

Temperature Limits to Trailing Activity in the Australian Arid-Zone Meat Ant *Iridomyrmex purpureus* form *viridiaeneus*

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Abstract

Trailing activity is restricted to the hours of daylight and is further limited by the temperature of the air surrounding the ant (T_a) and by the net radiant heat load. Activity in winter begins well after sunrise and continues until late afternoon averaging c. 7.4 h per day. Midsummer activity occupies two distinct periods, one commencing at dawn and the other in late afternoon; the two together total about 6.8 h per day. The upper and lower values of T_a between which ants are active are 43.5°C and 14°C. Radiant heat input is dissipated from the ants by convective heat loss.

Introduction

Iridomyrmex purpureus form *viridiaeneus* Viehmeyer is a common species of ant in the Australian arid zone (Halliday 1978). It is a trailing species, and workers follow well defined tracks, often several hundred metres in length, which run between the nest and a food resource. Because these trails are kept clear of vegetation and debris, foraging ants are completely exposed to incoming radiation, both from the sky and the soil. Workers are black in colour and this results in absorption of a high proportion of the incoming solar radiation (0.3–3 μm) and of solar radiation reflected from the ground and vegetation. Animal tissues, irrespective of colour, absorb almost all incident long-wave radiation (2–50 μm) so that the ants will also receive a large heat load due to long-wave radiation from the sky, vegetation and soil surface (Campbell 1977). Total heat loads in north-western New South Wales are large, especially in summer when at midday the total incoming radiation from the sky reaches 1300 W m^{-2} , and that from the ground reaches c. 900 W m^{-2} (Dawson 1972; Campbell 1977). In addition, soil surface temperatures frequently exceed 60°C, which leads to further heat gain by conduction from the soil surface and perhaps from the heated layer of air just above. Under these conditions it appears unlikely that the ants could maintain trailing activity throughout the day in summer. This investigation examined activity patterns of ants under field conditions in relation to environmental temperatures on the trail and radiation heat loads received. Although activity periods of *I. p. viridiaeneus* have been studied when temperatures were not extreme (Mobbs *et al.* 1978), no information is available concerning the relation of trailing activity to temperature conditions on the trail and radiation heat loads received by the ants. Consequently, this study, which emphasized the behaviour of the ants under summer conditions, was undertaken.

Materials and Methods

Several nests of form *viridiaeneus* were examined from 1976 to 1979, on a north-west facing slope in Sandstone Paddock, Fowlers Gap Research Station in the upper western division of New South Wales.

Activity of the ants was monitored by counting, at 15- or 30-min intervals, the number of ants passing a given point on the trail in 1 min; incoming and outgoing foragers were counted separately and data were expressed as ants per minute. The counting site was always within a few metres of the nest and care was taken to avoid disturbing the nest or trail. The colonies examined in the summer of 1976-78 had only one main trail, leading to a tree or shrub where excretions of sapsucking insects (Homoptera) were utilized as a source of food. In January and July 1979, different colonies were studied and several main trails were apparent, some exploiting food sources other than trees.

Solar radiation was measured with a Solar Radiation Instruments hemispherical solarimeter. Total sky and soil radiation were measured with S.R.I. net radiometers used as single-sided instruments; outputs from these instruments were recorded in millivolts with an Elaviscip battery operated recorder (1976-78) or a Honeywell Versapoint 12 channel potentiometric recorder operated from 12-V batteries through an inverter. Temperatures 1-2 mm above the trail (T_a) and soil surface temperatures (T_s) were measured with 38-SWG copper-constantan thermocouples. Thermocouples were calibrated against a standard mercury thermometer and readout was either direct, in degrees Celsius, on a Bailey Instruments laboratory thermometer (model Batt IV) (in 1976-78) or in millivolts on the Honeywell recorder with ice bath reference junctions (in 1979). Alfoil radiation shields were fitted to thermocouples used to measure T_a , and for measurement of T_s thermocouple junctions were placed just below the soil surface. A maximum and minimum thermometer was used to determine minimum overnight temperatures in tree canopies. Soil radiation temperature (T_{rs}) was calculated from the equation: $T_{rs} = \sqrt[4]{R + \sigma}$, where R is the measured long-wave radiation flux density ($W\ m^{-2}$) and σ is the Stefan-Boltzman constant.

