together with an indication of the size of ant and its direction of travel. At the beginning and end of each observation, which is the mean time in seconds for about 20 individuals, the temperature was read from a thermometer, the bulb of which was placed against the wall or board, some 10 or 15 millimeters from the trail.

As the observations are made within a few yards of a special station maintained by Mr. Hoge for the United States Weather Bureau, we have available, for all the observations on speed, continuous graphical records of the precipitation, wind-velocity, temperature, and barometric pressure, as well as semi-daily cloud and psychrometric observations.

It was found from the first observations that the kinetic response for these ants is essentially a function of temperature alone—other meteorological conditions (except rain, of course) having very little if any direct effect on speed. Even the influence of light and time of day are extremely small compared with the influence of temperature. If the speed is de-

pendent mainly on the velocity of chemical reactions, this result should be expected.

The quantities in the sixth column of table I are the observed mean time required for an ant to travel 30 centimeters, at the corresponding temperature, and the probable error of that mean; uncertainties of timing, frequently contribute nearly a tenth of a second to the probable error. The seventh column contains v , the average speed, reduced to centimeters per second.

Temperature is plotted against speed in figure 1. Observations made at station A are plotted as dots, and those made at station Y as crosses. Two observations of low weight (Nos. L2A and L27A) are plotted as open circles; the recorded temperatures are undoubtedly high, because the timing of ants was begun too soon after introducing the cardboard shade

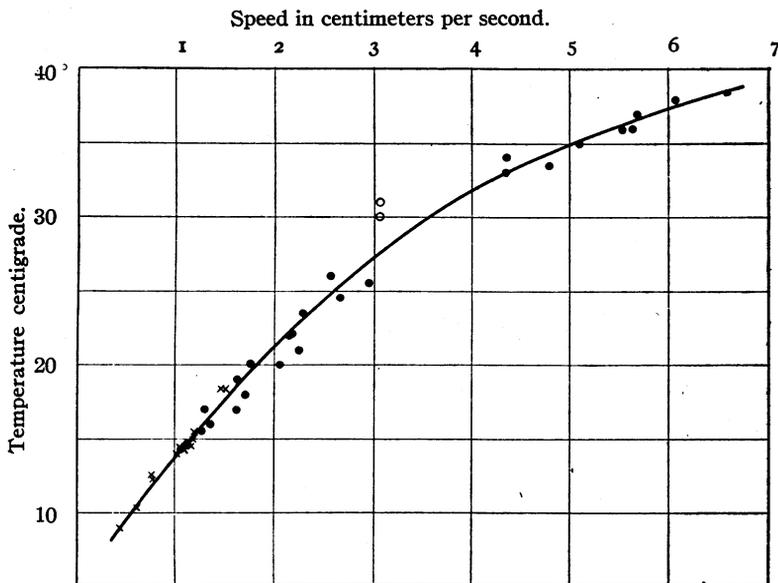


FIG. 1. The temperature-speed curve for *Liometopum apiculatum*.

and the artificial lowering of temperature is responded to much more quickly by the ants than by the mercury thermometer. (Observations made in January 1920 at stations F and G confirm the supposition that the two measures in question were erroneous and should be rejected in a mathematical discussion of the curve.)

The quantities in the eighth and ninth columns of table I are, respectively, the percentage difference in speed for inbound and outbound ants, and the percentage difference in speed for large and small workers. These observations of systematic differences were designed to give evidence of the effect on speed of fatigue and mass. A positive value of $(i - o)/0.01v$

indicates that during that observation ants travelled faster toward the nest than away. A positive value of $(M - m)/0.01v$ indicates a greater average speed for the larger workers. The percentage differences are grouped in table II in order of decreasing temperature.

