

## RESEARCH ARTICLE

# Foraging strategy of wasps – optimisation of intake rate or energetic efficiency?

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## ABSTRACT

In endothermic wasps, foraging is an expensive activity. To maximise the benefit for the colony, wasps can optimise either the intake rate or energetic efficiency of a foraging trip. We investigated the foraging behaviour of vespine wasps under variable environmental and reward conditions. We trained them to forage for 0.5 mol l<sup>-1</sup> sucrose solution from an artificial flower in a flow-through respiratory measurement chamber, and simultaneously measured their body temperature using infrared thermography to investigate interactions between thermoregulation and energetics. Measurement of carbon dioxide release (for energetic calculations) and load mass enabled the direct determination of foraging efficiency. An unlimited reward increased the wasps' energetic effort to increase the suction speed through high body temperatures. With reduced reward (limited flow), when an increased body temperature could not increase suction speed, the wasps decreased their body temperature to reduce the metabolic effort. Solar heat gain was used differently, either to increase body temperature without additional metabolic effort or to save energy. The foraging efficiency was mainly determined by the flow rate, ambient temperature and solar heat gain. In shade, an unlimited sucrose flow and a high ambient temperature yielded the highest energetic benefit. A limited flow reduced foraging efficiency in the shade, but only partly in sunshine. Solar radiation boosted the efficiency at all reward rates. Wasps responded flexibly to varying reward conditions by maximising intake rate at unlimited flow and switching to the optimisation of foraging efficiency when the intake rate could not be enhanced due to a limited flow rate.

**KEY WORDS:** Energetics, Foraging, Motivation, Metabolic rate, Thermoregulation, Wasps

## INTRODUCTION

Vespine wasps undergo an annual life cycle in which the colonies grow slowly after the foundation of the nest in spring by the queen but faster in summer and towards the end in autumn. Thus, efficient foraging is crucial for colony development. Wasps capture smaller or less mobile insects and forage for nectar and honeydew. Their high agility during foraging is achieved through a high body temperature by means of endothermic heat production (e.g. Heinrich, 1984; Coelho and Ross, 1996; Eckles et al., 2008; Kovac and Stabentheiner, 1999, 2012; Kovac et al., 2009; Kovac et al., 2015). For a proper take off and stable flight they need to


reach a minimum threshold temperature of their flight muscles (Coelho and Hoagland, 1995). The thoracic temperatures thereby can exceed 40°C (Heinrich, 1984; Kovac and Stabentheiner, 1999; Kovac et al., 2009). Additionally, a high body temperature accelerates foraging on liquid sources. Quite similar to water-collecting honeybees, the suction speed in drinking wasps is enhanced by a high thorax temperature (Kovac et al., 2015), which leads to an elevated head temperature and thereby increases suction speed (Kovac et al., 2010; Stabentheiner and Kovac, 2014, 2016).

During foraging flights in the temperate climate of central Europe, wasps are exposed to highly variable environmental conditions that challenge their thermoregulatory capability and energetic expenditure (Kovac and Stabentheiner, 2012; Kovac et al., 2015). Generally, foraging at low temperatures results in higher energetic costs for endothermic insects (Stabentheiner and Kovac, 2014, 2016; Coelho et al., 2016). A high body temperature as a result of endothermic activity can only be achieved by high energy expenditure. During foraging at sources with high energetic gain (e.g. 1.5 mol l<sup>-1</sup> sucrose solution at unlimited flow) wasps exhibit thorax temperatures above 35°C (Kovac et al., 2015). When only poor food sources are available, wasps have to minimise their own energetic effort to optimise foraging efficiency. Foraging strategies of social insects balance energy expenditure of individual foragers against the net energetic gains of the colony (e.g. Seeley, 1986, 1991; Varjú and Núñez, 1991; Balderrama et al., 1992; Moffatt, 2000, 2001). This net energetic gain (of the colony) could be improved by maximising the number of an individual's foraging trips per time interval (intake rate) and/or by optimising foraging efficiency (balancing gains and costs). Honeybees that feed on sucrose solutions at an unlimited flow rate maximise their net intake rate. They invest both their own heat production and heat gain from solar radiation to increase their body temperature to a level that guarantees a high suction speed, but they optimise energetic efficiency if the intake rate is limited by the food source, i.e. when a higher body temperature would not guarantee a higher intake rate (Stabentheiner and Kovac, 2016). As wasps have a similarly high energetic expenditure during foraging as honeybees (Kovac et al., 2015; Stabentheiner and Kovac, 2014, 2016), the question arises of whether they apply the same strategies to optimise foraging.

