

# Foraging in *Solenopsis invicta* (Hymenoptera: Formicidae): Effects of Weather and Season

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**ABSTRACT** Foraging activity of the red imported fire ant, *Solenopsis invicta* Buren, was monitored at bait traps for 1 yr to determine how weather and season affected foraging. Soil temperature at 2 cm was the best individual predictor of foraging rates at our study site ( $R^2 = 59\%$ ); workers foraged from 15 to 43°C, with maximal rates between 22 and 36°C. Season explained another 19% of sample variation in a multiple regression with soil temperature; this was because foraging was unusually low in late fall. Rain reduced foraging rates by ca. 40% and explained an additional 3% of the variation. Workers did not exhibit a tendency to forage more at night because neither time of day nor night/day were significantly correlated with foraging rates. Relative humidity, saturation deficits, soil moisture, and wind were also unrelated to foraging. Average weight of individual foragers increased ca. 30% with increasing soil temperature and decreased 15% with the advancing season. Soil-temperature data were used to calculate periods of foraging activity for an open pasture, a nearby shaded woodlot, and seven additional locations in the southeastern United States. Activity periods were distinctly shorter in shady habitats and higher latitudes. Low temperatures limited activity much more frequently than high temperatures.

**KEY WORDS** *Solenopsis invicta*, foraging rates, activity, temperature, soil moisture, humidity

THREE MAJOR FACTORS control foraging in ant colonies: internal needs, food resources, and the physical environment. Internal needs are primarily a function of hunger and rates of brood production (Wallis 1962, Howard & Tschinkel 1980). Food resources affect foraging rates through distribution, availability, and nutritional value (Taylor 1977, Howard & Tschinkel 1981, Traniello et al. 1984). The physical environment affects foraging primarily through changes in humidity, soil moisture, daylight, and temperature. Humidity and soil moisture (Talbot 1943) influence water loss in foraging workers and the abundance of prey items (Marsh 1985). Light affects the navigation of foragers and their daily foraging cycles (Wehner 1976, Bernstein 1979). Temperature controls transit rates (Holt 1955, Rissing 1982, Marsh 1985) and metabolic efficiency (Peakin & Josens 1978). Ants also have critical maximum and minimum temperatures above or below which foraging does not occur (Bernstein 1979).

Foraging in the red imported fire ant, *Solenopsis invicta* Buren, is clearly affected by changes in the physical environment (Rhoades & Davis 1967, Markin et al. 1974, 1975). Our objective was to determine how well such physical changes were correlated with foraging rates and which factors were most important. The following factors were

measured: air temperature, surface temperature, ground temperature, humidity, soil moisture, daylight, cloud cover, wind, and rain.

## Materials and Methods

Our investigations were conducted just east of Tallahassee, Fla., in a large open cow pasture. Our study site contained 87 mounds per hectare with an average population of  $161,000 \pm 59,000$  workers per mound (SD,  $n = 41$ , unpublished data). Vegetation consisted of well-grazed pasture grasses covering 95–100% of the ground. A few blackberries were also scattered across the site. Soil was a well-drained sandy loam over a sandy red clay subsoil.

Foragers were trapped in disposable glass culture tubes (13 by 100 mm) baited in one end with pieces of frankfurter (0.5 g). A silver-colored open-topped plastic box (11 by 11 by 3.5 cm) was placed upside down over each bait tube to protect it from direct sun and the feet of marauding cows. Ants reached the bait tubes by crawling under the edges of the box as it rested on the grass. Each sample run consisted of 12 bait traps set out at ca. 7-m intervals along the same trap line. Traps were left out for 30 min, then stoppered and stored for counting.

