Economics of comb wax salvage by the red dwarf honeybee, *Apis florea*

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Abstract

Colonies of *Apis florea*, which only abscond a short distance, usually return to salvage old nest wax; but, those colonies, and all other honeybee species which go considerably further, do not. Wax salvage would clearly be counter-productive unless the energy input/energy yield threshold was a profitable one. There are two possible trade-offs in this scenario, the trade-off between the energy expended to recover the wax (recovering hypothesis) as against that of replacing the wax by new secretion (replacing hypothesis). In order to compare the two hypotheses, the fuel costs involved in salvaging wax on one return trip, the average flower handling time, flight time and relative values for substituting the salvaged wax with nectar were calculated. Moreover, the energy value of the wax was determined. Net energy gains for salvaged wax were calculated. The energy value of the salvaged wax was 42.7 J/mg, thus too high to be the limiting factor since salvaging costs are only 642.76 mJ/mg (recovering hypothesis). The recovery costs (642.76 mJ/mg) only fall below the replacement costs for absconding distance below 115 m thus supporting the replacing hypothesis. This energetic trade-off between replacing and recycling plus the small absconding range of *A. florea* might explain why *A. florea* is probably the only honeybee species known to salvage wax and it parsimoniously explains the underlying reasons why *A. florea* only salvages wax from the old nest if the new nesting site is less than 100–200 m away—energetically, it pays off to recycle.

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Keywords *Apis florea* – Trade-off – Wax salvage

Introduction

The secretion of wax and construction of combs represents a large metabolic investment by honeybees, so that desertion or loss of the nest constitutes a substantial energetic expenditure (Hepburn et al. 1984). Nonetheless, nest desertion by absconding or migrating colonies is a common feature of tropical honeybees (Hepburn and Radloff 1998; Oldroyd and Wongsiri

2006). Despite the possible cost effectiveness of cannibalising wax from a deserted nest and reusing it in the construction of a new one, this behaviour has been reported thus far in only one species, the red dwarf honeybee, Apis florea (Akratanakul 1977; Dutton and Free 1979; Booncham 1995; Wongsiri et al. 1997).

However, there is a peculiar element to this wax-salvage behaviour. Colonies, which abscond a relatively short distance, less than about 200 m, usually return to salvage old nest wax (Booncham 1995); conversely, those which go considerably further, as in seasonal migrations, do not (Seeley et al. 1982). Thus, just as the timing of comb construction in temperate honeybees requires the right balance between the energy costs of construction and the opportunity costs of missed nectar flows (Pratt 2004), so too are the dwarf honeybees faced with decisions on the expenditure of energy. Wax salvage would clearly be counter-productive unless the energy input/energy yield threshold was a profitable one. The energetic trade-off could be either between the energy of the wax recovered as against the energy invested to do so (recovering hypothesis) or, alternatively, the energy invested to replace the wax as against the energy invested to recycle the wax (replacing hypothesis).

Here we examine these hypotheses and report the results of measurements on absconding colonies of the red dwarf honeybee to measure the energetic efficacy of wax recovery and provide a first approximation for calculating the energetics of wax-salvage behaviour.

Materials and methods

Observations

Observations and experiments on six queenright colonies of *A. florea* were performed on the Ratchaburi Campus, King Mongkut's University of Technology Thonburi, in Chom Bueng, Thailand (13.37N, 99.35E) during April–August 2008. The colonies were collected one at a time from a nearby forest, moved at dusk, and suspended under an open-sided bamboo kiosk. Before placing the colony in the kiosk, the total colony was weighed and the bees removed from the comb and separately weighed. The average mass of 100 workers was determined to extrapolate average individual bee weights. Measurements of the size of the comb (length, breadth and width) were recorded and the bees were then returned to the comb and allowed to settle for 24 h before the experiment commenced.