We hypothesize that, in any case, wasps optimise foraging energetics, i.e. they will maximise the total gain whenever possible and reduce costs if possible and necessary. It has remained an open question, however, whether they in the first place maximise foraging speed (net energy gain rate) or foraging efficiency (net energy gain), or both, like honeybees. However, wasps do not forage in a constant environment, but in one that is highly variable. Therefore, we investigated how they respond to environmental changes such as ambient temperature and solar radiation, but also availability of food resources. We simultaneously measured their thermoregulatory behaviour, metabolic rate (CO<sub>2</sub> release) and foraging gain (load mass). In extension to previous experiments (Kovac et al., 2015), we

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experimented in this study closer to natural conditions with lower food quality and reward rates ( $0.5 \text{ mol l}^{-1}$  sucrose at unlimited and limited flow rate), e.g. similar to wasps collecting droplets of honeydew. The combined consideration of environmental parameters and functional requirements enables us to understand the wasps' choice of foraging strategies and to generate general rules of energetic optimisation of endothermic insects that forage for liquids.

## MATERIALS AND METHODS

### Location and experimental setup

Experiments were conducted in September and October 2006 within the same series and experimental setup as previously described by Kovac et al. (2015) (for more methodical details see also Stabentheiner et al., 2012). Briefly, 15 free-flying vespine wasps [*Vespula germanica* (Fabricius 1793)] were lured and trained in a garden close to an external laboratory facility in order to measure body temperature, respiration and load mass. They were marked individually with colour dots on thorax and abdomen and were trained to collect  $0.5 \text{ mol l}^{-1}$  sucrose solution from an artificial flower in a respiratory measurement chamber ( $\sim 7.9 \text{ ml}$  inner volume; Fig. 1). The artificial flower was constructed from a cap of a plastic vial as described in Stabentheiner et al. (2012) and Kovac et al. (2015). Sucrose solution was supplied unlimited or at limited flow rates ( $15$  or  $8.3 \mu\text{l min}^{-1}$ ) to the artificial flower by a perfusor (B-BRAUN Perfusor Compact, Melsungen, Germany). To get access to the measurement chamber, the wasps had to walk via a short tunnel over a balance (AB104, METTLER-TOLEDO, Greifensee, Switzerland), where, before and after foraging, they were weighed to the nearest  $0.1 \text{ mg}$ . The crop load was calculated from the mass difference before and after foraging. Immediately after entering the chamber, the chamber lid was closed and, after the wasps had finished drinking the sugar solution, the lid was opened manually by the experimenter. During the foraging stay, the chamber was kept closed, airtight. The duration of foraging was deduced from infrared video sequences recorded during the entire foraging stay, defined as the time span from entering to leaving the measurement chamber.

### Environmental parameters: ambient temperature and solar radiation

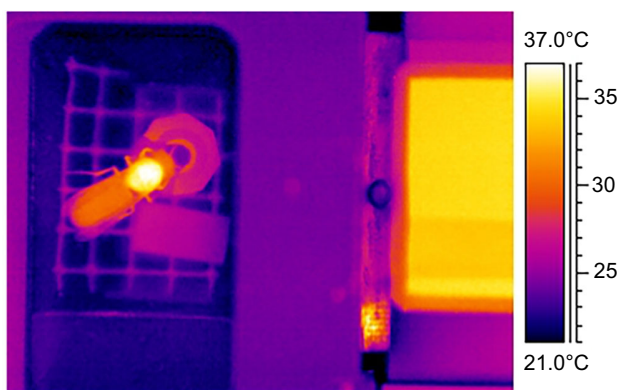
The variable environmental conditions manipulated experimentally were ambient air temperature ( $T_a$ ) and solar radiation in the