Forager samples were collected weekly during the hottest period of the day (ca. 1400 hours EST, January 1985–January 1986). On alternate weeks, we also collected a sample in the early morning (ca. 0730 hours) and one in the late evening (ca. 2130 hours). These additional samples allowed us

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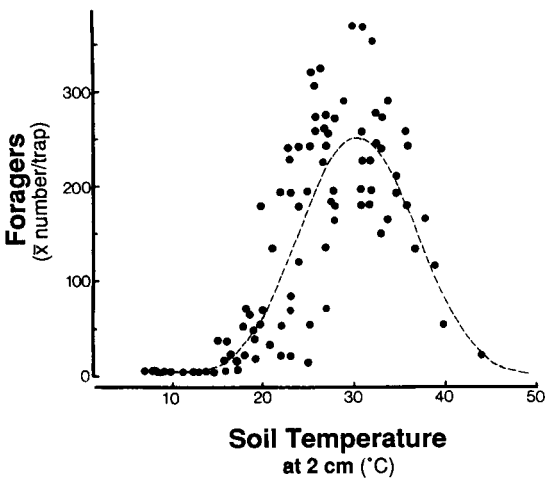


Fig. 1. Mean number of foragers per trap plotted against soil temperature at 2 cm. Each point is the average of 12 traps in one sample run. Dashed line plots the regression equation:  $\log y = -2.64 + 0.33x - 0.0054x^2$  ( $F = 55.5$ ;  $df = 2, 75$ ;  $P < 0.001$ ;  $R^2 = 59\%$ ).

to compare daytime rates with nighttime rates and rates during maximum and minimum daily temperatures.

Our trapping procedure permitted investigation of bait discovery and forager recruitment within a fixed time period. Four limitations of our baiting procedure should be specified as follows. 1) Our bait was highly attractive and concentrated. Smaller, scattered, or lower-quality food might have initiated different foraging responses. 2) Baits were covered by plastic boxes, so our results reflect recruitment to shaded food sources. Temperatures under the boxes at midday averaged  $1.3^\circ\text{C}$  cooler than exposed surface temperatures. 3) Recruitment rates probably interacted with the sample period (30 min) because transit speeds are higher at higher temperatures (Holt 1955, Marsh 1985). 4) Both the surface area of the bait and trap size (Wilson 1962) were limiting factors at temperatures when  $>500$  foragers packed into some of the bait tubes.

In conjunction with each sampling period, we measured relative humidity and percent soil moisture. Humidity was measured with a sling psychrometer held 30 cm above the ground. Soil moisture was measured by removing four plugs of soil 5 cm deep, which were weighed before and after drying. Wind and percent cloud cover were also estimated for each sample period.

We measured temperature at seven different positions: 1) air temperature (10 cm above ground, shaded probe), 2) unshaded soil-surface temperature, 3) air temperature within the trap, 4) mound temperature 2 cm deep, 5) soil temperature at 2 cm, 6) soil temperature at 15 cm, and 7) soil temperature at 40 cm. Air, surface, and trap temperatures were measured at one location; mound and soil temperatures were collected from four loca-

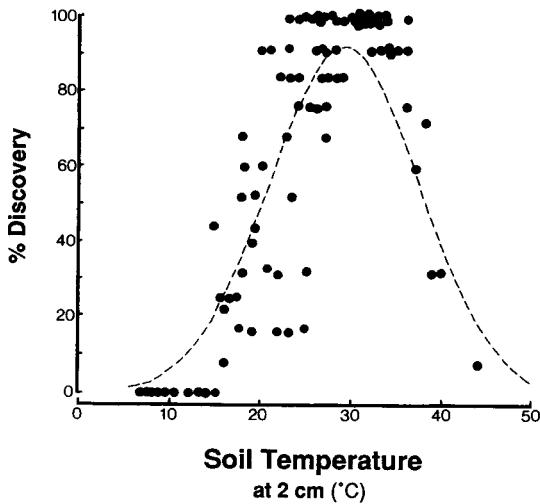
tions and averaged. Trap temperatures were collected only during the last half of the study (June–January). We also measured soil temperatures in a nearby shaded woodlot that received ca. 15% of the light striking the pasture site. Temperature data from the woodlot allowed us to estimate periods of foraging activity in shaded habitats. All temperature data were collected with a YSI Telethermometer and thermister probes. Foraging rates were correlated with various aspects of weather and season using multiple regression techniques.