At dusk the next day, the brood comb extending below the crown and its supporting twig (Fig. 1a) was cut away and removed to induce absconding. The rationale for removing the brood area of the comb is that colonies on the verge of absconding usually wait until the sealed brood has emerged before leaving the now empty natal nest. Removal of the brood comb usually obviates this step (Woyke *1976*). After removing the brood nest, the queen was caged and placed in a box along with workers scraped from the comb. Then the comb crown attached to its twig was weighed as was the newly separated brood comb. Finally, the colony was returned to the comb crown and suspended in the kiosk (Fig. 1b).

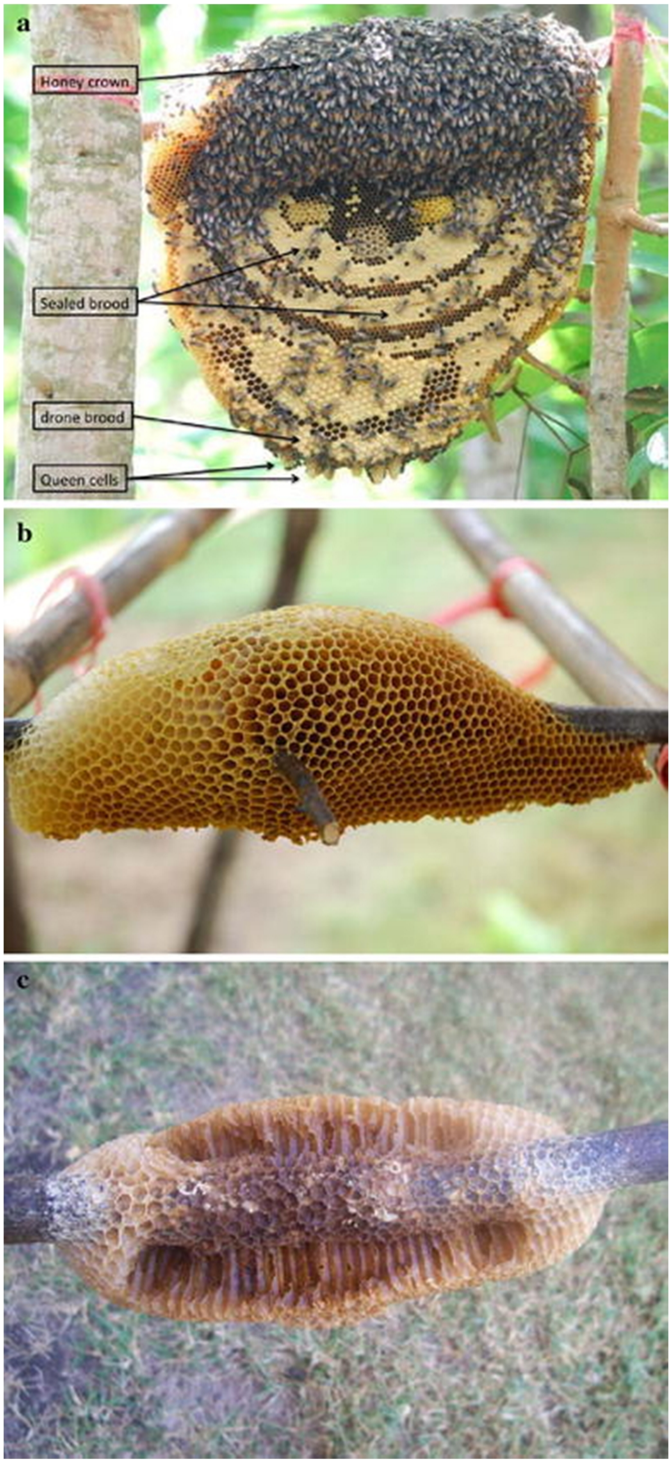

Fig. 1 **a** The single comb nest of *Apis florea* (bees removed) consists of a bulbous waxen "crown" replete with honey surrounding a twig and below which is the fan-shaped brood comb. The very white wax surrounding the fan is newly secreted wax; the greater area consists of capped developing brood while the empty darkish group of cells at the centre is brood cells from which an earlier generation has already emerged but in which the queen has not yet laid a new series of eggs. To induce absconding, the comb below the crown is cut away. **b** The isolated "crown" comb above the twig as it appears immediately after a colony of *Apis florea* has absconded. **c** The isolated "crown" comb above the twig as it appears 1 week after a colony of *Apis florea* has absconded and during which wax-salvaging foragers have stripped it of wax

