2001

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Published in *Oikos* 95:3 (December 2001), pp. 425–430; doi: 10.1034/j.1600-0706.2001.950307.x

Accepted June 5, 2001; published online December 16, 2003.

Feeding and survival in parasitic wasps: Sugar concentration and timing matter

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Abstract
Sugar consumption can increase the longevity and lifetime fecundity of many species of parasitic wasps. Consequently, for these insects the availability of sugar sources in the field is important for their reproductive success. As sugar sources can be highly variable in quantity, space and time, the chances of finding a sufficient amount of sugar to increase longevity might be very low. Therefore, the reward from a single feeding event can be critical for the forager's fitness. We measured the longevity of the parasitoid *Cotesia rubecula* after a single honey meal differing in sugar concentration (25, 47, 86% w/w) and timing (day of emergence and 24 h later). Survival was analyzed with Cox's Proportional Hazards Model. The risk of starving to death in sugar-fed wasps was reduced by 0–73% in comparison to unfed wasps, depending on sugar concentration and timing. Longevity was significantly increased by sugar concentration and by feeding later in life. Our results suggest that in the field, adult *C. rubecula* has to locate food at least once per day to avoid starvation.

Many species of parasitic wasps can increase their reproduction through feeding on supplemental sugar sources (Leius 1961a, 1961b; Syme 1975; Chippendale 1978; England and Evans 1997; Heimpel et al. 1997a). Sugar feeding usually results in an increase in longevity that is often positively correlated with a higher fecundity (Wolcott 1942; Leius 1961b; Sahragard et al. 1991; Hagley and Barber 1992; Morales-Ramos et al. 1996; Heimpel et al. 1997a). Successful sugar foraging is considered to be a critical factor that influences the lifetime reproduction of parasitic wasps in the field (Wäckers and Swaans 1993; Sirot and Bernstein 1996; England and Evans 1997; Jacob and Evans 1998; Heimpel et al. 1998), but little has been done on the estimation of realistic lifetimes of sugar-feeding wasps when sugar is not constantly and easily available. In many habitats foods and hosts of parasitic wasps are spatially separated or not available at the same time, resulting in rare food encounters.

Taking into account the spatial and temporal variability of sugar sources in the field we address the specific question of how much a single sugar meal affects survival in adult *Cotesia rubecula* (Marshall) (Hymenoptera: Braconidae). The estimation of longevity and reproduction of parasitic wasps in the field should not rely on data obtained from cage experiments with ad libitum sugar conditions. Considering the different qualitative, spatial and temporal scales at which sugar sources occur in the field (Jervis et al. 1993), this would lead to a drastic overestimation of the lifetime reproduction of wasps. The quantity and quality of sugar sources in the field vary as they can be obtained from various sources such as floral and extrafloral nectar, other plant materials rich in sugars, homopteran honeydew and even nectar-like fluids from a few fungi (DeBach and Rosen 1974; Jervis 1998). The sugar concentration in the majority of nectars ranges from 15% to 75% (Harborne 1992) and dried honeydew can nearly be pure sugar (Zoebelein 1956; Jervis et al. 1992). Sugar concentration also varies within one flower over time, even within the course of one day (Mohr and Jay 1990). Therefore, the chances of finding sufficient food on a regular basis to increase longevity might be very low.

Given a low frequency of sugar encounters in the field, the benefit from a single sugar meal becomes critical for survival. Therefore, we investigated the effect of a single sugar meal on survival in order to estimate minimum feeding frequencies in the field. In our experiments we used female *C. rubecula* as they depend on sugar to increase longevity and do not feed on hosts (Nealis 1986; Wäckers and Swaans 1993). In laboratory experiments wasps were allowed to feed once on a honey solution and their longevity compared with unfed wasps. As foraging wasps can encounter varying sugar concentrations in the field, honey was offered in a low, medium and high sugar concentration. We also varied the time when wasps were allowed to feed by providing food on two different days to test the effect of temporal availability of food on longevity. During the experimental procedure volume consumed and feeding duration were recorded to compare the feeding behavior between the different feeding treatments.