## Results

**Individual Factors.** Temperature was clearly the primary physical factor affecting foraging rates. The average number of *S. invicta* per trap ( $y$ ) was best predicted by fitting a model of the form:  $\log y = b_0 + b_1x + b_2x^2$ , where  $x$  is one of the seven temperatures measured. Sample runs averaging  $<10$  ants per trap ( $n = 14$ ; Fig. 1) were deleted from the analyses to stabilize variance of the log-transformed data. All measured temperatures were strongly correlated with foraging ( $P < 0.01$ ) except trap temperature ( $P > 0.05$ ). Soil temperature at 2 cm was the best predictor of foraging rates. This factor accounted for almost 59% of sample variation (Fig. 1). By comparison, air temperature, soil temperature at 15 cm, and soil temperature at 40 cm explained 30, 43, and 37% of sample variation, respectively. Mound temperatures, surface temperatures, and trap temperatures accounted for only 17, 14, and 8%, respectively, of the variation.

*S. invicta* foraged when soil temperatures at 2 cm were between 15 and  $43^\circ\text{C}$ ; however, maximal rates were only achieved between 22 and  $36^\circ\text{C}$  (see Fig. 1). This range of activity is very similar to ranges reported for *S. invicta* by other observers (Lofgren et al. 1975, Markin et al. 1975). *S. invicta* regularly foraged with surface temperatures  $>40^\circ\text{C}$ . Surface temperatures exceeded  $40^\circ\text{C}$  in 14% of our samples; the mean number of foragers in these samples was 167 (range, 13–285). In fact, foraging even occurred when surface temperatures were  $>50^\circ\text{C}$ .

Colonies were assumed to have discovered and recruited to any trap that contained at least 10 foragers. Discovery rates (Fig. 2) are different from forager numbers (Fig. 1) in that discovery is primarily a function of scouting efficiency, whereas forager numbers are primarily a function of recruitment efficiency. In other words, forager numbers are probably best viewed as a measure of retrieval potential, but discovery rate is a measure of search effort; nevertheless, the plot of discovery rates (Fig. 2) was quite similar to forager numbers (Fig. 1) except that the discovery curve rose and fell more rapidly. Between 22 and  $36^\circ\text{C}$  almost 90% of traps were discovered (Fig. 2). (We should note that interspecific competition was not an important factor in our study;  $<1\%$  of bait traps contained other species of ants.)



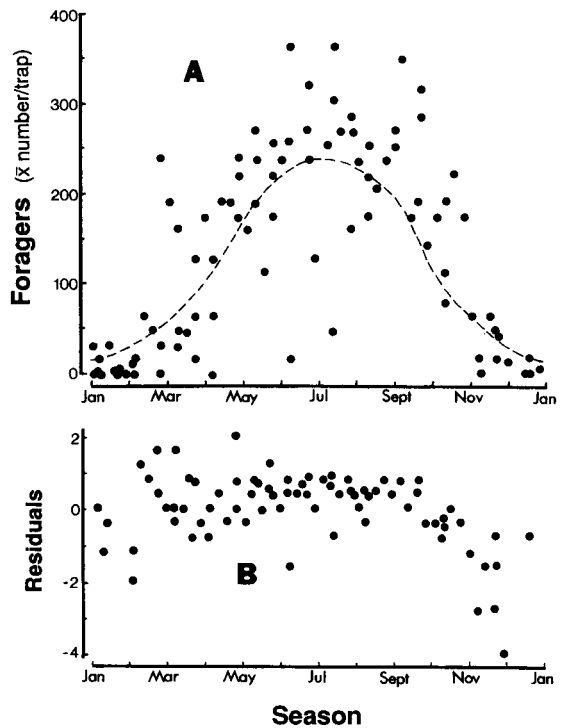
**Fig. 2.** Percentage of traps discovered and recruited to after 30 min plotted against soil temperature (2 cm). Dashed line plots the regression equation:  $\log y = -0.770 + 0.186x - 0.00318x^2$  ( $F = 34.7$ ;  $df = 2,75$ ;  $P < 0.001$ ;  $R^2 = 47\%$ ).