The rate of movement along the trail was determined as follows. A 30-m tape was laid alongside the trail and the time for individual ants to travel 20-30 m recorded. To facilitate recognition of ants, animals carrying easily recognizable burdens, but which moved at the same rate as unladen ants, were selected.

To enable calculation of the surface area of ants, the dimensions of the legs, antennae, head, trunk and gaster were measured under a binocular microscope fitted with a calibrated ocular micrometer and calibrated eyepiece graticules. The legs, antennae and trunk were treated as cylinders and the head and gaster as cones. The ants used were mounted on entomological pins for ease of handling.

Ants were identified by Dr P. J. M. Greenslade, CSIRO, and voucher specimens are deposited in the Australian National Insect Collection.

Results

Activity, Radiation Fluxes and Temperatures

The ants studied were strictly diurnal in their trailing activity, although activity at the nest surface was observed before trailing began in the morning and briefly after dusk. Activity was monitored on cloudless days in December 1976 and 1977, January 1979 and June 1978 and July 1979, providing data for midsummer and midwinter conditions.

On summer days, ants were active during two periods: from dawn to mid-morning and from mid-afternoon to dusk (Table 1; Fig. 1), the exact duration of these periods varied according to the prevailing weather conditions. Measurements were made of trailing activity, radiation fluxes, soil and air temperatures on the above dates; data for 10 January 1979 are shown in Fig. 1. The number of ants leaving the nest in the morning began to decline about an hour before trailing activity finally ceased. The numbers of incoming ants reached a peak shortly after this, but thereafter declined rapidly, reaching zero about 30 min after ants stopped leaving the nest. Table 2 gives the temperature and radiation levels at these two critical times (commencement of decline in outgoing activity and

Table 1. Activity periods on ant trails

Times in summer are Australian Central Summer Time and in winter Australian Central Standard Time

Season	Date	Morning		Afternoon	
		Trailing starts	Trailing ends	Trailing starts	Trailing ends
Summer	8.xii.1976	—	1100	—	—
	10.xii.1976	—	1100	—	—
	7.xii.1977	0615	1115	1700	—
	8.xii.1977	0600	1045	1730	2010
	9.xii.1977	—	1000	1830	—
	10.i.1979	0615	1100	1835	2035
	11.i.1979	0620	1015	1840	2035
Winter	20.vi.1978	1000	—	—	1645
	21.vi.1978	0945	—	—	1700
	22.vi.1978	0930	—	—	1715
	15.vii.1979	0830	—	—	1630

