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Bees get a head start on honey production

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Nectar concentration is assumed to remain constant during transport by honeybees between flowers and hive. We sampled crop contents of nectar foragers on *Aloe greatheadii* var. *davyana*, a major winter bee plant in South Africa. The nectar is dilute (approx. 20% w/w), but the crop contents of bees captured on flowers are significantly more concentrated. In returning foragers, the concentration increases further to 38–40%, accompanied by a volume decrease. The doubling of sugar concentration suggests that nectar is regurgitated onto the tongue and evaporated during foraging and on the return flight. Processing of the dilute nectar into honey thus begins early, aided by low ambient humidities. This has implications for honeybee thermoregulation, water balance and energetics during foraging, and for the communication of nectar quality to recruits.

Keywords: crop contents; nectar concentration; dilute nectar; aloes

1. INTRODUCTION

In choice experiments, honeybees prefer sugar concentrations of 30–50% w/w (Waller 1972). However, under field conditions, they collect nectar over a much wider range of concentrations (Seeley 1986), and the attractiveness of dilute nectars depends on the other nectar sources available. Using dilute nectar as a food source increases the quantity of excess water that must be carried to the hive and evaporated during the ripening of honey. This process could begin before unloading of the crop contents in the hive, but Park (1932) observed no increase in the sugar concentration in honeybee crops between the nectar source and the hive entrance when bees were collecting nectars of approximately 30%. Since this thorough study, it has been generally accepted that the nectar concentration in the forager's crop is an accurate indication of the nectar concentration of the flowers it has been visiting, and Park (1932) recommended this as a convenient method of sampling nectar (Roubik & Buchmann 1984; Roubik *et al.* 1995).

We have investigated changes in crop concentration in honeybees, *Apis mellifera scutellata*, foraging on the nectar of *Aloe greatheadii* var. *davyana* (Asphodelaceae), an important indigenous plant for South African beekeepers because it flowers during the winter dry season when other nectar sources are few (Williams 2002). Its nectar contributes substantially to the honey crop but is relatively dilute, and we hypothesized that early concentration of the crop contents could be advantageous to the bees.

2. MATERIAL AND METHODS

We investigated honeybees foraging in the following two natural field sites with hives present on a temporary basis and dense populations of aloes: Roodeplaat Nature Reserve (795 ha; 28°39' E, 25°66' S) and Rust de Winter (28°23' E, 25°12' S), both in Gauteng Province. At each site, we selected two of the less aggressive hives for capture of foragers.

All measurements were made between 09.00 and 13.00 on 11 and 12 July 2004. We captured 50 bees on flowers approximately 200 m from the hives at each site, after they had collected nectar for more than 20 s (average duration of visit; H. Human 2004, personal observation). The bees were compressed dorsoventrally to induce regurgitation and the crop contents were collected from the mouthparts in capillary tubes (Roubik & Buchmann 1984). Crop contents were expressed within 10 min of capture and their volume and concentration measured. In addition, we measured the concentration of residual nectar in the flower visited. At Roodeplaat, we also captured 50 departing foragers in order to measure the fuel reserves for flight. At both sites, we blocked the two hive entrances between 10.00 and 11.00 and captured 50 returning foragers in Ziploc plastic bags. These were placed on ice to prevent crop content utilization and to facilitate handling.

Volumes (μl) were determined from the column length in haematocrit tubes (length 75 mm/75 μl) and concentrations were measured as % w/w sucrose equivalents with a pocket refractometer (Bellingham & Stanley Ltd, Tunbridge Wells, UK). Sugar contents (mg) were calculated as the product of volume, concentration and density. Temperature and relative humidity were measured at flower height (approximately 75 cm) with a thermohygrometer (Model TES 1365, TES Electrical Corp., Taiwan).

Crop volumes and sugar contents were compared using Mann–Whitney *U*-tests. Nectar and crop concentrations were analysed with Kruskal–Wallis ANOVA followed by Mann–Whitney *U*-tests. Bonferroni corrections were applied for paired combinations. Analyses were performed with STATISTICA v. 6.0 (1984–2004). The level of significance was $p < 0.05$.

3. RESULTS

The flowering season of *A. greatheadii* var. *davyana* is characterized by a wide diurnal temperature range and very low daytime humidities. The vapour pressures at the beginning and end of the 4 hour sampling period were 3.47 and 3.73 mb, respectively, at Roodeplaat, and 5.74 and 4.69 mb, respectively, at Rust de Winter.