measurement chamber. Measurements were conducted during 5–10 foraging trips of one individual at the same environmental condition. Experimental ambient temperature was regulated from  $12$  to  $35^\circ\text{C}$  in about  $5^\circ\text{C}$  intervals by immersing the brass measurement chamber (Fig. 1) in a water bath (Julabo F33 HT, Seelbach, Germany). If possible, the same wasp was measured first in the shade (artificial shading) and then in bright sunshine at the same experimental ambient temperature. After this series we measured another individual, but the same wasp could also be measured at different temperatures on different days. Wasps foraging under intermediate, partly cloudy conditions were also evaluated and taken into consideration. Ambient air temperature in the measurement chamber was measured about  $1 \text{ cm}$  next to the wasps by a Type K thermocouple (OMEGA Thermo Products, Stratford, WI, USA). Solar radiation was measured using a custom-manufactured photoelectric miniature global radiation sensor (FLA613GS/Mini spezial, measurement range of  $380$ – $1100 \text{ nm}$ ; Ahlborn, Holzkirchen, Germany) in a second chamber beside that containing the artificial flower. Air temperature in the measurement chamber, radiation and outside air temperature were recorded with an ALMEMO® data logger (2890-9, Ahlborn; for details see Stabentheiner et al., 2012; Kovac et al., 2015). Results were divided into three categories according to the mean solar radiation during the foraging stay: (a) bright sunshine ( $>500 \text{ W m}^{-2}$ , mean values:  $548/569/618 \text{ W m}^{-2}$  for unlimited/ $15 \mu\text{l min}^{-1}/8.3 \mu\text{l min}^{-1}$  flow rate), (b) partial sunshine ( $100$ – $500 \text{ W m}^{-2}$ , mean values:  $385/392/412 \text{ W m}^{-2}$ , respectively), and (c) shade ( $<100 \text{ W m}^{-2}$ , mean values:  $13/20/25 \text{ W m}^{-2}$ , respectively).

### Energy turnover

The wasps' energy turnover was determined from their respiratory metabolism ( $\text{CO}_2$  production), which is commonly used as an indirect measure of an organism's metabolic rate.  $\text{CO}_2$  emission was measured with a flow-through measurement setup in serial mode using a differential infrared gas analyser (DIRGA; URAS 14, ABB, Zürich, Switzerland) operating at a flow rate of  $240 \text{ ml min}^{-1}$ . Digital data readout via the RS-232 interfaces of the DIRGA was done by Centrol 5 software (Harnisch, Austria). Depending on the experimental situation (duration of stay, influenced by ambient temperature and solar radiation), the rise and decay (washout) times of the  $\text{CO}_2$  signal resembled or even exceeded the visit duration. Thus, the insects' energy turnover could not be measured by cutting out a section of the respiratory trace and simple averaging. Therefore, we integrated the wasps' total  $\text{CO}_2$  emission per stay (including 2 min of washout) and divided the integral by the duration of the stay inside the respiratory chamber. The loss of measurement gas during chamber opening after the insects' visits was compensated for by calibrations as described in Stabentheiner et al. (2012). Briefly,  $\text{CO}_2$  was injected into the measurement chamber via a syringe by a perfusor to achieve a stable measurement signal. Then, the perfusor was turned off and the chamber was kept closed, or the perfusor was turned off and the chamber was opened for  $\sim 5 \text{ s}$  (the duration of chamber opening when a wasp left the chamber). During this period, the chamber was flushed with fresh air because the pump and mass flow controller were still active. In this way, we got two calibration curves of the  $\text{CO}_2$  quantity in the system in dependence on the 'turnover' (concentration $\times$ flow) at the time when the perfusor was turned off. The difference between these two curves represented the  $\text{CO}_2$  loss caused by chamber opening (Stabentheiner et al., 2012).

As the wasps differed noticeably in size and mass, the mass-specific energy turnover and  $\text{CO}_2$  production was calculated per



**Fig. 1.** Thermogram of a wasp foraging for sucrose solution from an artificial flower inside a respiratory measurement chamber. The air inlet is located at the bottom of the image; the outlet is in the chamber floor to the right of the wasp. The thorax is heated by activation of the flight muscles; part of the heat has reached the head and the abdomen. Ambient temperature ( $T_a$ )  $\sim 23^\circ\text{C}$ . Right-hand rectangle: proprietary infrared reference radiator.

milligram body mass. For calculation of the energy gain, the conversion of the crop load from mass (mg) to volume (ml) units was performed based on a sucrose solution density of  $1.0638 \text{ g cm}^{-3}$  for  $0.5 \text{ mol l}^{-1}$  at  $20^\circ\text{C}$  (i.e. measured values corrected for density variation due to temperature). Energy gain from sugar was calculated by using a calorific value of  $16.8 \text{ kJ g}^{-1}$  sucrose (compare Hartfelder et al., 2013). The respiratory quotient was assumed to be 1.0, as determined by Maschwitz (1966), for resting and moving wasps, because they were feeding solely on sucrose solution also during the training period preceding the experiments. Therefore, the energy turnover ( $P$ ; measured in W) could be calculated directly from the  $\text{CO}_2$  production rate ( $\dot{V}_{\text{CO}_2}$ ; measured in  $1 \text{ O}_2 \text{ s}^{-1}$ ) without the need to convert to  $\text{O}_2$  consumption:  $P = \dot{V}_{\text{CO}_2} \times \text{caloric equivalent}$ , in which the caloric equivalent for sucrose-feeding wasps is  $21,117 \text{ J l}^{-1} \text{ O}_2$ .