Time of day, night/day, percent cloud cover, wind, rain, percent soil moisture, relative humidity, and saturation deficits were all unrelated to foraging when viewed individually. None of these factors explained  $>3\%$  of variation in the number of foragers per trap.

Season was the only other individual factor that had a significant effect on foraging (Fig. 3A), but most of this effect was apparently due to seasonal variation in soil temperatures (2 cm). The correlation with season was greatly reduced after adjusting for the effects of soil temperature (Fig. 3B); nevertheless, foraging rates still fell considerably in the late fall (Fig. 3B) even after this adjustment.

**Multiple Regression Analyses.** We performed a series of multiple regressions to determine which combination of factors offered the best prediction of foraging rates. Humidity, saturation deficit, soil moisture, wind, night/day, and time of day were still not significant even in these analyses. Careful inspection of residuals also failed to reveal hidden patterns in any of these factors. Likewise, combination variables including multiples and differences between variables were also ineffective. Several temperature variables were colinear or strongly associated with each other. For example, high temperatures at 2 cm were generally associated with high temperatures at 15 cm and so forth; this situation could have obscured relatively subtle interactions among the different temperature measurements.

Soil temperature at 15 cm was significant as a second factor ( $T = 3.14$ ,  $P < 0.01$ ), but its effect disappeared when season was added to the model. The best two-factor model for the average number of foragers per trap ( $y$ ) included the curvilinear



**Fig. 3.** (A) Mean number of foragers per trap plotted against season. Dashed line plots the regression equation:  $\log y = 1.10 + 0.095x - 0.0018x^2$ , where  $x$  is in weeks ( $F = 40.3$ ;  $df = 2,75$ ;  $P < 0.001$ ;  $R^2 = 51\%$ ). (B) Effect of season on forager number adjusted for soil temperature. Standardized residuals were obtained from the regression of forager numbers on soil temperature (2 cm) using the model in Fig. 1.

effects of both soil temperature (2 cm,  $a$ ) and season in weeks ( $b$ ):

$$\log y = -2.5 + 0.29a - 0.0051a^2 + 0.060b - 0.0012b^2$$

This model accounted for 78% of sample variation ( $F = 68.7$ ;  $df = 4,73$ ;  $P < 0.001$ ).

Rain and percent cloud cover were the only factors to explain significant amounts of variation in the model after soil temperature (2 cm) and season were added. However, rain eliminated the significance of cloud cover when both were entered together. The model including the effect of rain ( $c$ ) is given below:

$$\log y = -2.4 + 0.29a - 0.0053a^2 + 0.063b - 0.0013b^2 - 0.24c$$

This model accounted for 81% of sample variation ( $F = 67.3$ ;  $df = 5,72$ ;  $P < 0.001$ ). Rain just before or during the sampling period reduced the number of foragers at the baits by ca. 42% ( $n = 11$ ).