TABLE I
OBSERVATIONS OF TEMPERATURE AND SPEED

Obsn.	Date (1919)	Time (P. S. T.)	Temp. (Cent.)	No. Ants.	Seconds and P. E.	Speed (cm/sec)	$\frac{f-o}{0.01v}$	$\frac{M-m}{0.01v}$	Remarks		
L 1A	May, 25	11:20 A.M.	34°	22	6.9 ± 0.1	4.35	- 4	- 1	Sunshine		
L 2A		11:35 A.M.	30	18	9.8	0.3	3.05	- 5	+ 4	Shaded with cardboard	
L 3A		11:46 A.M.	35	21	5.9	0.1	5.08	- 5	- 3	Sunshine	
L12A*		5:25 P.M.	21	20	13.4	0.3	2.23	+13	+ 6	Tree-shadows	
L13A		8:35 P.M.	16	18	22.1	0.2	1.36	+ 4	- 2	Dark	
L16A		10:38 P.M.	15.5	17	23.5	0.5	1.27	+17	- 1	Dark	
L17A*		26	1:28 A.M.	14.5	15	27.3	0.7	1.10	+ 1	- 2	Dark
L20A			4:00 A.M.	14.5	18	27.2	0.6	1.10	+ 6	- 3	Dawn beginning
L22A			0:55 P.M.	38.5	42	4.55	0.05	6.60	- 9	+ 7	Sunshine
L23A*		27	2:25 A.M.	17	19	23.5	0.4	1.28	+ 9	+ 5	Dark
L25A*			10:55 A.M.	33.5	26	6.3	0.1	4.77	+ 8	0	Sunshine
L27A*			11:25 A.M.	31	24	9.8	0.2	3.06	- 4	+ 1	Shaded with cardboard
L28A*			11:40 A.M.	37	22	5.29	0.08	5.67	+ 6	+10	Sunshine
L29A			4:47 P.M.	26	24	11.7	0.2	2.56	- 1	+ 2	Tree-shadows
L31A			5:24 P.M.	23.5	18	13.1	0.2	2.29	- 8	- 7	Cloudy
L32A	6:15 P.M.		22	22	13.8	0.3	2.17	-13	+ 8	Twilight, cloudy	
L33A	8:15 P.M.		20	20	16.1	0.2	1.86	- 6	0	Dark	
L35A	11:42 P.M.		18	24	17.6	0.5	1.70	+12	+ 2	Dark, two hours after rain	
L36A	June, 4		9:22 A.M.	20	24	14.7	0.3	2.04	0	- 7	Cloudy
L38A		11:24 A.M.	36	22	5.43	0.08	5.62	- 6	- 1	Sunshine	
L39A		11:40 A.M.	38	20	4.95	0.07	6.06	- 2	+ 8	Sunshine	
L40A		11:53 A.M.	36	21	5.43	0.13	5.52	- 3	- 3	Shaded with glass	
L41A		0:02 P.M.	33	20	6.95	0.13	4.32	- 3	- 1	Shaded with cardboard	
L44A		4:40 P.M.	25.5	25	10.2	0.2	2.94	+ 5	0	Tree-shadow	
L46A		5:11 P.M.	24.5	20	11.3	0.2	2.65	+10	+12	Tree shadows	
L47A		10:55 P.M.	17.5	20	18.6	0.4	1.61	+ 8	- 2	Dark	
L48A		5	9:20 A.M.	19	26	18.5	0.4	1.62	- 9	+ 7	Shadow of wall
L50A*			10:05 A.M.	22	19	13.9	0.4	2.16	-19	- 2	Shadow of wall
L54Y			1:40 P.M.	14	20	29.6	0.9	1.01	+12	+14	Tree-shadows
L56Y		Dec. 21	2:16 P.M.	14.5	24	25.8	0.4	1.16	- 8	+19	Weak sunshine
L57Y			3:44 P.M.	12.6	20	39.0	1.1	0.77	- 6	+12	Tree-shadows
L58Y			4:36 P.M.	10.3	20	46.9	1.6	0.64	+27	+ 4	Weak sunshine
L59Y			6:15 P.M.	9.0	16	68.1	2.6	0.44	+11	+15	Dark
L60Y	22		11:42 A.M.	14.5	20	27.0	0.8	1.11	-20	+ 6	Tree-shadows
L61Y			11:56 A.M.	14.5	20	28.5	1.0	1.05	-25	+15	Tree-shadows
L62Y			0:47 P.M.	15.5	22	25.4	0.8	1.18	-14	0	Tree shadows
L63Y			3:40 P.M.	18.0	21	25.9	0.8	1.16	- 9	+ 9	Mottled shadow
L64Y	23		2:47 P.M.	18.6	20	20.2	0.5	1.48	- 2	+ 2	Weak sunshine
L65Y			4:08 P.M.	18.5	20	20.8	0.6	1.44	+13	+ 3	Weak sunshine
L66Y		7:15 A.M.	12.5	20	38.7	0.9	0.77	- 4	+ 5	Shadows at sunrise	