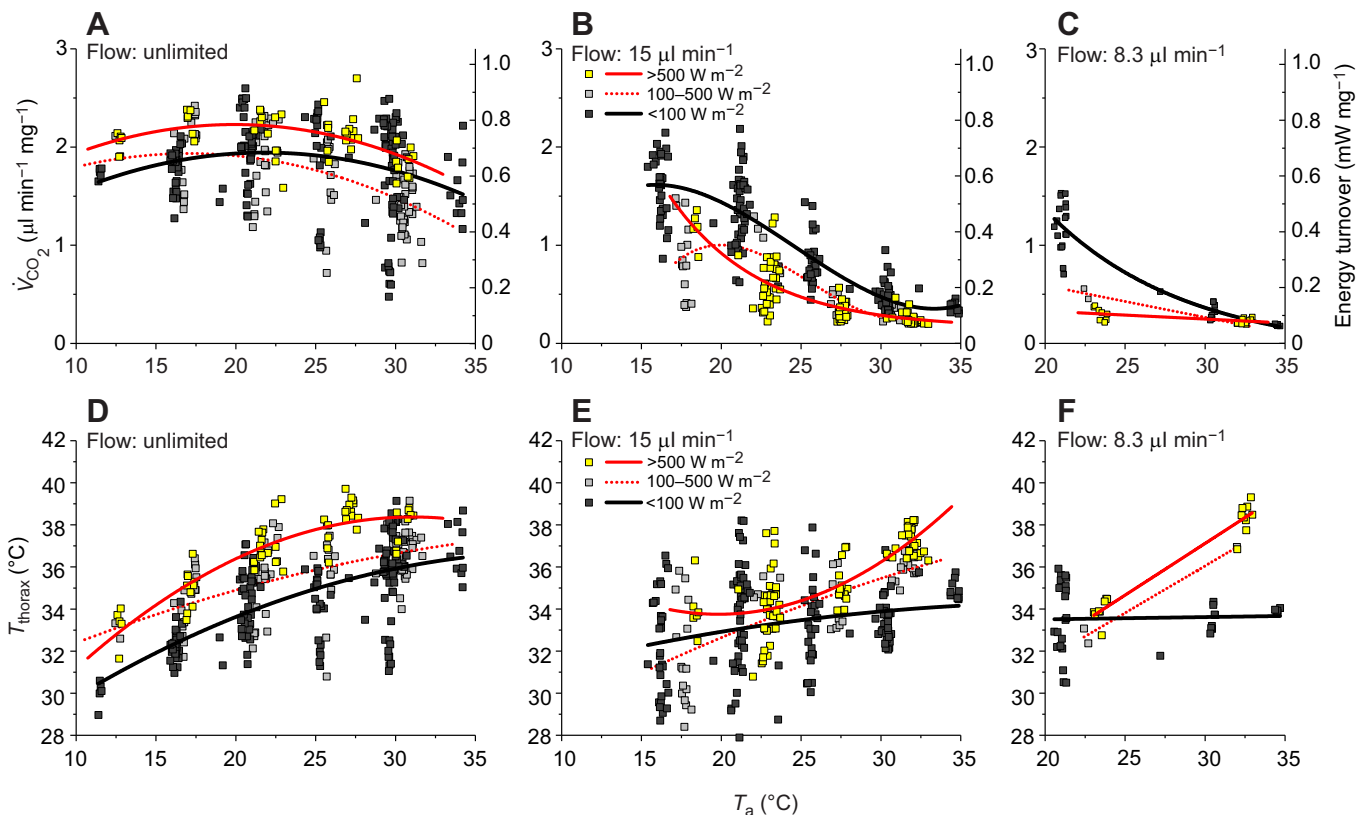
### Forager body temperature

The lid of the measurement chamber consisted of a brass frame covered with a plastic film, which was transparent for radiation both in the infrared and visible range (Stabentheiner et al., 2012). This allowed thermographic measurement of the wasps' body surface temperature (ThermaCam SC2000 NTS, FLIR Systems, Wilsonville, OR, USA) and observation of their behaviour during foraging. The infrared camera was calibrated against a proprietary Peltier-element-driven reference radiator placed close to the measurement chamber (but not inside) within the infrared picture (Fig. 1; accuracy  $\leq 0.4^\circ\text{C}$ ; Stabentheiner et al., 2012). The

