

SUCROSE INTAKE AND PERCENT EFFORT BY THE RED IMPORTED FIRE ANT, *SOLENOPSIS INVICTA* BUREN (HYMENOPTERA: FORMICIDAE)

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Abstract Sucrose intake rate and percent effort (a variable which describes the amount of energy an insect uses to feed on a liquid) was quantified for *Solenopsis invicta* Buren. In other words, how much energy does the insect gain and how much energy is lost in the feeding event? In order to understand this more closely, two variables important in liquid feeding, viscosity and sucrose concentration, were controlled independently. Three series of solutions were prepared to test these variables separately: base series (BS, no alteration to sucrose solutions), constant viscosity series (CVS, multiple sucrose concentrations all with the same viscosity as a 50% sucrose solution), and constant concentration series (CCS, 30% sucrose solutions with increasing viscosities). Viscosity seemed to affect the solution intake rate of *S. invicta* more than sucrose concentration of the solution. Percent effort increased with increasing sucrose concentration in the BS and CCS ranging from 17.53 to 95.8% and 40.09 to 100%; however, the sucrose intake rate decreased dramatically in the CCS to less than 2 μg sucrose/min at the highest viscosity level. Levels of solution and sucrose intake rate and percent effort were stable. This information on how viscosity and sucrose concentration affect feeding behavior in ants may assist in future formulations of baits for the control of these pests.

Key Words Solution intake rate, viscosity, sucrose concentration

INTRODUCTION

The mechanics of liquid feeding in nectarivorous insects have been studied extensively (honeybees: Schmid-Hempel et al., 1985; Farina and Nunez, 1995; Tezze and Farina, 1999; bumblebees: Harder, 1986; Lepidoptera: Kingsolver and Daniel, 1979; May, 1985; Josens and Farina, 1997, 2001; ants: Josens et al., 1998; Paul et al., 2002; Paul and Roces, 2003). In ants, the choice of a food source and/or amount of load taken has been explained by variables such as available surface area (Wilson, 1962; Silverman and Roulston, 2001), distance of the food source from the nest (Taylor 1977), and level of starvation (Howard and Tschinkel, 1980, 1981; Josens and Roces, 2000). The morphological characteristics of the insect's mouthparts and the physical properties of the solution, along with the pressure difference created by the insect while feeding, however, may describe the actual dynamics of liquid intake (Kingsolver and Daniel, 1979).

Kingsolver and Daniel (1979) proposed a model to explain the sucking nectar feeding behavior in butterflies. One relation in this model quantified the negative pressure produced by the cibarial pump needed to transport the liquid through the proboscis. A number of variables in this equation describe the dimensions of the proboscis which explain head loss due to friction. Compared to lepidopterans, ants would have much less head loss due to a much shorter feeding apparatus; however, the feeding method of some ants, such as *Solenopsis invicta* Buren, does match the sucking feeding method that this model describes (sucking versus lapping feeding methods, Aye, 1995).

Two variables are critical in insect liquid feeding and are readily measured: intake rate and viscosity (μ). Intake rate has often been measured to quantify feeding dynamics for many nectar-feeding insects such as butterflies and honeybees (Josens, 2002; Josens et al., 1998; Farina and Núñez, 1995; Harder, 1986). However, the method of controlling viscosity to measure the impact of other variables and viscosity itself is fairly new (Josens and Farina, 2001; Farina and Josens, 1994). Using the method developed by Farina and Josens (1994), and the principles outlined by Kingsolver and Daniel (1979), a relation (percent effort) may be used to relatively quantify the energy an insect uses to feed on a liquid: % effort = $(\mu * \text{Intake Rate}) / \text{Max}(\mu * \text{Intake Rate})$.

According to this relation, a larger value will indicate the insect is using more energy to imbibe the liquid. The pressure drop is only relatively estimated, because values for the dimensions of the feeding apparatus and, therefore, velocity of the liquid, are not measured in this study. However, the size of the mouthparts is assumed to change only nominally from ant to ant in the worker caste. This information may provide a clue to how much the insect works to feed on liquids of different viscosities.