The following morning, colonies were observed continuously until they absconded and the distance flown to the new nest site measured when possible, usually about 100 m. However, many colonies flew further and we lost them in the forest at these greater distances. Observations on the comb crowns for the following 48 h showed that no forager of these far-flown colonies returned to salvage wax. None of these colonies is included in the analysis since they were lost to us so that it was not possible to measure the absconding distance. When one of the six queenright colonies absconded, the crown comb and supporting twig were weighed and re-hung (Fig. 1b). When returning wax-scavenging bees arrived at the comb crown, 13 different coloured craft paints were used to mark individual bees on the thorax enabling us to identify those returning more than once for wax collection. The comb crown was weighed once after 24 h and again 1 week later to determine the amount of wax collected following absconding (Fig. 1c). Finally, five individual foragers laden with salvaged wax in both their corbiculae were caught and the total weight of wax/bee measured. After 1 week, the comb crown wax remaining on the twig was removed and the twig weighed to determine what the original comb crown weight had been.

The crop loads of 20 randomly collected nectar foragers of neighbouring queenright colonies and the wax loads of five workers of each of the absconded colonies were measured to obtain the relevant data for the energetic calculations, and the time needed to load the wax.

Energy considerations

Energy values of samples of beeswax from *A. florea* were measured using standard calorimetric analysis in a modular calorimeter (MC-1000 Operators Manual) and are expressed in megajoules/kilograms (=J/mg). The average energy value for honey is 1,271.936 kJ/100 g (National Honey Board, USA 2010) and bees need about 6.25 kg of honey to produce one kilogramme of wax (Weiss 1965). The values are based on A. mellifera but due to the lack of data for A. florea are taken as reasonable estimates. The amount of floral nectar required to produce 6.25 units of honey was calculated based on an average sugar content of nectar (25%, Root 1972) in relation to honey (80%, White and Doner 1980).

The following data were taken as constants for *A. florea*: flight speed (4.81 m/s) and mass specific metabolic rate during flight (400 W/kg thorax) (Dyer and Seeley 1987). The cost of a single salvaging trip to obtain wax (mJ) and the energetic costs involved in securing the amount of floral nectar necessary to produce the same amount of wax were calculated. Furthermore, the distance at which the cost of salvaging wax is equal to the cost of substituting floral nectar to obtain the energetic equivalent of salvage wax was also calculated.

Results

The rather variable results on wax salvage by six colonies of *A. florea* are shown in Table 1. Colony size varied from 3,715 to 25,200 bees and there was no significant correlation between colony size and weight of the original comb ($r = -0.33$, $P = 0.520$). The observed absconding distances of the colonies were 51.5 ± 27.9 m (mean ± SD) to a new nesting site with a range of 15–89 m. Pre-absconding net comb crown mass averaged 79.1 ± 96.1 mg. Slightly over half of this wax, 42.2 ± 66.5 mg, was salvaged within 24 h and, by the end of 1 week, only an additional

4.11 mg had been removed. Thus, nearly 60% of the wax available was quickly removed which staves off competition from any other scavenging colonies.