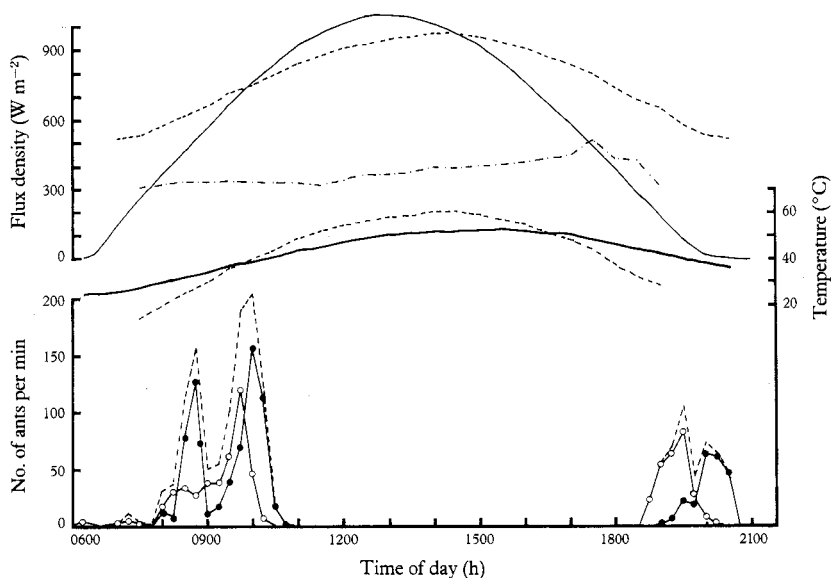


Fig. 1. Activity of ants on trails in relation to air temperature at trail level, soil radiation temperature and radiation fluxes on a summer day, 10 January 1979. Sunrise c. 0600 h Central Summer Time. Activity: ○ outgoing ants; ● incoming ants; --- total ants on trail. Temperatures: — air temperature; - - - soil temperature. Radiation flux: . . . total solar radiation; - . . . solar long-wave radiation; — solar short-wave radiation.

cessation of all trailing), and similar data for the resumption of activity in late afternoon. The fullest data are available for January 1979 but good agreement is apparent between them and values obtained on other occasions during summer.

Activity patterns of the ants were rather different in winter (Fig. 2). Trail running began well after sunrise and continued throughout the day, ceasing around sunset.

Table 2. Temperature and radiation at the time when ants' activity on the trail declines and ceases in the morning, and resumes in the afternoon, in summer

Time of day is Australian Central Summer Time. Air temperature is measured 1 mm above the trail

Date	Time of day (h)	Air temp. (°C)	Radiation flux density (W m ⁻²)			
			Long-wave radiation		Short-wave radiation	
			Ground	Sky	Ground	Sky
Morning, activity starts to decline						
10.i.1979	1000	38.4	543	332	766	214
11.i.1979	0930	39.5	521	346	651	206
7.xii.1977	0930	—	—	—	706	—
8.xii.1977	0930	—	—	—	697	—
Mean		38.9	532	339	705	210
Morning, activity ceases						
10.i.1979	1100	43.7	608	330	927	240
11.i.1979	1015	43.2	561	340	786	222
7.xii.1977	1130	—	—	—	952	—
8.xii.1977	1100	—	—	—	920	—
10.xii.1976	1100	—	—	—	906	—
Mean		43.4	585	335	898	231
Afternoon, activity resumes						
10.i.1979	1830	43.7	492	431	288	194
11.i.1979	1845	43.7	479	470	240	189
7.xii.1977	1700	—	—	—	464	—
8.xii.1977	1730	—	—	—	488	—
Mean		43.7	486	451	370	192

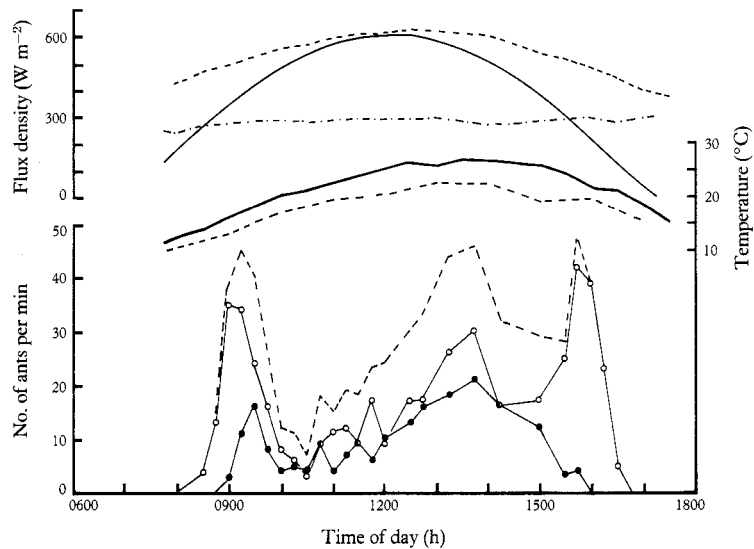


Fig. 2. Activity of ants on trails on a winter day, 15 July 1979. Symbols as in Fig. 1. Sunrise c. 0645 h Central Standard Time.