Along with the amount of energy spent feeding, another important factor is the amount of energy gained from a feeding event. The energy intake rate has been reported in many experiments (Paul and Roces, 2003; Josens et al., 1998; Kingsolver and Daniel, 1979). By comparing the energy gained and spent (above) at a feeding event for each viscosity and sucrose concentration level, relationships may emerge that may explain feeding behaviors of nectar-feeding ants more closely.

MATERIALS AND METHODS

Three series of solutions were prepared: base series (BS), constant viscosity series (CVS), and constant concentration series (CCS) (Farina and Josens, 1994; Tezze and Farina, 1999; Josens and Farina, 2001). The BS is pure sucrose-water solutions at 10, 20, 30, 40, and 50% (w/w) sucrose. Because viscosity increases exponentially with increasing sucrose concentration, a chemical (Tylose: Clariant, Charlotte, NC) was added to each solution to match the viscosity of a 50% sucrose solution which made the constant viscosity series (CVS). A small amount of Tylose will increase the viscosity of a solution significantly while only changing the density slightly. The last series controls the sucrose concentration at 30% while the viscosity is varied (CCS). The ants did not hesitate to imbibe the Tylose solutions.

Two colonies of *S. invicta* were collected from Baton Rouge, LA. Each series of solutions were tested with at least six individual foragers from these two colonies. Large trays (580 mm x 350 mm x 90 mm) with Teflon-coated (Dupont, Wilmington, De) sides were used to house each colony. Before tests began and between tests, ants were fed 20% (w/w) sugar water, frozen crickets, and water ad libitum.

Bioassays were performed in the same manner for each series of solutions. Colonies were starved for 96 hours to achieve uniform hunger before tests began (O'Brien and Hooper-Bùi, unpublished data). One at a time, colonies were connected to a smaller foraging arena by a wooden bridge where a droplet of sucrose solution was presented (Josens et al., 1998). A small group of foragers were allowed access to the arena and allowed to feed. After the foragers are allowed back to the colony to presumably recruit others, single ants were allowed on the bridge and weighed (in mg) by capturing the ant in a 6 mm genitalia vial. The ant was placed in the foraging arena after initial weighing. The feeding time was considered the total time the ant was in contact with the droplet and was measured in minutes and seconds. After feeding, the ant was captured once again on her way back to the colony and weighed. At least three ants from each colony were measured for each solution for a total of at least six ants measured per solution. The amount taken (mg) is the initial weight subtracted from the final weight, and the volume taken (crop load, in μl) is the amount taken divided by the density of the solution (Lide, 2002). The solution intake rate ($\mu\text{l}/\text{min}$) was calculated by dividing the crop load by the feeding time. The energy intake rate (μg sucrose/ min) is the amount of sucrose in the sample (μg sucrose/ ml) multiplied by the intake rate.

Data Analysis Two-way ANOVA (two by five factorial) was performed on the intake rates and sucrose intake rates for the CVS and BS. One-way ANOVA was used for the CCS series. At least six individuals were measured for each combination. Means were separated using Tukey adjustment (SigmaStat SPSS 3.0 2003).

RESULTS

Mean intake rates of the base series and constant viscosity series are plotted for each sucrose concentration (Figure 1). BS and CVS were found to be significantly different ($F = 30.96$, $df = 1$, $P < 0.001$). In the CVS, intake rates were not different either from each other nor from the intake rates of 40% and 50% sucrose solutions in the BS. Intake rates in the BS decreased after 30% sucrose solution, though not significantly. Sucrose intake rates for the BS and CVS were calculated from the solution intake rates and are plotted in Figure 2. Significant differences were found between these series for the sucrose intake rates as well ($F = 21.25$, $df = 1$, $P < 0.001$). In general, the sucrose intake rates are the same for all sucrose solutions in the CVS, whereas the sucrose intake rates in the BS increased to $9.58 \mu\text{g}$ sucrose/ min at 30% sucrose. Lastly, intake rates for the constant concentration series are plotted in Figure 3. The 30% sucrose base solution (viscosity = 0.0287) is significantly different from all other solutions in the series ($F = 12.73$, $df = 3$, $P < 0.001$). The three other solutions (all with increasingly higher viscosities) were fed on at lower intake rates.