Table 1 The weights of the workers of the colonies absconded, the comb, the crown and the total amount of salvaged wax taken (unit is mg)

Colony	**Bee weight**	**Comb weight**	**Crown weight**	**Total taken**
1	78.02	186.82	112.53	112.01
2	308.93	114.24	30.46	28.22
3	290.28	81.71	8.24	5.42
4	529.96	226.81	44.63	34.90
5	413.80	57.03	18.30	12.81
6	251.25	352.07	260.21	241.63
Mean	312.04	169.78	79.06	72.50
SD	152.83	109.84	96.11	91.23

There was no significant correlation between colony size and the amount of wax taken ($r = -0.46$, $P = 0.356$). In fact, the smallest colony (3,715 bees) salvaged 76.6 mg wax which is significantly greater than the 7.04 mg salvaged by the largest colony (25,200 bees). The salvaged wax loads in both corbiculae of five individual foragers ranged from 0.7 to 1.2 mg and averaged 1.12 mg. The mean gross energy of the *A. florea* wax was 42.7 ± 0.1 J/mg.

There was a highly significant correlation between the amount of wax present in the crown on absconding and the amount subsequently salvaged: the greater the amount of crown wax available, the more taken ($r = 0.99$, $P < 0.001$). Furthermore, the workers stayed on average 6.3 min (±2.1) to salvage one load of wax. The crop content of nectar foragers ranged from 7 to 13 µl with an average of 8.18 µl (±2.0).

Energetics of salvaging wax

The costs involved in salvaging wax by a worker and in substituting the salvaged wax with nectar were determined using the following parameter values (for the complete list and references see Table 2):

Table 2 Parameters, symbols and values used to calculate the net energy gains for salvaging wax

Parameter	**Symbol**	**Value**	**References**
Absconding distance	d	51.5 m	This study
Foraging distance	D	Mean 51.5 m	This study, based on "d"
		Median 268 m	Dyer and Seeley (1991)
Mass specific metabolic rate of flying bee	r_f	0.4 mW/mg	Dyer and Seeley (1987)
Mass specific metabolic rate of non-flying bee	r_s	0.05 mW/mg	Schmid-Hempel et al. (1985)
Increase % of mass metabolic rate for each mg of additional weight		1%/mg	Schmid-Hempel et al. (1985)
Mass of bee	m_b	26.165 mg	This study
Mass of wax load	m_w	1.12 mg	This study
Mass of nectar load	m_n	9.91 mg	This study
Flight speed	v	4.81 m/s	Dyer and Seeley (1987)
Handling time for wax salvage	t_w	378 s	This study
Handling time for nectar collection	t_n	159 s	This study
Number of trips to collect nectar for one load of wax	T	2.26	This study
Amount of honey needed to produce 1 kg of wax	To calculate the amount of nectar needed to replace the wax	6.25 kg	Weiss (1965)
Energy of honey	To calculate the energy intake of the nectar	1,271.936 kJ/100 g	National Honey Board, USA (2010)
Nectar load		8.18 µl	This study
Specific weight of nectar	To calculate the mass of a nectar load	1.1125 of water	

Mass specific metabolic rate of flying bee (r_f) = 0.4 mW/mg

Mass specific metabolic rate of non-flying bee (r_s) = 0.05 mW/mg

Mass of bee (m_b) = 26.165 mg

Mass of wax load (m_w) = 1.12 mg

Mass of nectar load (m_{n}) = 9.91 mg

Absconding distance (d) = 51.5 m

Flight speed (v) = 4.81 m/s

Handling time for wax salvage (t_{w}) = 378 s (6.3 min)

Handling time for nectar collection (t_{n}) = 159 s

Number of trips to collect nectar for one load of wax (T) = 2.26

Cost involved in salvaging wax in one return trip

$$E_{\text{wax}} = (E_{\text{wax}}\text{\_OUT} + E_{\text{wax}}\text{\_HANDLE} + E_{\text{wax}}\text{\_IN}) \tag{1}$$

where E_{wax}_OUT denotes the energy spent on the flight out, E_{wax}_HANDLE the energy used during handling the wax and E_{wax}_IN the energy spent on the flight back with the wax load. The energy spent by a worker on the flight out is given by

$$E_{\text{wax}}\text{\_OUT} = r_{\text{f}} \cdot m_{\text{b}} \cdot d/v \tag{1a}$$

giving E_{wax}_OUT = 112.1 mJ.