Material and methods

Insects and experimental preparation

C. rubecula is a solitary endoparasitoid that attacks larvae of the cabbage white butterfly, *Pieris rapae* L. (Lepidoptera: Pieridae), living on *Brassica* plants. The *C. rubecula* females used in the experiments originated from strains collected from commercial crop fields near Adelaide, South Australia. To avoid inbreeding, once in a year wild males were caught in the area of Adelaide and were mated with females from the culture. Females were allowed to parasitize second instar *P. rapae* feeding on cabbage plants (*Brassica oleracea* L. cv. 'Green Coronet'). Plants with hosts were available in 25 cm wide and 35 cm high rectangular cages (made with aluminum frames covered with gauze). Light and temperature conditions were set to L:D 14:10 and 25°C. Wasp cocoons were collected from the rearing cages and kept in a clear, air-ventilated 2-l plastic container until adult emergence. As about 90% of adults emerge within a few hours after onset of light in the morning, newly emerged females were separated from the cocoon stock about 3 h after this event to allow time for mating and to obtain a uniform age group. Three to four females were held together in a clear 2-l plastic container deprived of hosts and food but with access to a water-soaked cotton wick, until used in experiments.

Experimental procedure

Honey solutions (Kangaroo Island 'Canola' Honey) containing nectar from *Brassica* flowers were used as sugar diets because they were easy to prepare and resemble flower nectar *Cotesia rubecula* wasps would encounter in *Brassica* crop fields. These sugar diets were available as a drop of undiluted honey, 50% (v/v) or as 25% (v/v) honey-water solutions. Tap water was used as a control. The corresponding sugar concentrations were determined using an optical refractometer (Atago N1) and were expressed as 86%, 47% and 25% (w/w) sucrose equivalents, respectively. This method gives only an estimate of the overall sugar concentration of a solution, but does not indicate about the kinds of sugar or their proportions in the honey used. For this study an estimate of a low, medium and high overall sugar concentration was sufficient and therefore no further sugar analysis was carried out. Fifteen wasps were assigned to each of the eight feeding treatments that included three different sugar concentrations and a control on two different days. An ample drop of food was given once, either 9–12 h after emergence (Day 0) or on the following day, 33–36 h after emergence (Day 1). As median longevity of *C. rubecula* without food was known to be 2.5 d at 25°C from preliminary experiments, we chose these feeding times to present food to wasps early and late in life. In the feeding procedure an individual wasp was removed from her cage and fed on a 3-μl drop of honey solution placed on a piece of Parafilm. The aliquot had been dispensed from a nearly filled 10-μl microcapillary. After the wasp had fed she was returned to her cage. The end of feeding was observed as withdrawing of the wasp's mouthparts from the drop to commence extensive grooming or as walking away from the feeding location. As wasps were held with water before and after the feeding procedure, water offered in control treatment was ignored. Therefore, data collection and analysis of the feeding behavior were only carried out with diets containing sugar. Fluid consumption in the diluted sugar diets was measured by reading the difference between the filled capillary before placing the drop and after taking up the remainder. Evaporation of drops of the low and medium honey concentrations was measured at one point in time and final volume readings were adjusted accordingly assuming a linear evaporation rate. As pure honey was too viscous to be treated with a microcapillary, food uptake was measured using a microbalance (Microbalance LM 600, Beckmann). A small drop of honey was placed on a piece of aluminum foil, weighed and then offered to a wasp. After she finished feeding, the remainder was weighed again and the difference in weight recorded. The weight was then converted to volume after the weight/volume factor of honey had been obtained. Evaporation in pure honey was assumed to be negligible and was not recorded. Feeding time was recorded with a stopwatch.

After feeding once on one of the three sugar diets, wasps of the same age and feeding history were caged under the original culture conditions in groups of 3–4 in clear 2-l plastic cages. These contained a cotton wick soaked with water and a piece of paper towel as a resting place. The control consisted of unfed wasps. The cages were checked for dead wasps in the morning, at noon and in the evening each day until all individuals had died.

Data analysis

Fluid consumption and feeding duration were analyzed with a two-way factorial ANOVA where sugar concentration accounted for one factor and feeding day for the other. Data were log-transformed before analysis if inhomogeneous variances occurred. After interaction between factors had been tested, a multiple comparison of the means was carried out using planned orthogonal contrasts (SAS Institute 1995).