TABLE II
RELATION OF SPEED TO SIZE AND DIRECTION OF TRAVEL

INTERVAL OF TEMPERATURE	NUMBER OF OBSERVATIONS					Mean of $\frac{i - o}{0.01v}$	Mean of $\frac{M - m}{0.01v}$
	Total	Inbound Workers		Major Workers			
		Fast	Slow	Fast	Slow		
Station A							
38.5° to 30.5°	10	2	8	4	5	-2.2	+1.7
30.5 to 22.5	5	2	3	3	1	+0.2	+2.2
22.5 to 14.5	13	8	3	5	7	+3.5	+0.7
Total range	28	12	14	12	13	+0.8	+1.3
Station Y							
18.6 to 9.0	12	4	8	11	0	-2.1	+8.7

TABLE III
OBSERVATIONS OF TEMPERATURE AND AVERAGE FREQUENCY FOR 4570 ANTS

Ob- serva- tion	Date (1919)	TIME (P. S. T.)	TEMP. (CENT.)	INBOUND		OUTBOUND		Ratio of fre- quencies N_i/N_o
				Number	Fre- quency N	Number	Fre- quency N_o	
L 4A	May 25	0:55 P.M.	37°	150	0.95	150	1.14°	0.83
L 8C		3:46 P.M.	34.5	250	1.58	250	1.33	1.19
L11A		5:15 P.M.	21.5	250	2.05	250	1.27	1.61
L14A		8:40 P.M.	16	150	1.32	150	1.04	1.27
L15A		10:30 P.M.	15.5	100	0.88	100	0.65	1.35
L18A	26	1:37 A.M.	14.5	150	0.80	150	1.21	0.66
L19A		3:59 A.M.	14	250	0.94	250	0.82	1.15
L21A	27	0:56 P.M.	38.5	125	0.44	125	0.42	1.05
L24A		2:35 A.M.	17	125	0.87	125	0.48	1.81
L26A		11:10 A.M.	36	100	0.41	100	0.86	0.48
L30A		5:00 P.M.	25.5	200	1.42	200	1.27	1.12
L34A		8:25 P.M.	20	150	1.14	150	1.36	0.84
L37A	28	9:30 A.M.	19.5	110	0.74	110	0.70	1.06
L45A		4:51 P.M.	25.5	100	0.85	100	0.85	1.00
L51A	5	10:12 A.M.	23	50	0.20	100	0.76	0.26

In order to determine the relation of number of ants running to time of day and to temperature, the series of observations were made at station A which are recorded in table III and summarized for time of day and temperature in tables IV and V. The frequencies N_i and N_o show the average number of inbound and outbound ants passing a given point on the trail per second—a quantity obtained by dividing the number of ants, fifth and seventh columns, into the intervals of time required for their passage. When the ratio N_i/N_o exceeds unity, more ants are going in

TABLE IV
FREQUENCY AND TIME OF DAY

TIME OF DAY	NUMBER OF OBSERVATIONS	MEAN FREQUENCY		
		In	Out	Ratio
0 to 6 A.M.	3	0.87	0.84	1.04
6 to 12 A.M.	3	0.45	0.77	0.58
0 to 6 P.M.	6	1.22	1.05	1.16
6 to 12 P.M.	3	1.11	1.02	1.09
All	15	0.97	0.94	1.03*

TABLE V
FREQUENCY AND TEMPERATURE

TEMPERATURE (Centigrade)	NUMBER OF OBSERVATIONS	MEAN FREQUENCY		
		In	Out	Ratio
14.5° to 22.5°	8	1.09	0.94	1.16
22.5 to 30.5	3	0.82	0.96	0.86
30.5 to 38.5	4	0.84	0.94	0.90
All	15	0.97	0.94	1.03*

* If the terminal territories of different files do not overlap, this ratio in the long run should be unity or less.

than out. In tables IV and V the quantity N_i/N_o is the ratio of average frequencies for the corresponding intervals of time or temperature; it has a different and better meaning than the average ratio of frequencies for the same intervals.