At Roodeplaat, there was no significant difference between crop volumes of bees captured at flowers and those entering the hive ($p = 0.063$; figure 1*a*). However, we measured a significant increase in concentration from the residual nectar to the crop contents of bees captured at flowers, and a further significant increase in the crop contents of returning foragers (figure 1*b*; $p < 0.001$). In bees captured at the flowers and at the hive entrance, the sugar content of the crops was not significantly different (figure 1*c*; $p = 0.780$). The crop of 50 bees departing to collect nectar contained 1.09 ± 1.27 s.d. μl of fluid, with a concentration of $67.7 \pm 4.7\%$, giving a mean sugar content of 1 mg.

At Rust de Winter, the crop volumes of bees captured at flowers were significantly higher than those of returning foragers (figure 1*a*; $p < 0.001$). The crop contents of bees captured at flowers and returning to the hive had significantly higher concentrations than residual nectar, and the concentration in crops of returning foragers was significantly higher than in bees captured at flowers (figure 1*b*; $p < 0.001$). The sugar content of the crops was significantly higher in bees captured at the hive entrance than in those captured at flowers (figure 1*c*; $p = 0.017$).

Bees at Rust de Winter returned with an average of 7.2 mg sugar in their crops. Based on the residual nectar concentration of 21.8%, bees would need to

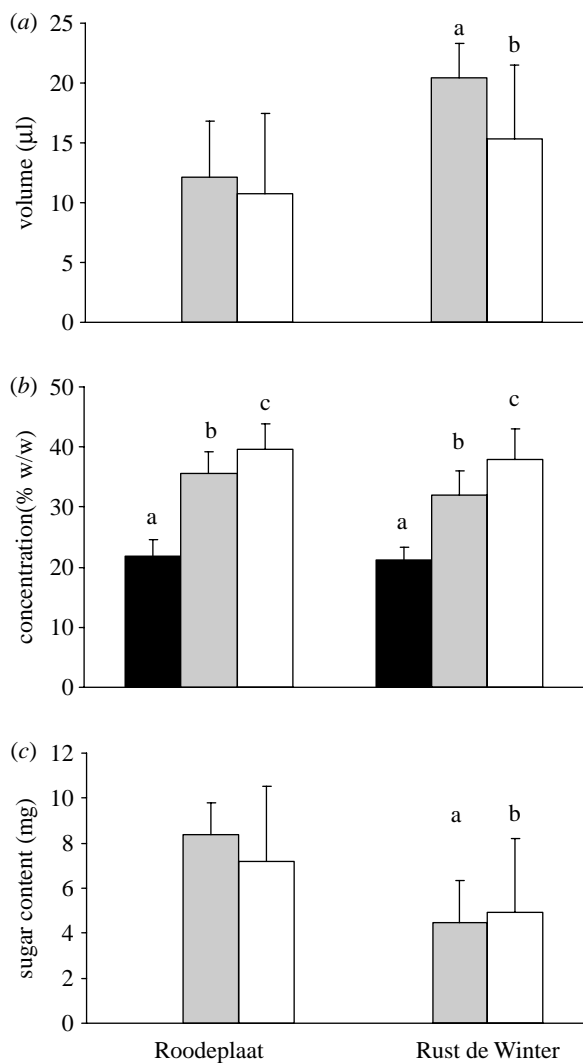


Figure 1. Honeybees (*A. m. scutellata*) foraging on the nectar of *A. greatheadii* var. *davyana*—comparison of nectar and crop contents. (a) Volume in μl , (b) concentration in % w/w and (c) sugar content in mg of crop contents of bees captured at flowers and returning to the hive at Roodeplaatt and Rust de Winter (means \pm s.d., $n=50$). Concentration of residual nectar after honeybee visits is included in (b). No letters in common denote significant differences (Mann–Whitney U -test, significance level $p<0.05$). Data from the two sites were analysed separately. Black bars, residual nectar; grey bars, bees at flowers; open bars, returning foragers.

collect 33.0 mg of nectar to obtain this amount of sugar. From this, 14.8 mg of water was evaporated before return to the hive, leaving 11.0 mg of water in nectar with a concentration of 39.5%. Roodeplaatt bees collected smaller loads but also evaporated more than half of the nectar water before return to the hive.