Longevity was analyzed using survival analysis. The probability of survival is estimated as a function of time from a static point such as emergence. Survival curves were generated for Day 0 and Day 1 by plotting the proportion of wasps alive against time. Differences in survival curves for each feeding day were analyzed with a log-rank test (SAS Institute 1995). After that we estimated the quantitative effect of sugar concentration on survival with Cox's Proportional Hazards Analysis for each day separately (SAS Institute 1995). The quantitative effect of a variable is expressed as the risk ratio (also called hazard ratio). It characterizes the risk of death in the control group in comparison with the treatment group (Lang and Secic 1997). The reverse risk ratio calculates the risk of death after feeding and is used in the following to characterize the effect of sugar feeding on survival. For example, a risk ratio of 1 indicates that a sugar diet has no influence on survival. A value greater than 1 indicates a higher risk and a value lower than 1 a reduced risk of starving to death among sugar-fed wasps.

Results

Food intake

Sugar concentration and feeding day affected fluid consumption, sugar intake and feeding duration significantly (Table 1). Fluid consumed (Figure 1a) and time spent feeding (Figure 2) were similar on the low and medium sugar diet but both were significantly different from the high sugar diet. When feeding on the high sugar diet, fluid consumption was nearly half the consumption of the lower sugar diets but the feeding duration was twice as long. Due to different fluid volumes consumed, the actual sugar intake was the same on the medium and high sugar diet and significantly lowest on the low sugar diet (Figure 1b).

When fed one day after emergence (Day 1), fluid consumption (Figure 1a), actual sugar intake (Figure 1b) and feeding time (Figure 2) increased on all three sugar diets significantly (Table 1). The high sugar diet showed the strongest effect of feeding day on food consumption as sugar intake (Figure 1b) was nearly two times and feeding duration (Figure 2) nearly three times higher on Day 1 in comparison to the previous day.

Survival analysis

Median longevity (day at which 50% of the initial number of wasps are still alive) of the water-fed control group was 2.5 d and all wasps were dead after 3 d. Within both feeding days, sugar-feeding had a positive effect on survival (log-rank test, Day 0: $n = 60$, $\chi^2 = 31.80$, $p < 0.0001$ and Day 1: $n = 60$, $\chi^2 = 52.95$, $p < 0.0001$) (Figure 3).

Analysis of survival data with Cox's Proportional Hazards model showed a significant reduction in the risk of starving to death for each sugar diet, except for the low sugar diet given on Day 0 (Table 2). When fed on the medium or high sugar diet on Day 0, the risk of starving to death was reduced to 0.5 on average. This means that on the day where all unfed wasps are finally dead (probability of starving to death = 1), 50% of the fed wasps will be still alive. Generally, the risk of death was further reduced when wasps were fed on Day 1 instead of Day 0. The probability of death after feeding on Day 1 on the medium and high sugar diets was even reduced to 0.27 and 0.38, respectively; in other words, over 60% of wasps will be still alive on the day when all unfed wasps are finally dead. Feeding on a medium and high sugar diet produced similar results within both feeding days as the 95% confidence intervals of their risk ratios overlap broadly (Table 2). Whereas feeding on the low sugar diet on Day 0 did not affect survival, the same diet given one day later (Day 1) reduced the risk of death to 0.57, similar to the risk ratios of more concentrated sugar diets given on Day 0.

Table 1. Two-factorial analysis of variance of the factors sugar concentration and feeding day on feeding parameters of *C. rubecula* ($n = 90$).

Feeding parameter[1]	Sugar concentration		Feeding day	
	F	*P*	*F*	*P*
Volume consumed	25.9	< 0.001	23.8	< 0.001
Sugar intake	38.7	< 0.001	23.8	< 0.001
Feeding duration	76.4	< 0.001	75.4	< 0.001

1. data log-transformed.