attenuation of the infrared radiation by the plastic film was compensated for by covering a part of the reference source head with a stripe of the same film. This also minimised errors resulting from ambient reflections via the film surface. The body surface temperature was calibrated using the cuticular emissivity of honeybees ( $\epsilon=0.97$ ; Stabentheiner and Schmaranzer, 1987). Thermograms were digitally stored on a DOLCH FlexPac computer (Kontron, Augsburg, Germany) with 14 bit resolution at a rate of 5 Hz using ThermaCam Researcher software (FLIR Systems, Wilsonville, OR, USA). Thermographic measurements were evaluated with ThermaCam Researcher software (FLIR) controlled by a proprietary MS Excel (Microsoft) VBA macro. This macro also extracted the stored environmental data automatically from the logger files at the time of thermographic measurement. The thermoregulatory behaviour was evaluated during the entire foraging stay in such a way that thermograms were taken every 3–5 s. From these thermograms, the surface temperatures of head, thorax and abdomen were calculated.

### Data analysis

We measured four parameters: metabolic rate ( $\text{CO}_2$  release), body temperature, duration of foraging and load mass. The costs and gains of foraging were calculated on the basis of the metabolic data, foraging time and load mass (see above). Measured (thorax temperature,  $\text{CO}_2$  release, load mass, foraging time) and calculated (costs, gains and efficiency of foraging) parameters were analysed in dependence on ambient temperature, solar



**Fig. 2. Energetics and thermoregulation of wasps foraging sucrose solution ( $0.5 \text{ mol l}^{-1}$ ) in the shade and in sunshine at different reward rates in relation to ambient air temperatures near the wasps in the measurement chamber ( $T_a$ ).** Results in the shade are shown by black symbols, and in sunshine by yellow and grey symbols. (A–C)  $\text{CO}_2$  production rate ( $\dot{V}_{\text{CO}_2}$ ) and energy turnover; (D–F) thorax surface temperature. All parameters were measured simultaneously in all individuals. Symbols represent mean values of foraging stays.  $N=295$  unlimited flow rate,  $N=255$  limited flow of  $15 \mu\text{l min}^{-1}$ ,  $N=48$  limited flow of  $8.3 \mu\text{l min}^{-1}$ . For constants of fit curves and statistic details, see Tables S2 and S3.

radiation and reward rate. Foraging efficiency and intake rate were defined according to Seeley's calculations (Seeley, 1994): net energy efficiency = (gain-costs)/costs ( $\text{J J}^{-1}$ ); net rate of energy gain = (gain-costs)/time ( $\text{J s}^{-1}$ ).

Integration and baseline correction of metabolic data was done with Origin 8.1/9.1 (OriginLab) software. Curve fitting and statistics was done with Origin (OriginLab) and Statgraphics software (Statgraphics Centurion XVI, StatPoint Technology Inc.). Simple linear regressions and complex curve fittings (exponential and polynomial) were carried out to show the dependence of parameters on ambient temperature or duration of foraging. A 'general linear model' (GLM) statistics test was performed to test the influence of the experimentally given variables reward, temperature and radiation on the measured and calculated parameters. The difference between foraging in sunshine and shade was tested with Statgraphics using ANOVA. All statistical details are provided in Tables S1–S3.