4. DISCUSSION

Only partial crop loads were observed in returning bees in our study, in spite of the abundant nectar, which can be attributed to its low concentration (Varjú & Núñez 1991). The surprising finding is the substantial increase in the concentration of the crop contents that was already apparent in honeybees captured at flowers and increased further on the return flight. This is contrary to Park's (1932) findings that nectar is not concentrated in the crop

before returning to the hive, but only in the hive itself during the storage and honey ripening process. His experiments showed a slight dilution (averaging 1%) of the crop contents between the food source and the hive, and this dilution has been attributed to added glandular secretions (Pasedach-Poeverlein 1940; Oertel *et al.* 1951). In two stingless bee species (*Melipona*) collecting 50% sucrose in Costa Rica, sugar concentration of the load increased by only 0.2% between the feeder and the hive (Biesmeijer *et al.* 1999). In all these studies, artificial food sources were used. The possible explanations for our very different results are considered below.

Honeybee foragers depart with small amounts of sugar in their crops as fuel for flight. Beutler (1950) measured up to 1.25 mg sugar depending on the distance to the feeder and Visscher *et al.* (1996) measured up to 1 mg sugar in crops of departing water collectors. Our bees carried a similar small quantity of sugar (1 mg) on the outward trip; even if unused, it could not account for the increase in concentration at the flowers.

The tubular corolla of *A. greatheadii* var. *davyana* restricts evaporation and nectar is available all day at constant concentration. The deepest nectar, in the basal bulb of the flowers, is inaccessible to bees, but there is no significant stratification, nectar in the floral tube being only 1% more concentrated than that in the bulb (Human & Nicolson 2008). Bees are therefore not collecting superficial nectar that has been subject to evaporation.

Increases in concentration of the crop contents between flowers and nest have also been recorded in solitary mason bees and carpenter bees (Willmer 1986, 1988). In addition, the bees' haemolymph osmolality decreases between arrival at the flower patch and return to the nest site, showing a rapid mobilization of the ingested water. However, neither the dilution of haemolymph in solitary bees nor the excretion of dilute fluid by honeybees when transporting dilute nectar or water (Johansson & Johansson 1978; Visscher *et al.* 1996) can explain the removal of water from the crop without accompanying sugar. The primary function of the expandable crop of bees is to store nectar or water and it is also the site where invertase is added to the nectar to hydrolyse sucrose. Without impermeability of the cuticular lining, water would enter from the haemolymph down a steep osmotic gradient and dilute the crop contents (Nicolson 1998). Nectar is thus only available to bees when it passes from crop to midgut. When honeybees collecting water under desert conditions were fed radiolabelled water, no water left the crop on the return flight (500 m) to the hive (Visscher *et al.* 1996).

Evaporation from the mouthparts provides the only explanation for the removal of water from the crop contents. When heated under laboratory conditions, honeybees repeatedly regurgitate a droplet of nectar onto the proboscis and then withdraw the cooled droplet to achieve evaporative cooling of the head (Heinrich 1980). Over 40% of returning honeybees flying at high temperatures (40°C) in the Sonoran desert extruded a droplet of fluid on the tongue (Cooper *et al.* 1985). Similarly, wasps (*Vespa* sp.)

achieve substantial head cooling by regurgitation (Coelho & Ross 1996). In addition to the cooling effect, this process concentrates the crop contents of bees and is used by receiver bees to ripen honey before depositing it in cells.

Honeybees foraging on the aloes are likely to be evaporating dilute nectar on their tongues as they move between flowers and on the return flight to the hive. For these bees, the nectar concentrating function is important and the evaporative heat loss may be undesirable, but bees have a thermal refuge in the hive. The increased concentration is dramatic owing to the small nectar volumes carried and the very dry atmospheres prevailing during flowering (relative humidity commonly approx. 10% in the afternoons). Much of the water elimination required for honey production is achieved before arrival at the hive entrance. Low humidities favour further evaporation in the hive, so dilute nectar is not a problem for water balance at the colonial level. Obviously, bees should not be used to sample nectar concentrations. More importantly, our data raise questions about the communication system of bees: does the increased concentration of the crop contents sampled by recruits lead them to expect a higher quality food source than is actually available?

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