A multiple regression of the logarithm of percent discovery on the various weather variables was essentially the same as that just described for forager number. Together, soil temperature (2 cm), season,

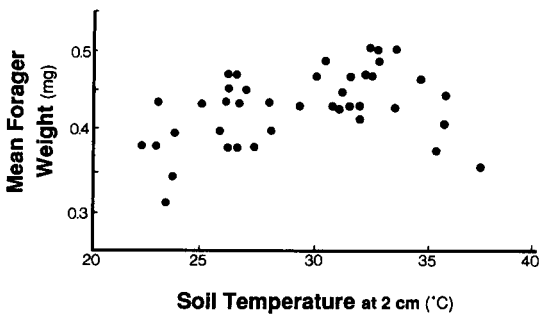


Fig. 4. Mean dry weights of individual foragers (adjusted for season) plotted against soil temperature. Weights ( $y$ ) were adjusted for season ( $x$ ) by adding nonstandardized residuals from the model  $y = 0.53 - 0.0024x$  ( $T = -2.55$ ;  $P < 0.02$ ) to the weight of foragers predicted on week 25.

and rain accounted for 68% of the variation in this dependent measure ( $F = 36.8$ ;  $df = 5,72$ ;  $P < 0.001$ ). We also ran multiple regressions without taking the logarithm of forager number or percent discovery. A curve including a cubic term for temperature produced results equivalent to the models described above, but we chose not to use these models because variance was not uniform, and extrapolated predictions were not realistic.

**Average Forager Weights.** To determine if different-sized workers foraged at different temperatures or different times of the day, we calculated the average forager weight for each bait trap (April–October). Within the range of maximal foraging (22–36°C), both soil temperature (2 cm,  $a$ ) and season ( $b$ ) were significant predictors of mean forager weight in milligrams ( $y$ ):

$$y = 0.32 + 0.0083a - 0.0033b$$

This equation explained 53% of the sample variation ( $F = 20.6$ ;  $df = 2,33$ ;  $P < 0.001$ ). Forager weights declined 15–18% across season and increased 25–31% over the temperature range indicated. Other factors, including forager number, did not add additional explanation to the model. Above 35°C, however, forager weights tended to decline again (Fig. 4).

**Periods of Foraging Activity.** The window of maximal foraging activity was between 22 and 36°C (Fig. 1). Reduced activity rates occurred up to ca. 44°C and down to 15°C. Based on these activity windows, we calculated foraging periods for our study site and a nearby shaded woodlot (Fig. 5). Temperature data were based on 55 d of soil temperatures (2 cm) collected weekly from December 1984 to January 1986.

Activity periods varied considerably with season and habitat (Fig. 5). At our study site in a sunny pasture, 59% of the year was in the maximal range, and 27% was in the reduced range. Approximately 15% of the year was too cold for any foraging. Soil temperatures were never so hot that foraging ceased

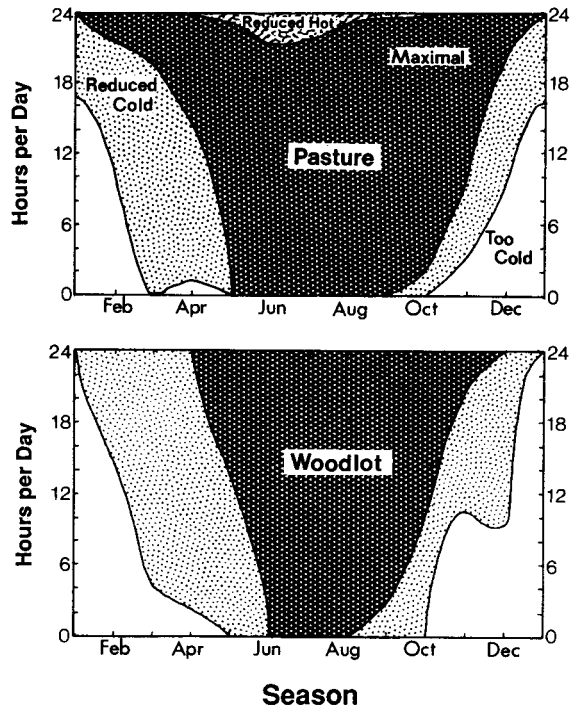


Fig. 5. Seasonal windows of foraging activity in Tallahassee, Fla., based on soil temperatures at 2 cm in an open pasture (top) and a shaded woodlot (bottom). The average number of hours per day in each activity range are plotted against season. Maximal range: 22–36°C, reduced hot: 36–44°C, reduced cold: 15–22°C, too cold: <15°C.

altogether, although high temperatures severely reduced activity on several occasions. Temperature was in the maximal range 90% of the time between May and October.