## RESULTS

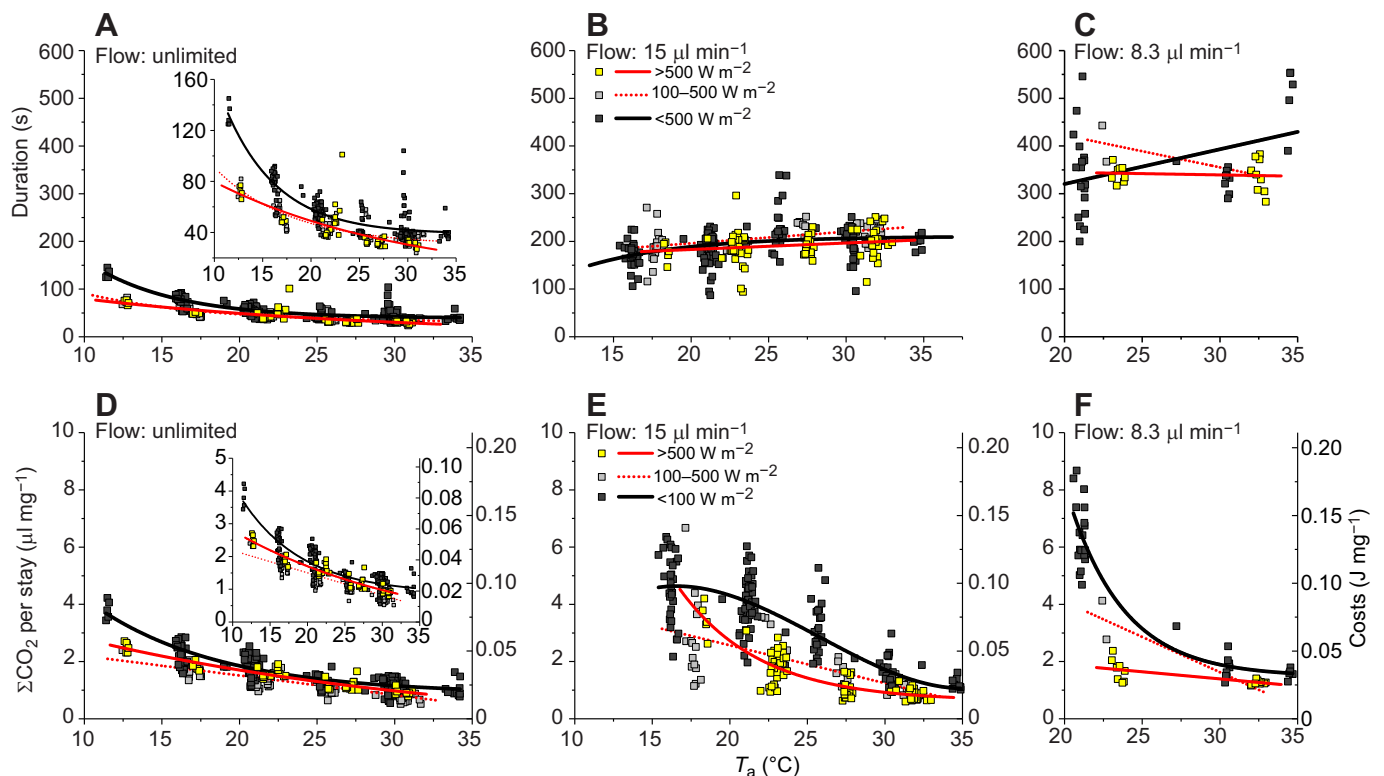
### Energetics and temperature

We evaluated 597 foraging stays of wasps at the artificial flower in the measurement chamber at a broad range of experimental ambient temperatures ( $T_a = 12\text{--}35^\circ\text{C}$ ). From the total of 597 visits, 295 measurements were made at an unlimited sucrose flow rate, 255 at a limited flow of  $15 \mu\text{l min}^{-1}$ , and 48 measurements at a limited flow of  $8.3 \mu\text{l min}^{-1}$ . As the wasps differed considerably in size and mass (mean mass at arrival:  $75.6 \pm 6.6 \text{ mg}$ , minimum:  $66.8 \text{ mg}$ , maximum:  $89.3 \text{ mg}$ ,  $N=597$  measurements;  $n=15$  wasps), the mass-specific metabolic rate was calculated per milligram body mass (Fig. 2A–C). The variability of the metabolic rate and

calculated energy turnover of individual wasps was very high. The experimentally given variables – reward rate, ambient temperature and radiation – had a significant influence on the metabolic rate ( $P < 0.0001$ , GLM; see Table S1). The wasps' mean energy turnover (derived from regressions) was in the range of about  $0.1\text{--}0.8 \text{ mW mg}^{-1}$  (about  $13\text{--}270 \text{ mW}$  per wasp). In all radiation categories, it decreased significantly with increasing ambient temperature ( $P < 0.01$ , ANOVA; for  $N$ , d.f. and other statistical details, see Tables S2, S3) with one exception (i.e. partial sunshine,  $8.3 \mu\text{l min}^{-1}$  limited flow rate, n.s., Fig. 2C). The wasps' mean energy turnover was mostly higher in bright sunshine than in the shade at an unlimited flow rate ( $P < 0.0001$ , ANOVA), but lower at limited flow rates ( $P < 0.0001$ , ANOVA). The experimentally given variables had also a significant influence on the thorax temperature ( $P < 0.0001$ , GLM; see Table S1). The variability of thorax temperature was very high, with mean values per stay ranging from  $\sim 28^\circ\text{C}$  to nearly  $40^\circ\text{C}$  (Fig. 2D–F; fit curves and statistics in Tables S2, S3). However, despite the differences in energy turnover between flow rates, the mean thorax temperature was mostly higher in sunshine ( $P < 0.0001$ , ANOVA), and it increased with ambient temperature ( $P < 0.0001$ , ANOVA) except in two categories ( $8.3 \mu\text{l min}^{-1}$  flow rate in partial sunshine and shade; n.s., Fig. 2F).