Radiation flux densities and relevant temperature parameters are presented in Table 3. As activity began at varying periods after sunrise it is likely that a temperature threshold for trail-running activity exists.

Foraging in Trees

During the periods without trail activity, i.e. in the middle of the day in summer and overnight in both summer and winter, large numbers of ants remained in the trees, or shrubs where honeydew was collected from homopterans. Provided that the temperature range was suitable, foraging continued in the trees. These ants began to return at the start of the next activity period and were replaced by fresh foragers. At no time were the trees unoccupied, and ants were vigorous in their defence of both the homopterans and the tree. Temperature conditions in the trees were similar to those of the air outside the canopy, but in the middle part of the day the ants kept to the shade of leaves and twigs unless disturbed. In midwinter, overnight temperatures in the trees fell to low levels. Thus in June 1978, minimum overnight temperatures of -0.5°C and 5°C were recorded in part of the canopy of a mulga tree occupied by ants. These animals seemed tolerant of such low temperatures, and began leaving the tree at approximately the same time as foragers began leaving the nest the next morning.

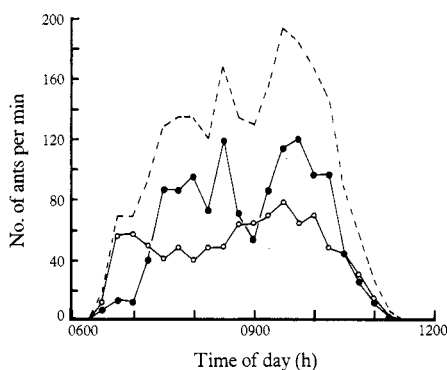


Fig. 3. Numbers of ants on the trail during the morning activity period on 7 December 1977. Time of day is Central Summer Time. ○ Outgoing ants. ● Incoming ants. --- Total ants on trail.

Speed of Locomotion on Trails

In many of the colonies studied, the trails leading to the food resource sites were long, frequently more than 100 m and exceptionally up to 500 m, so that ants were obliged to spend a considerable time travelling between the nest and the food site. An attempt was made to quantify this aspect of activity at one nest site in December 1977. The colony, at this time, had only one operative trail, c. 250 m long (although the ants actually covered a greater distance than this due to the unevenness of the trail surface). Measurements were made from 1830 to 2000 h on two successive days, at T_s of $35\text{--}45^{\circ}\text{C}$; an average speed ($\pm \text{SE}$) of $6.1 \pm 0.24 \text{ m min}^{-1}$ ($n=13$) was recorded. At this speed, the ants would take c. 40 min to travel the length of the trail, or 1.33 h for a round trip. This estimate is strengthened by data from Fig. 3, from which it is apparent that, in early morning, incoming ants were not encountered in any numbers at the counting site near the nest until 40 min after the start of large-scale trailing activity. It is interesting, also, that the number of ants leaving the nest (and presumably the foraging site

as well, although that end of the trail was not studied) declined markedly about 1 h before morning activity on the trail ceased altogether. With an approximate time of 40 min for an ant to travel the trail, it is possible to estimate the number of ants on the trail during periods of stable activity. On data from Fig. 3, between 0800 and 1030 h, when ant numbers passing the counting point were stable at 150 ants min^{-1} , the number on the trail would be *c.* 6000.

Critical Thermal Limits

The critical thermal maximum (CT_{max}) and minimum temperatures (CT_{min}) of form *viridiaeneus*, representing the upper and lower air temperatures at which locomotion was impaired (Kay and Whitford 1978), were measured in the field. This was achieved by monitoring T_a at the start and end of summer and winter activity periods.