In contrast, periods of activity were much shorter in a nearby shaded woodlot (Fig. 5); only 42% of the year was in the maximal range, 35% was in the reduced range, and 23% was too cold for foraging. Furthermore, soil temperatures at 2 cm never exceeded 30°C, and daily fluctuations averaged  $3 \pm 1.5^\circ\text{C}$  compared with  $10 \pm 5^\circ\text{C}$  in the pasture. We should note that *S. invicta* colonies were present in the woodlot, but they were much less abundant than in the open pasture. Shadiness or the lack of insolation clearly limited the time period available for *S. invicta* foraging.

Periods of foraging activity were estimated at seven additional sites in the southeastern United States (Table 1) based on soil temperatures at 5 cm. At our study site, interpolated values for 5 cm predicted foraging rates as accurately as those at 2 cm ( $R^2 = 56\%$ ). However, the upper and lower critical temperatures changed slightly to 14 and 40°C, respectively, while the maximal range remained essentially the same. The time period at each level of activity was determined by plotting maximum

**Table 1.** Percentage of year at different levels of foraging activity (activity levels were estimated from maximum and minimum daily soil temperatures at 5 cm for the years 1984–85 based on 1 d per week, except Tallahassee data are only from 1985 and temperatures at 2 cm (Fig. 5))

Location of weather station	°N latitude	Activity levels				
		Too hot	Reduced (hot)	Maximal	Reduced (cold)	Too cold
Mississippi						
State University	33.4	1.9	5.0	35	24	35
Stoneville	33.4	1.2	4.8	37	25	32
Alabama						
Auburn	33.6	0.2	3.3	36	28	34
Georgia						
Experiment	33.2	0.0	0.0	36	28	36
Byron	32.6	0.9	3.8	43	23	30
Tifton	31.5	0.1	2.5	47	26	24
Florida						
Quincy	30.6	0.0	0.2	49	25	25
Tallahassee						
(sunny pasture)	30.4	0.0	2.0	59	25	15
(shady woodlot)	30.4	0.0	0.0	42	35	23

and minimum daily temperatures against time of day, assuming minimums occurred 0.5 h after sunrise and maximums at ca. 1400 hours (Yao 1981).

At the nine locations examined, foraging would have been limited by high temperatures from 0 to 6% of the year. Soil temperatures rarely became so hot (>40°C) that foraging would have ceased entirely. Overall, low temperatures reduced or eliminated foraging activity much more often than high temperatures (Table 1). The period too cold for foraging was longer at the more northerly sites. Soil temperatures at 5 cm were not available from other areas of the *S. invicta* range, but soil temperatures at 10 cm indicate that in areas of South Florida and South Texas almost the entire year is in the maximal range.

### Discussion

Soil temperature at 2 cm was the best single predictor of *S. invicta* foraging rates. This relationship makes good sense because *S. invicta* colonies have an extensive system of foraging tunnels 2–7 cm below the soil surface that radiate out from the mound and divide into many branches (Markin et al. 1975). Exit holes are distributed throughout the foraging territory (Wilson et al. 1971) so that foragers generally need to travel <0.5 m above ground to reach any point in the territory (Markin et al. 1975). Consequently, >90% of a forager's trip is in the underground tunnel system and <10% is above ground (assuming a mean forager trip of 5 m). The fact that foragers spend relatively little time outside the tunnel system probably also explains why surface temperature, air temperature, relative humidity, saturation deficit, and even trap temperature are so poorly correlated with foraging rates.