The energy used by the worker during handling the wax is given by

$$E_{\text{wax}}\text{\_HANDLE} = r_{\text{s}} \cdot m_{\text{b}} \cdot t_{\text{w}}. \tag{1b}$$

giving E_{wax}_HANDLE = 494.5 mJ.

The energy spent on the flight back with the wax load is given by

$$E_{\text{wax}}\text{\_IN} = r_{\text{f}} \cdot m_{\text{b}} \cdot (1 + 0.01 \cdot m_{\text{w}}) \cdot d/v \tag{1c}$$

where the mass specific metabolic rate is increased by 1% for each mg of additional weight of wax (Schmid-Hempel et al. 1985), giving E_{wax}_IN = 113.3 mJ.

Entering the values of Eq. 1a–1c into Eq. 1 results in:

$$E_{\text{wax}} = 112.1\,\text{mJ} + 494.5\,\text{mJ} + 113.3\,\text{mJ} = 719.89\,\text{mJ},$$

the cost involved in salvaging wax in one return trip or the costs are 642.89 mJ/mg wax salvaged.

Cost involved in substituting the salvaged wax with nectar

In order to produce 1.12 mg of wax (equal to 1 load of 1 worker), 7 mg of honey is needed (6.25 mg honey/mg wax, Weiss 1965). Honey has a sugar concentration of about 80% and nectar has a concentration of about 25%; thus, to take in the same amount of energy, the bees must harvest 22.4 mg nectar (7 mg × 80/25), ignoring the energy needed to convert the nectar into honey for simplicity. The average crop load was 8.81 µl, and the specific weight of a 25% nectar solution is 1.1125; so workers carry 9.91 mg. From this it follows that bees require 2.26 foraging trips to garner 22.4 mg of floral nectar.

However, there is the question of the availability of floral nectar, which clearly affects the time required to collect 9.91 mg. If we use a simple example of rape, Brassica, a single flower produces 9–27 mg in 24 h (Farkas 2008). Taking the lower end of the range, and assuming a linear production over 24 h, this would result in 0.375 mg/h available per flower. Therefore, a worker has to visit 26.4 flowers, spending 6 s per flower (Farkas 2008) and requires a handling time of 159 s to fill the crop.

Energetics of substituting wax with nectar

$$E_{\mathrm{nectar}} = T \cdot (E_{\mathrm{nec}}\text{\_OUT} + E_{\mathrm{nec}}\text{\_HANDLE} + E_{\mathrm{nec}}\text{\_IN}) \tag{2}$$

where E_{nec}_OUT is the energy used flying out, E_{nec}_HANDLE the energy used during handling the nectar and E_{nec}_IN the energy invested flying back with the nectar load.

The energy spent by a worker on the flight out is given by:

$$E_{\mathrm{nec}}\text{\_OUT} = r_{\mathrm{f}} \cdot m_{\mathrm{b}} \cdot D/v \tag{2a}$$

where D is the average foraging distance. Assuming the same distance as in Eq. 1a,

$D = 51.5$ m, giving E_{nec}_OUT = 112.1 mJ.

The energy used by the worker during handling the nectar is given by:

$$E_{\mathrm{nec}}\text{\_HANDLE} = r_{\mathrm{s}} \cdot m_{\mathrm{b}} \cdot t_{\mathrm{n}} \tag{2b}$$

giving E_{nec}_HANDLE = 208.0 mJ.

The energy spent on the flight back with the nectar load is given by:

$$E_{\mathrm{nec}}\text{\_IN} = r_{\mathrm{f}} \cdot m_{\mathrm{b}} \cdot (1 + 0.01 \cdot m_{\mathrm{n}}) \cdot D/v \tag{2c}$$

where the mass metabolic rate is increased by 1% for each mg of additional weight of nectar (Schmid-Hempel et al. 1985), giving E_{nec}_IN = 123.2 mJ.