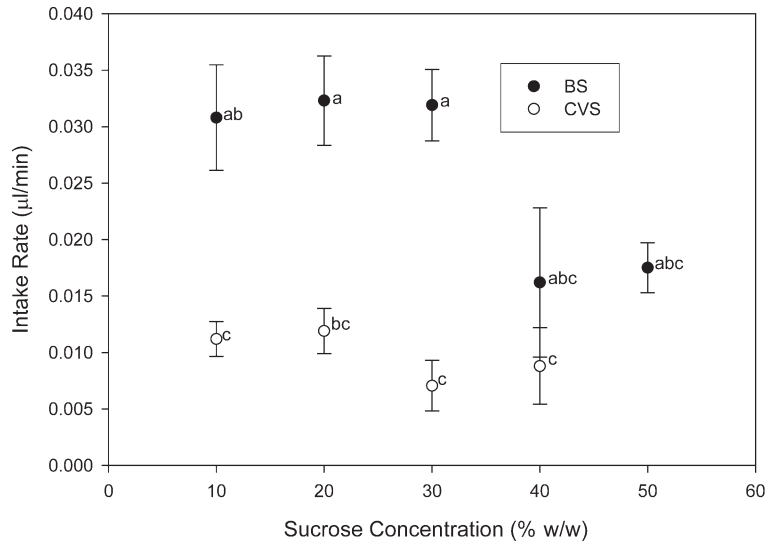


Figure 1. Mean solution intake rates are shown for each sucrose solution in the base series (closed circles) and constant viscosity series (open circles). Data points with different letters are significantly different at $\alpha = 0.05$ (Tukey adjustment).

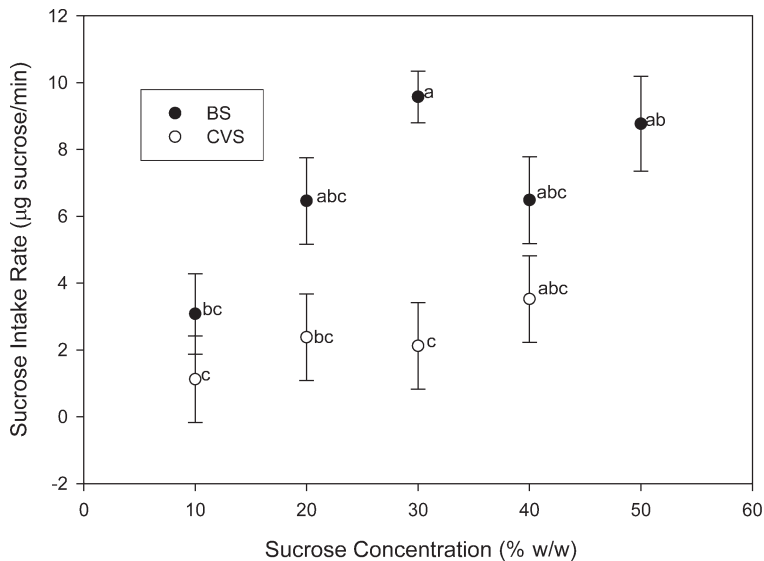


Figure 2. Mean sucrose intake rates are shown for each sucrose solution in the base series (closed circles) and constant viscosity series (open circles). Data points with different letters are significantly different at $\alpha = 0.05$ (Tukey adjustment).

Table 1 shows percent effort and sucrose intake rate for each solution tested. Percent effort increased with increasing sucrose concentration in the BS and CCS ranging from 17.53 to 95.8% and 40.09 to 100%; however, the sucrose intake rate decreased dramatically in the CCS to less than 2 µg sucrose/min at the highest viscosity level. The CVS showed values in the middle for percent effort in the range of 38.64 and 65.19%. The sucrose intake rates in the CVS were also stable but low with rates not surpassing 3.52 µg sucrose/min.

DISCUSSION

Viscosity seems to affect the solution intake rate of *S. invicta* more than sucrose concentration of the solution. At concentrations of more than 30% in the BS, the intake rate decreases to that which is similar to viscous solutions in the CVS, which are relatively stable for all sucrose concentrations. In contrast, the intake rates in the CVS

measured in the moth *Macroglossum stellatarum* decrease with increasing sucrose concentration, similar to the BS (Josens and Farina, 2001). The moth was able to imbibe (create a highly negative pressure) the viscous, diluted solutions at a similar intake rate as the diluted solutions in the BS. Perhaps the size of the insect plays a major role in liquid feeding.