### Duration, load mass and energetic costs

The duration of foraging stays depended on the reward rate and the radiation conditions ( $P < 0.05$ , GLM; see Table S1) but not on the ambient temperature ( $T_a$ ) in the measurement chamber. At an unlimited sucrose flow rate, the duration of foraging stays decreased with  $T_a$  in all three radiation categories (mean range:  $25\text{--}135 \text{ s}$ , Fig. 3A;  $P < 0.0001$ , ANOVA). At a limited flow rate, we observed



**Fig. 3.** Duration of stay and costs of wasps foraging sucrose solution ( $0.5 \text{ mol l}^{-1}$ ) in the shade and in sunshine at different reward rates in relation to ambient air temperature near the wasps in the measurement chamber ( $T_a$ ). Results in the shade are shown by black symbols, and in sunshine by yellow and grey symbols. (A–C) Duration of stay; (D–F) costs. Insets show same graph in larger scaling.  $N=295$  unlimited flow rate,  $N=255$  limited flow of  $15 \mu\text{l min}^{-1}$ ,  $N=48$  limited flow of  $8.3 \mu\text{l min}^{-1}$ . For constants of fit curves and statistic details, see Tables S2 and S3.



no clear strategy, i.e. either a slight increase or decrease with  $T_a$  ( $P < 0.0001$ , ANOVA) or independence from  $T_a$  (mean range: 170–430 s; Fig. 3B,C). The load mass of foraged sucrose solution was highly variable (with a range from 30 to 80 mg, Fig. S1A–C), but means of the three reward categories differed only slightly, albeit significantly, from each other [unlimited:  $52.95 \pm 6.35$  mg ( $N=306$ ),  $15 \mu\text{L min}^{-1}$ :  $55.15 \pm 6.83$  mg ( $N=268$ ), and  $8.3 \mu\text{L min}^{-1}$ :  $57.9 \pm 8.03$  mg ( $N=48$ );  $P < 0.01$ ,  $t$ -test]. The load mass increased in most cases slightly with  $T_a$  ( $P < 0.0001$ , ANOVA), except in all foraging categories in bright sunshine.

The costs of foraging (calculated from the amount of  $\text{CO}_2$  release during the foraging stay, Fig. 3D–F) depended strongly on the reward rate, and on the ambient temperature and radiation ( $P < 0.0001$ , GLM). The costs of foraging were found to be mostly lower in sunshine than in the shade [ $P < 0.01$ , ANOVA, except at  $8.3 \mu\text{L min}^{-1}$  limited flow rate in partial sunshine (n.s.); Fig. 3F] and decreased with increasing ambient temperature [ $P < 0.01$ , except at  $8.3 \mu\text{L min}^{-1}$  limited flow rate in partial sunshine (n.s.), ANOVA]. The mean costs of foraging (derived from the regression functions) were in the range of about  $0.01$ – $0.15 \text{ J mg}^{-1}$  body mass.

### Energy efficiency and net gain rate

The efficiency of foraging depended strongly on the reward rate, and on the ambient temperature and radiation ( $P < 0.0001$ , GLM; see Table S1). The efficiency of foraging increased with  $T_a$  in most experimental conditions ( $P < 0.01$ , ANOVA, Fig. 4A–C), except at  $8.3 \mu\text{L min}^{-1}$  flow rate in partial sunshine (Fig. 4C), and it was always higher in sunshine than in the shade ( $P < 0.0001$ , ANOVA). The mean efficiency derived from regressions increased from about

$8 \text{ J J}^{-1}$  at  $8.3 \mu\text{L min}^{-1}$  flow rate ( $T_a \sim 20^\circ\text{C}$ ) to more than  $150 \text{ J J}^{-1}$  at an unlimited sucrose flow ( $T_a > 30^\circ\text{C}$ ).