Table 3. Temperature and radiation at the time when ants' trailing activities start and cease, in winter

Time of day is Australian Central Standard Time. Air temperature is measured 1 mm above the trail; soil temperature is measured with thermocouples

Date	Time of day (h)	Temp. ($^{\circ}\text{C}$)		Radiation flux density (W m^{-2})			
		Air	Soil	Long-wave radiation		Short-wave radiation	
				Ground	Sky	Ground	Sky
Morning, activity begins							
20.vi.1978	1000	—	17.3	—	—	—	372
21.vi.1978	0945	—	15.5	—	—	—	441
22.vi.1978	0930	—	15.0	—	—	—	279
15.vii.1979	0830	13.9	11.8 ^A	373	264	87	266
Afternoon, activity ceases							
20.vi.1978	1645	—	12.7	—	—	—	0
21.vi.1978	1700	—	13.3	—	—	—	0
22.vi.1978	1715	—	14.5	—	—	—	0
15.vii.1979	1630	20.7	17.7 ^A	405	277	35	128

^ASoil radiation temperature.

Workers ceased all trail-running and surface nest activity when T_a reached 43.5°C (Table 2; Fig. 1). At this point, T_b must have been slightly greater than T_a , for reasons discussed below. The ants, however, showed no signs of locomotory dysfunction, and presumably CT_{max} was even higher, possibly about 45°C .

In winter, trail-running began when T_a reached 14°C (Table 3; Fig. 2). At this temperature locomotion was clearly impaired and individuals were frequently observed to stumble, but as T_a rose their running became more rapid and better coordinated. The lower lethal temperature was evidently lower than CT_{min} , as ants tolerated overnight temperatures of -0.5°C in tree canopies and temperatures below zero are expected on from seven to ten nights per annum at Fowlers Gap (Bell 1973). The freezing point of the ants' haemolymph is likely to be about -0.8°C , but freezing is unlikely until much lower temperatures are reached, due to supercooling. Low overnight temperatures are unlikely to cause mortality due to freezing of the tissues.

Discussion

Trail-running is restricted to daylight hours but within this period it is also limited by T_a , the radiant heat input of the ants, or both. It is difficult to link the cessation of trail-running with any single environmental factor, because all the temperature and radiation parameters are dependent on solar radiation and are interrelated. Thus solar radiation absorbed by the soil raises the soil surface temperature, warming the air above it and causing increased emission of long-wave radiation. Some of this energy is absorbed by carbon dioxide, water vapour molecules and dust in the air, and is reradiated back to earth. Additionally, some solar short-wave radiation is reflected from vegetation and the ground. It is probable that activity ceases when the capacity of the ants to cool themselves is exceeded by heat input, and body temperature approaches lethal levels. To clarify this situation the radiant heat loads of ants on the trail have been calculated from the data presented above, by the equation:

$$R_n = L_{oe} - 0.5[a_s S_t (1 + \alpha)] - 0.05[a_L (L_{iu} + L_{id})],$$

modified from Campbell (1977), where R_n is the net radiant flux density in watts per square metre, L_{oe} the long-wave emittance from the ant's body surface, L_{iu} and L_{id} the long-wave irradiances for the upper and lower surfaces, α the albedo of the soil surface, a_s and a_L the short-wave and long-wave absorptivities, and S_t the total short-wave flux density. Values for R_n in midsummer have been calculated for various body temperatures and indicate a large net heat load for the ants at the three critical periods (Table 4). Heat is also produced by metabolism, and this component has been calculated, from data on oxygen consumption given by Ettershank (1971), as $5.61 \mu\text{W}$ per ant at 42°C . This value probably underestimates actual heat production while ants are running. It is not possible to calculate the other component of the heat load, i.e. heat gain by conduction, but this is likely to be small in ants as the area of body surface in contact with the soil is negligible (Hadley 1970). Evaporative heat loss has been calculated from the data of Nel (1965) who found an evaporative water loss rate of $0.31 \mu\text{l h}^{-1}$ per ant, a rate sustainable for at least 6 h without adverse effects on the ant. Such a rate of evaporation would result in a heat loss of 0.21 mW per ant. A heat budget can now be constructed for an average forager and quantified for the time at which trailing ceases (a body temperature of 43.5°C has been assumed as this represents air temperature at that time). Net radiation input (16.3 mW) plus metabolic heat (0.006 mW) equals evaporative heat loss (0.21 mW) plus convective loss, which, by difference, is 16.1 mW per ant, and represents the major route (98.7%) of heat loss. Convective heat loss is only possible if body temperature (T_b) is greater than T_a . A cool ant emerging onto the trail would, therefore, warm up rapidly until T_b exceeded T_a , when convective heat loss would stabilize T_b . However, as heat input increases during the day T_a rises (Fig. 1), causing a concomitant rise in T_b . Thus T_b remains slightly above T_a , and when it approaches a harmful level activity on the trail must cease and the ants retire to cooler microclimates, either in the resource trees or the nest. It follows, then, that the most critical parameter affecting activity is T_a around the ant, and activity must stop when this approaches levels inducing heat coma. It is noticeable that the T_a when activity resumed in late afternoon was virtually identical with that at which activity stopped in the morning, although R_n was very much smaller (Tables 2, 4). Clearly activity could