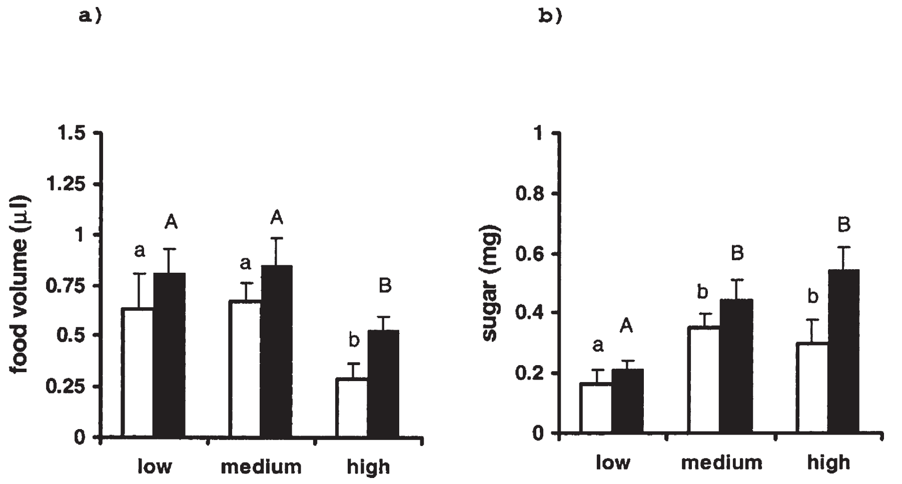

Figure 1. Food consumption (mean + 95% conf. interval) by *C. rubecula* in a single meal. Three different sugar diets were provided on the day of emergence (Day 0) or one day later (Day 1). a) Fluid volume consumed and b) sugar amount consumed. □ = Day 0, ■ = Day 1. Different letters above bars indicate statistical differences; for each sugar concentration, there was a statistical difference between Day 0 and Day 1.

Discussion

If food patches are spatially or temporarily separated from host patches, sugar encounters might be rare events in the life of parasitic wasps. In this study we measured the effect of a single sugar meal on the survival of female *Cotesia rubecula* wasps. Our results showed that sugar concentration as well as timing of the food encounter play an important role in extending longevity.

The influence of feeding on survival was linked to the amount of sugar consumed, which varied between feeding days, but only partly between different sugar diets. By providing an ample drop of honey solution, the quantity of sugar consumed was limited by the feeding capacity of the wasp and the physical properties of the sugar diets. The amount of food consumed was higher on the day after than on the day of emergence, suggesting a higher feeding capacity in the wasps that have depleted carbohydrate reserves. On the low and medium sugar diet, wasps were observed to feed until their gut was completely filled. While feeding, the abdomen increased in size balloon-like and the membranes between the abdominal segments became visible. Fluid consumption in the low and moderate sugar diets was probably limited by the stretching ability of the abdomen. Studies in blowflies have shown that abdominal stretch receptors are likely to be responsible for the termination of feeding (Stoffolano 1995). However, on pure honey *C. rubecula* consumed only a fraction of the volume that was consumed on the diluted diets. Similar results were observed in the food intake of ants (*Camponotus mus*), filling their crops only partially on sucrose concentrations over 70%. As *C. rubecula* consumed a highly concentrated amount of sugar on pure honey, the termination of feeding on honey could be explained through the osmotic pressure of sugar on the insect fluid system. A negative feedback between the osmotic pressure of the haemolymph and the rate of sugar passage through the intestine was found to limit sugar consumption in *Drosophila* flies (Chippendale 1978).

Feeding on pure honey differed from the diluted diets not only in the volume consumed but also in time spent feeding. Feeding duration on pure honey was relatively long, suggesting that similarly high sugar concentrations in the field (i.e. concentrated honeydew) might have a strong impact on daily time allocation. A wasp spending a long time on a highly concentrated sugar source makes her an easy target for predators (Morse 1986; Maingay et al. 1991) and delays her return to host searching and egg laying. The long feeding duration on pure honey suggests a reduced rate of fluid intake due to high viscosity. An exponential increase in viscosity is a major characteristic of increasing sugar concentration (Kingsolver and Daniel 1995), a factor that affects the handling of food in insects (Heyneman 1983). For example, Josens et al. (1998) reported an exponential increase in feeding time with increasing sugar concentration in ants. Optimal sugar concentrations for parasitic

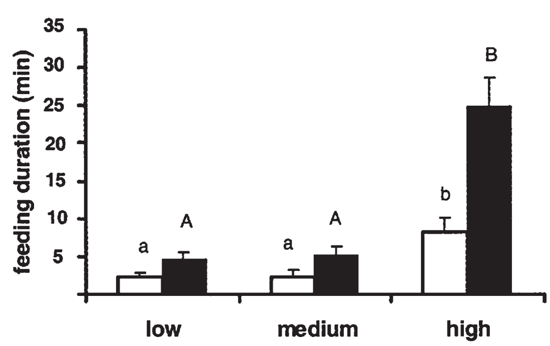

Figure 2. Time spent feeding (mean + 95% conf. int.) by *C. rubecula* in a single meal. Three different sugar diets were provided on the day of emergence (Day 0) or one day later (Day 1). □ = Day 0, ■ = Day 1. Different letters above bars indicate statistical differences; for each sugar concentration, there was a statistical difference between Day 0 and Day 1.