*S. invicta* workers foraged over a range of 27°C of soil temperature (Fig. 1) but 39°C of surface temperature (12–51°C). This wider range of surface temperatures indicates that the tunnels may expand a colony's range of foraging temperatures by as much as 40%. This hypothesis could be tested by monitoring foraging activity in colonies that had been denied use of their tunnel system, forcing them to travel overland.

Supposedly, ants inhabiting lower latitudes have evolved narrower ranges of foraging temperatures to reduce competition with other ants in their communities (Bernstein 1979). Colonies of *S. invicta* at our study site clearly did not follow this trend. Workers foraged over a range of surface temperatures considerably wider than that predicted for an ant at 30°N latitude (Bernstein 1979) and even more so for one that originated in Brazil at 15–20°S latitude.

Exposure to temperatures >42°C are potentially lethal for *S. invicta* workers (Francke et al. 1985); yet workers still foraged at surface temperatures well in excess of this, presumably because the tunnel system substantially limited the time workers were exposed to these temperatures.

Season is an important predictor of *S. invicta* foraging (Fig. 3; Markin et al. 1974). Rates fell off rapidly in the late fall even after accounting for the effects of soil temperature (Fig. 3B). A number of seasonal factors may contribute to this effect. One major factor is probably a decreased preference for protein foods (e.g., frankfurters) during the winter when brood production is low (Markin et al. 1974). Most protein is fed directly to the larvae (Sorensen et al. 1983); in fact, laboratory colonies do not even collect protein foods unless larvae are present (personal observations). Similarly, M. B. Stein reported (personal communication)

that field colonies prefer carbohydrate baits to protein ones during the winter months.

Rainfall probably reduced foraging by temporarily plugging exit holes, washing away pheromones, or physically striking the workers. The heavy cloud cover usually associated with rain might also impair the navigating ability by impairing sun compass orientation (Hölldobler 1976), but this seems unlikely because nighttime darkness did not inhibit foraging.

Soil moisture might affect foraging in particularly dry years or in drier portions of the *S. invicta* range, but we saw no evidence of this during our study even though soil moisture fell as low as 2%. We should note, however, that foragers may be more selective when foraging low-quality food items (Taylor 1977, Traniello et al. 1984); in such cases, the higher costs potentially associated with low soil moisture and humidity might still be an important consideration. Our lack of correlation between soil moisture and foraging rates contrasts with the positive results of Rhoades & Davis (1967) at a study site 50 km from ours. This discrepancy may have occurred because we monitored recruitment to large baits while they estimated unbaited scouting activity. Their evidence may also have been coincidental because it was only analyzed graphically and did not account for potentially confounding effects of temperature interacting with humidity.

The average weight of individual workers recruited to baits increased 25–30% from 22 to 36°C. A similar response was observed in the ant *Formica neorufibarbis* Wheeler (Bernstein 1976). Average head width of *F. neorufibarbis* foragers increased ca. 15% from midmorning to early afternoon, presumably in response to increased temperature. Large *S. invicta* workers may forage at higher temperatures because their reduced surface/mass ratio makes them more heat tolerant and less subject to desiccation. Above 36°C, however, average worker weights appeared to drop off, indicating either a contradiction or that only small or old workers were risked at higher temperatures. Average forager weights also declined 15–18% across season (April–October); this probably resulted because the percentage of large workers in *S. invicta* colonies tends to decline as winter approaches (Markin & Dillier 1971).

Periods of foraging activity vary considerably in different areas of the *S. invicta* range (Table 1). Up to 36% of the year was too cold for foraging at more northern sites compared with 15% in Tallahassee. In contrast, foraging is probably year-round in South Florida and South Texas. Insolation or the exposure to direct sun substantially increases foraging periods. In the sunny pasture, 59% of the year was in the maximal range compared with 42% in the shaded woodlot (Fig. 5). In many habitats, insolation is patchy and highly variable; such variation is probably important in explaining differences in foraging activity between habitats, within

habitats, and even within the territories of the individual colonies.

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