only resume when adequate convective heat loss was possible at a T_b below lethal levels.

Table 4. Net radiation heat loads on ants as activity declines and ceases in the morning, and resumes in the afternoon, in summer

For method of calculation, see text. Mean data from Table 2 were used, on the assumption that an ant consists of two horizontal surfaces for receiving and emitting radiation. Values of constants used were: a_s , 0.9; a_L , 0.95; α , 0.2. The long-wave emittance, L_{oe} , was calculated for each body temperature by means of the Stefan-Boltzmann equation, $\phi = \sigma T$, where ϕ is the radiation flux density, in watts per square metre, for an emissivity of 1. The mean (\pm SE) surface area of ants was measured as $52.2 \pm 1.05 \text{ mm}^2$

Body temp. (°C)	L_{oe} (W m ⁻²)	Load as activity falls Per m ² (W)	Per ant (mW)	Load as activity ceases Per m ² (W)	Per ant (mW)	Load as activity resumes Per m ² (W)	Per ant (mW)
30	479	277.6	14.5	402.9	21.0	145.4	7.6
35	511	245.6	12.8	370.9	19.4	113.4	5.9
40	545	211.6	11.0	336.9	17.6	79.4	4.1
43.5	569	187.6	9.8	312.8	16.3	55.4	2.9
45	581	175.6	9.2	300.9	15.7	43.4	2.3
50	617	139.6	7.3	264.9	13.8	7.4	0.4

In winter, heat loads are still substantial (Table 5). Although the net load at midday is high, T_a did not exceed 27°C and heat gained would be lost convectively without T_b approaching a critical level. Towards the end of the activity period conditions favour net heat loss, but again T_b is unlikely to fall below T_a and activity can continue until T_a falls below the lower critical level for activity. It is difficult to measure T_b of small ants directly, because of their size and the hardness of the exoskeleton. If thermocouples are used serious errors may be introduced by

Table 5. Net radiant heat loads on ants in midwinter (July 1979)

Calculations are similar to those used in Table 4; data are from Table 3 and Fig. 2. Values of α used were 0.2, 0.3 and 0 respectively for the three periods shown. Symbols are explained in the text

Body temp. (°C)	L_{oe} (W m ⁻²)	Load as activity begins Per m ² (W)	Per ant (mW)	Load at midday Per m ² (W)	Per ant (mW)	Load as activity ceases Per m ² (W)	Per ant (mW)
10	364	82.2	4.3	324.1	16.9	17.6	0.9
15	391	55.2	2.9	297.1	15.5	- 9.5	-0.5
20	419	27.2	1.4	269.1	14.0	-37.5	-2.0
25	448	1.8	0.1	240.1	12.5	-66.5	-3.5
30	479	-32.8	-1.7	209.1	10.9	-97.5	-5.1

conduction of heat into or out of the animals along the wires, due to the small body mass involved. Consequently, recent work on thermal limits of ants has utilized critical thermal maxima (CT_{max}) and minima (CT_{min}) to define their limits of temperature tolerance. These values represent the acute upper and lower air temperatures at which locomotion is impaired (Kay and Whitford 1978) and are more meaningful in ecological terms than upper and lower lethal temperatures. CT_{max} in form *viridiaeneus* is in the same range found for diurnal species of