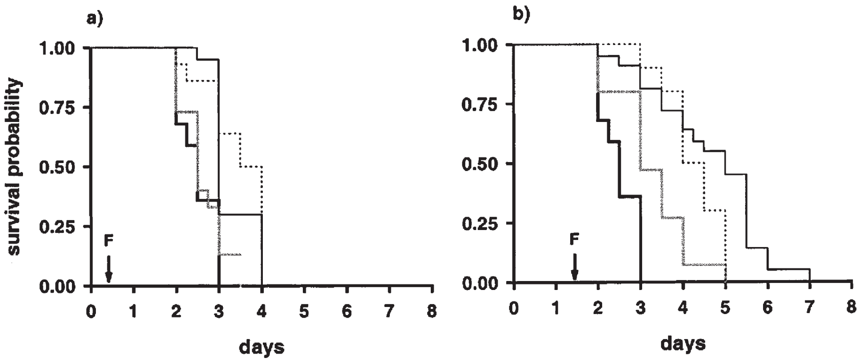

Figure 3. Survival probabilities of *C. rubecula* after a single meal on three different sugar diets. Survival after meal (F) given **a)** on the day of emergence (Day 0) and **b)** one day after emergence (Day 1). Legend: ▬ water control, ▬ low sugar diet, — medium sugar diet, ······ high sugar diet.

Table 2. Cox's Proportional Hazards Analysis for each feeding day (n=60). Each sugar diet (low medium high) is an explanatory variable on the survival time of *C. rubecula*. Risk ratios were obtained from each sugar diet/control-pair and characterize the risk of starving to death after feeding on a particular sugar diet in comparison to the control (risk ratios < 1 indicate a lower risk and ratios > 1 a higher risk of death).

	Sugar concentration					
	Day 0			Day 1		
	low	medium	high	low	medium	high
risk ratio	0.95	0.56	0.50	0.57	0.27	0.38
95% conf. int.	0.68–1.32	0.40–0.78	0.34–0.73	0.38–0.83	0.17–0.42	0.24–0.60
P	0.764	0.0006	0.0003	0.0025	< 0.0001	< 0.0001

wasps such as *C. rubecula* seem to be just below 50% sugar, as a high amount of sugar can be consumed in a relatively short feeding time.

According to the survival data collected in this study, the majority of wasps feeding on the medium sugar diet were still alive two or more days after the feeding event, but a few wasps did not survive the following day. These data suggest that food should be available once every day to prevent starvation in all wasps. As energy reserves and consequently life expectancy can decline at a different rate depending on factors such as temperature and locomotory activities, food requirements may vary accordingly. For example, on a warm day the energy metabolism of a wasp will increase (Downer 1981; Woodring 1985) and consequently a higher feeding frequency is needed to replace energy reserves. Flying is an energy-demanding process in hymenopteran insects and uses up carbohydrate reserves (Nayar and Van Handel 1971; Wigglesworth 1972; Steele 1981; Neukirch 1982; Friedman 1985), so wasps flying a lot during the day need to feed more often than wasps resting most of the time.

The extent to which sugar-feeding contributes to survival in the field will depend finally on the impact of other mortality factors such as predators (Völkl et al. 1996; Heimpel et al. 1997b; Völkl and Kroupa 1997) or harsh weather conditions (Weisser et al. 1997). For example, Heimpel et al. (1997b) studied the predation on two parasitoid species in the field and concluded that during three months in autumn the medium longevity of *Aphytis* wasps will be less than a day due to predator encounters. For a large proportion of a wasp population feeding can be irrelevant if they get killed early by extrinsic mortality conditions. However, assuming a low impact of mortality factors other than starvation sugar feeding becomes beneficial for survival and fecundity of parasitic wasps such as *Cotesia rubecula* in the field. Our study demonstrated that the effect of sugar feeding on survival should not be estimated from cage experiments with ad libitum sugar conditions but instead with the minimum feeding frequency needed to avoid starvation. Combining the minimum feeding frequency with the chances to find sugar sources in a particular habitat can lead to a realistic estimation of the expected lifetime of parasitic wasps in the field if extrinsic mortality factors are not important.

Acknowledgments

The manuscript benefited from critical readings and clarifying discussions by J. J. van Alphen, F. Wäckers, N. Schellhorn, and M. Cargill. GS was funded by IPRS (Australia).

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