Entering the values of Eq. 2a–2c into Eq. 2 results in:

$E_{\text{nectar}} = 2.26 \cdot (112.1\ \text{mJ} + 208.0\ \text{mJ} + 123.2\ \text{mJ}) = 1{,}001.85\ \text{mJ}$.

Net energy gain $= E_{\text{nectar}} - E_{\text{wax}} = 1{,}001.85\ \text{mJ} - 719.89\ \text{mJ} = 281.96\ \text{mJ}$.

The energy gain for salvaging the wax instead of replacing it with nectar would be 282 mJ under the condition that average absconding distance and average foraging distance are both 51.5 m.

By setting Eq. 1 equal to Eq. 2 and solving for d, the absconding distance, one obtains the maximum distance at which energetically salvaging and collecting nectar cost the same:

$$d(D) = \frac{(E_{\text{nec}} - E_{\text{wax}}\text{\_HANDLE})}{\frac{r_f \cdot m_b}{v} \cdot (2 + 0.01 \cdot m_w)} = 115.9\ \text{m}.$$

Obviously, this depends on the average foraging distance D. At a distance of 115.9 m, the energy spent salvaging wax would be equal to the energy spent substituting the wax with nectar under the assumption that the average foraging distance is 51.5 m. Using the median foraging distance estimated by Dyer and Seeley (1987) of 268 m, salvaging wax would be energetically beneficial up to 607 m (Fig. 2). The data from Punchihewa et al. (1985) are similar to our observations that the median foraging distance is below 150 m (see Figs. 3 & 8 of Punchihewa et al. 1985).