Myrmecocystus from deserts of New Mexico (Kay and Whitford 1978) and the leafcutter ant of Arizona, *Acromyrmex* (Gamboa 1976). Although trailing activity in midsummer ceased at a T_a of c. 43.5°C, numbers of ants entering the trail fell sharply at T_a 39°C, an hour before trailing finally ceased. The time required to run the length of the trail was c. 40 min; this can be seen, therefore, as a behavioural adaptation to minimize the chances of ants being caught in the open when conditions become too severe for activity. Very few ants were found to be trapped on the trail in this way.

CT_{\min} for form *viridiaeneus* has been estimated at 14°C, and it is probable that these ants can be active throughout most winter days at Fowlers Gap. For example, on 21 June 1978, ants were active by 1000 h after a cold night with frost at dawn. The lower threshold of activity appears to be at an air temperature at trail level of c. 14°C, which is achieved by 1000 h or earlier on a clear day, even in midwinter when the declination of the sun is minimal. A similar pattern of activity for ants has been observed in September in the nearby Kinchega National Park (Mobbs *et al.* 1978).

It is evident from the combined data for summer and winter that periods of activity are controlled both by daylength and T_a . Trailing does not occur after dark even when temperatures are suitable, and in daylight hours trailing occurs only if conditions permit body temperature to be maintained within the required range 14–45°C. It is interesting to compare the amount of foraging time available in summer and winter. In midsummer, ants were trailing for an average of 6.8 h per day (mean for 5 d) but in midwinter for a mean of 7.4 h per day (mean of 4 d). From the data presented by Mobbs *et al.* (1978), in September 11 h foraging was possible. Activity in summer is limited by high temperatures although daylight hours are relatively long, but in winter short days and low temperatures restrict foraging. In spring, and presumably in autumn, favourable temperature conditions and daylength combine to allow better utilization of potential foraging time. In practice foraging occurs over a longer time than trailing, as ants left in the trees and shrubs continue to collect honeydew from homopterans during non-trailing periods.

Form *viridiaeneus* is by no means unique in its strictly diurnal foraging pattern. Ants of the genus *Pogonomyrmex* from the Chihuahuan desert are also diurnal and are active at high temperatures (Whitford and Ettershank 1975). Many other species alter their foraging patterns on a seasonal basis and become nocturnal or crepuscular in the summer months, e.g. *Novomessor cockerelli* (E. Andre) (Whitford and Ettershank 1975).

The preceding discussion has been confined to the consideration of thermal limitations to activity of ants, but in hot, arid conditions it is also necessary to consider water balance. Evaporative water loss from workers of *Iridomyrmex detectus* (Smith) (= *Iridomyrmex purpureus purpureus*) to still air at 25°C and 0% RH was about 0.3 mg h⁻¹ per ant, and total body water of workers is equivalent to 73% wet weight (Nel 1965). No data were given by Nel for lethal water loss in form *purpureus*, but in desert ant species from New Mexico this value varies from 30 to 45% loss of body weight (Whitford *et al.* 1975). If a conservative value of 30% loss in body weight is accepted as the lethal water loss in form *viridiaeneus*, each ant could lose approximately 3 mg of water before death. Evaporative water loss under trail conditions in the summer is likely to be greater than that measured

by Nel (1965). If a value twice that measured in the laboratory is adopted (0.6 mg h^{-1} per ant), this would allow 5 h of trail activity, equivalent to 1.8 km travelled under summer conditions, before water loss reached a lethal level. In practice trail lengths have been observed to be very much shorter, a common length being 100–250 m (Greenslade 1975; this paper), and it is likely that more distant food sources may prove uneconomical in terms of return for time expended, due to the length of time spent in travel. In the situations observed in summer the maximum foraging period seldom exceeded 5 h, and trail length, 250 m. In such a situation, with honeydew the major food resource, it is unlikely that evaporative water loss restricts activity.

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