Similar to the solution intake rate discussed above, sucrose intake rates in the CVS were also stable. In other words, ants fed on viscous solutions at the same rate while each gaining the same amount of energy. At first glance this may not make sense; however, the percent effort in the CVS shows a decrease with increasing sucrose concentration (Table 1). This may explain the constant sucrose intake rates.

Table 1. The percentage effort and mean sucrose intake rate are shown for each solution tested.

	SUCROSE CONC (% w/w)	VISCOSITY (cm ² /s)	% EFFORT	SUCROSE INTAKE RATE (µg sucrose/min)
BS	10	0.013	17.53	3.078
	20	0.019	26.87	6.458
	30	0.028	39.1	9.575
	40	0.061	43.26	6.481
	50	0.125	95.8	8.767
CVS	10		61.29	1.124
	20	0.125	65.19	2.379
	30		38.64	2.119
	40		48.16	3.521
CCS		0.0287	40.09	9.575
	30	0.0749	52.8	4.833
		0.1863	72.92	2.682
		0.3552	100	1.929

In the base series, ants fed on dilute solutions at almost the highest intake rate, then the rates decreased after 30% sucrose. The moth, *M. stellatarum*, was also shown to feed on dilute solutions at a maximal intake rate (Josens and Farina, 2001) as well as bumble bees (Harder, 1986). Nevertheless, another ant species, *Camponotus mus*, imbibed dilute liquids at a slower rate (Josens et al., 1998). They later found that the level of starvation, or individual motivation, influenced the rate at which these ants fed (Josens and Roces, 2000). In our study, however, fire ants were starved for 96 hours, which is the amount of starvation time needed to simulate behavior similar to that which occurs in the field (O'Brien and Hooper-Bùi, unpublished data). Josens et al. (1998) starved *C. mus* colonies for only 48 hours.

In contrast to the CVS, solution and sucrose intake rates in the CCS decrease with increasing viscosity. Viscosity seems to be the most influential variable in liquid feeding for this insect. Viscosity also negatively affected *M. stellatarum* feeding (Josens and Farina, 2001). However, no difference was found between the intake rates of the solutions with high viscosity (Figure 3). Given that *S. invicta* is a much smaller insect compared to the moth, the viscosity levels used in this study were too viscous for the ant to handle, which would explain these results. This series would need to be tested with smaller viscosity values on ants.

In conclusion, viscosity of liquid solutions affects *S. invicta* feeding behavior much more than does the chemosensory effects of the sucrose concentration of the solution. Some bait formulations being developed may be more viscous than others. This data may help in future formulations of baits designed to control these pests.

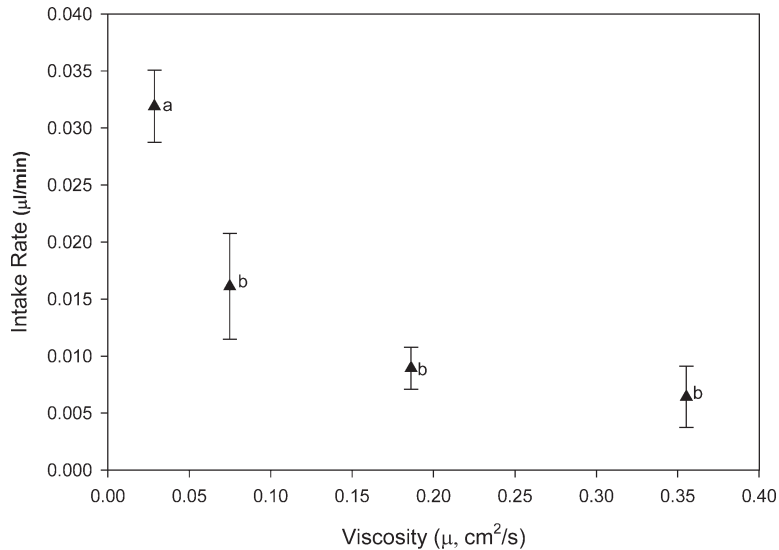


Figure 3. Mean solution intake rates are shown for each viscosity level in the constant concentration series in which all solutions contain 30% sucrose. Data points with different letters are significantly different at $\alpha = 0.05$ (Tukey adjustment).

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