The following summary of conclusions may be based upon the tables and figure; a discussion of the properties of the temperature-velocity curves reserved for a later communication.

1. From the measurement of the speed of a thousand individuals of the species *Liometopum apiculatum*, an empirical curve is obtained that for any temperature throughout a range of 30° centigrade gives the speed with an average probable error of 5% for one observation. Conversely, from a single observation of the ant-speed, the temperature can be predicted within 1 degree centigrade.

2. The activity is less erratic for higher temperatures. Thus, the percentage probable error, derived for each observation from the deviations of the individual timings, decreases on the average with increasing temperature and speed from about 4% to less than 2%; but for only one observation does the probable error exceed a millimeter a second.

3. As the temperature rises 30° centigrade the speed changes fifteen fold, increasing uniformly from 0.44 to 6.60 centimeters a second. For a large species of *Eciton*, probably *burchelli*, observed by Beebe in British

Guiana, a normal speed of 7.6 centimeters a second is recorded,⁷ and on a later occasion as speed of 15.2 centimeters a second.⁸

4. There appears to be little, if any, real difference in speed towards and away from the nest. Large and small workers have practically the same speed for all temperatures during the summer months; after two months of low temperature, the large workers are conspicuously more active than the small workers (ninth column of table I).

5. This species of ant runs as numerously in the night as during daylight hours; maximum activity falls between noon and midnight, according to the scarcely sufficient observations summarized in table IV. Within the limits of 14° and 38° centigrade, temperature appears to have little effect on the number of ants running in the files.

¹ Wheeler, W. M., *Proc. Amer. Acad. Arts and Sci.*, Boston, **51**, 1915 (255-286), p. 259

² Mayr, G., *Verh. Zool. Bot. Gesell. Wien.*, **5**, 1855 (273-478), p. 319.

³ Wheeler, W. M., *Proc. Amer. Acad. Arts and Sci.*, Boston, **52**, 1917 (457-569).

⁴ Wheeler, W. M., *Ibid.*, p. 521; and *Bull. Amer. Mus. Nat. Hist.*, New York, **21**, 1905 (321-333).

⁵ Woodworth, C. W., *Univ. of Cal. Pub.*, Berkeley, Cal., Agr. Exp. Sta. Bull. **207**, 1910 (53-82).

⁶ Shapley, Harlow, *Bull. Ecol. Soc. Amer.*, Tuscon, Ariz., **3**, 1919, No. 4.

⁷ Beebe, William, *Jungle Peace*, New York, 1919, p. 229.

⁸ Beebe, William, *Atlantic Monthly*, Boston, October 1919 (454-464), p. 458.

THE INFLUENCE OF IONS ON THE OSMOTIC PRESSURE OF SOLUTIONS

BY JACQUES LOEB

THE ROCKEFELLER INSTITUTE FOR MEDICAL RESEARCH, NEW YORK

Communicated February 21, 1920

I. The osmotic pressure of solutions is usually measured indirectly, namely, by the determination of the freezing-point. Direct measurements have thus far been rare for the reason that it is difficult to prepare membranes permeable for water but not for the solute. The measurements thus far obtained on non-electrolytes by Morse,¹ and by the Earl of Berkeley² and their collaborators show that the actual values observed are not far from those expected according to van't Hoff's theory.

The difficulties in the preparation of semipermeable membranes are considerably diminished when we substitute colloidal solutions for solutions of crystalloids. By using solutions of proteins, collodion membranes satisfy the demand of semipermeability.

Gelatin is a very convenient protein for the purpose of such experiments. Like proteins in general, it is an amphoteric electrolyte being capable of forming salts with acids as well as with bases. The hydrogen ion concentration at which gelatin is neither in combination with acid nor with base is $10^{-4.7}N$ ($p_H = 4.7$ in Sørensen's logarithmic symbol). This