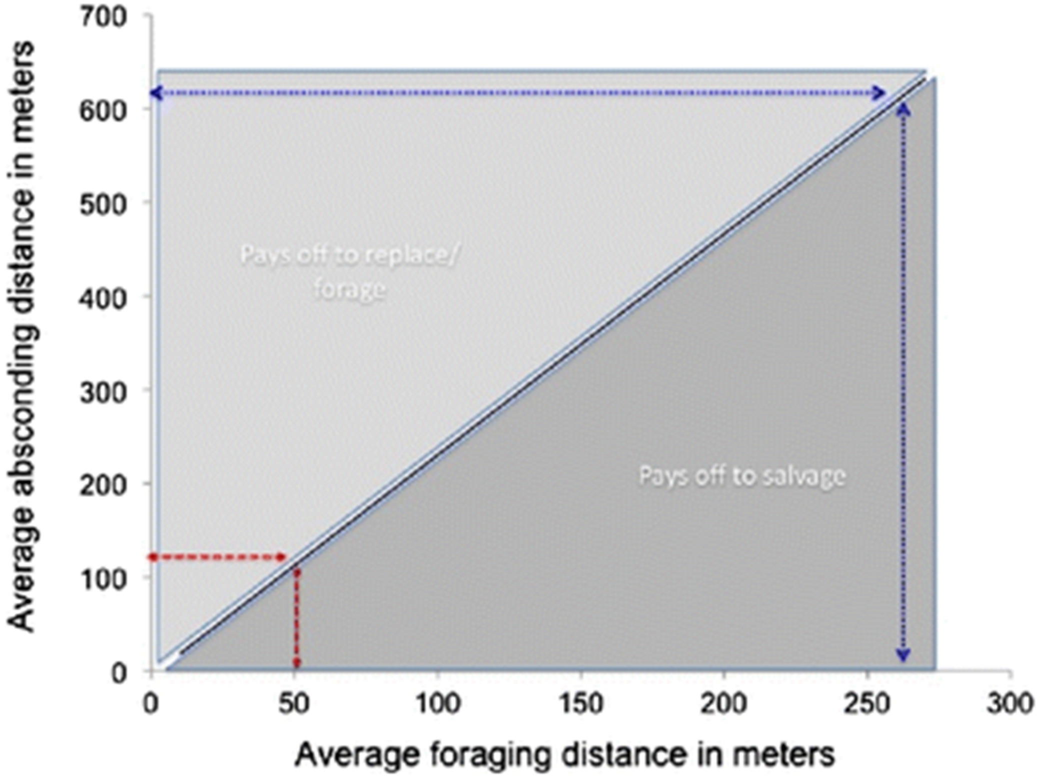

Fig. 2 Relationship between average foraging distance and absconding distance—the *dashed line* represents the situation when the energy invested for salvaging equals the energy invested to replace the wax with nectar based on an average foraging distance of 51.5 m (this study). The *dotted line* is the same calculation assuming a median foraging distance of 268 m (Dyer and Seeley 1991). Above the *diagonal line* it would be energetically beneficial to collected nectar, below it would be more beneficial to salvage the wax

Discussion

To make a single return flight to the old comb to salvage wax, a worker spends 112.1 mJ for the flight, for handling the actual wax it takes 378 s and uses 494.5 mJ, and to carry the wax load home a further 113.3 mJ, equalling a total 719.9 mJ. The energy value of a wax load recovered is 47.8 J. Since one salvaging trip costs only 1/70 of the energy recovered (719.9 mJ or 0.7 J), an even longer flight distance of several kilometres would still be beneficial if the trade-off were between energy invested and energy recovered.

The observations and calculations support the replacing hypothesis that wax salvaging is a trade-off between the energy invested to recycle the wax as against the energy replacing it. Salvaging wax does not yield an energetic gain if the absconding distance is greater than 115 m (under the assumption that the average foraging distance is 51.5 m). If the average foraging distance is actually smaller, e.g. nectar sources are closer to the new nest site, the cut-off distance is less (Fig. 2). That energetic trade-off and the unique behavioural ecology of A. florea, e.g. small absconding range, might be the reason why A. florea is the only species of honeybees that has been reported to salvage wax. Apis florea only salvages the crown of the comb, which is where honey and pollen are stored, most likely for efficiency reasons. The main part of the comb is used for brood rearing so during the brood cycles the silk of the pupae remains in the cells (Hepburn 1986). This silk however reinforces the combs, which substantially increases both the tensile strength and the stability of the cells (Pirk et al. 2004) and therefore makes it more difficult to harvest the pure wax.

Indeed the trade-off scenario holds for other species like A. mellifera which has an average foraging distance of about 1,000 m (Seeley 1985) and a minimum absconding range of about 6,000 m (Schneider 1990). If our model is parameterized for these values then salvaging is not energetically profitable for this species (Figure S1; Table S1). An average foraging distance of 1,000 m means that wax salvaging would only be beneficial with an average absconding distance of below 468 m. The costs for a wax trip (6 km one way) would be around 71.6 J and to replace the wax with nectar would cost only 6.8 J. Generalising these considerations would explain why it is not beneficial for any other species, except possibly, Apis andreniformis, to salvage wax.

The six absconding colonies flew an average distance of 51.5 ± 27.9 m to a new nesting site and, within these limits, there was no significant correlation between distance moved and the amount of wax salvaged. Distance between the new and old nest site is an important parameter since colonies, which abscond further than 100 m away do not return to salvage wax (Seeley et al. 1982). Indeed, the energetic trade-off scenario described here supports that observation.

To salvage the wax from an old nest site around 200 m away would only be feasible if the average foraging distance is above 75 m (Fig. 2). The proposed trade-off between energy recovery and distance gives a parsimonious explanation why such behaviour is only observed in *A. florea*, despite the fact that worker bees of all honeybee species can be observed salvaging abandoned propolis, wax and honey stores. Published data on foraging distances show that *A. florea* workers can travel about 800 m to forage on artificial feeders and this suggests that absconding is less related to tapping new resources than to microclimatic parameters related to the nest itself. The energetic trade-off nicely explains the underlying reasons why *A. florea* only salvages wax from the old nest if the new nesting site is less than 100 m away—energetically, it pays off to recycle.

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