The net energy gain rate also depended strongly on the reward rate, the ambient temperature and radiation ( $P < 0.0001$ , GLM; Fig. 4D–F). The net energy gain rate increased with the ambient temperature from about 1 to more than  $4 \text{ J s}^{-1}$  at an unlimited flow rate ( $P < 0.0001$ , ANOVA; Fig. 4D–F), but remained at a constant low level at limited flow rates ( $0.8$  and  $0.5 \text{ J s}^{-1}$  at  $15$  and  $8.3 \mu\text{L min}^{-1}$  flow rate, respectively; Fig. 4E,F). It was significantly higher during foraging in the sun than in the shade at an unlimited flow ( $P < 0.0001$ , ANOVA; Fig. 4D).

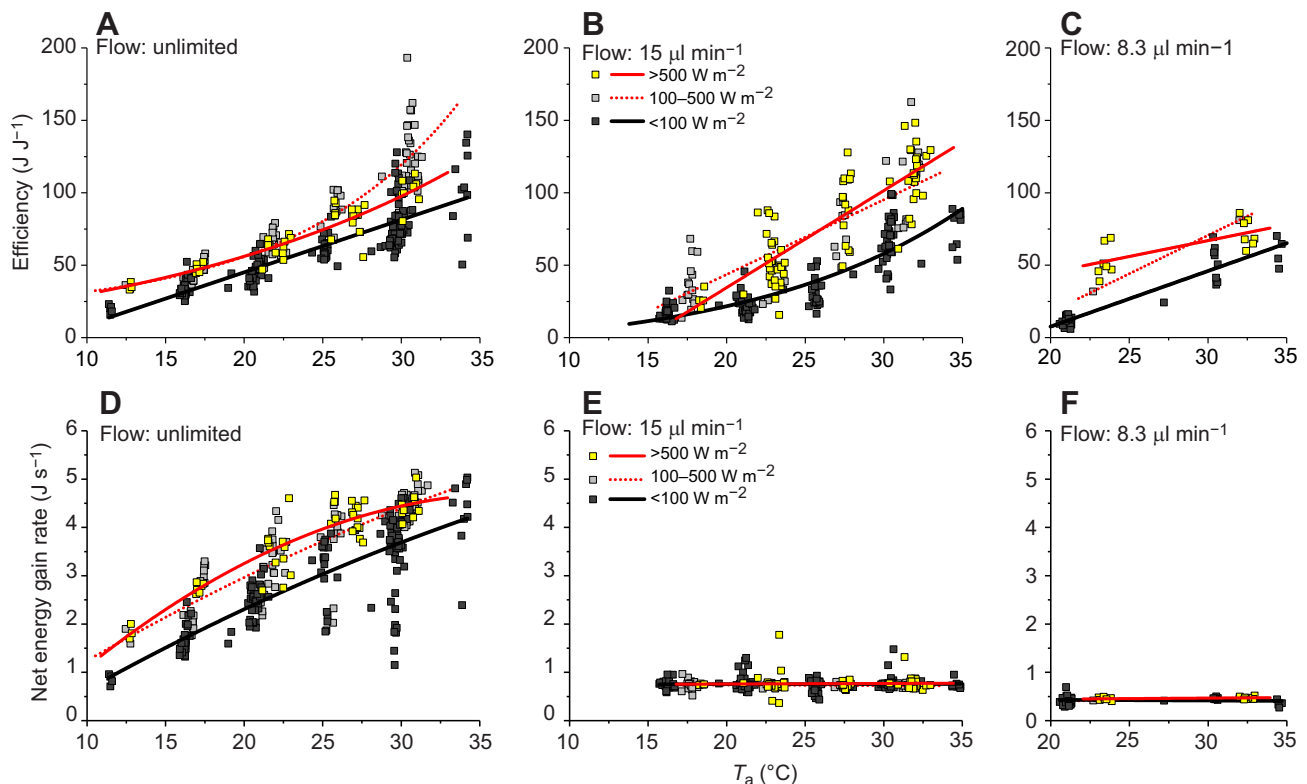
The comparison of energy efficiency with the net energy gain rate revealed a strong correlation at unlimited flow rate ( $P < 0.0001$ , ANOVA; Fig. 5A), but no dependence at limited flow rates (Fig. 5B,C).

The energy efficiency depended on the ingested volume of sucrose at an unlimited flow rate in partly sunshine and in the shade ( $P < 0.0001$ , ANOVA; Fig. S2A) but not in bright sunshine. At a limited flow rate, no correlation between efficiency and ingested sucrose volume was detectable (Fig. S2B,C). For fit curves and statistical details, see Tables S1–S3.

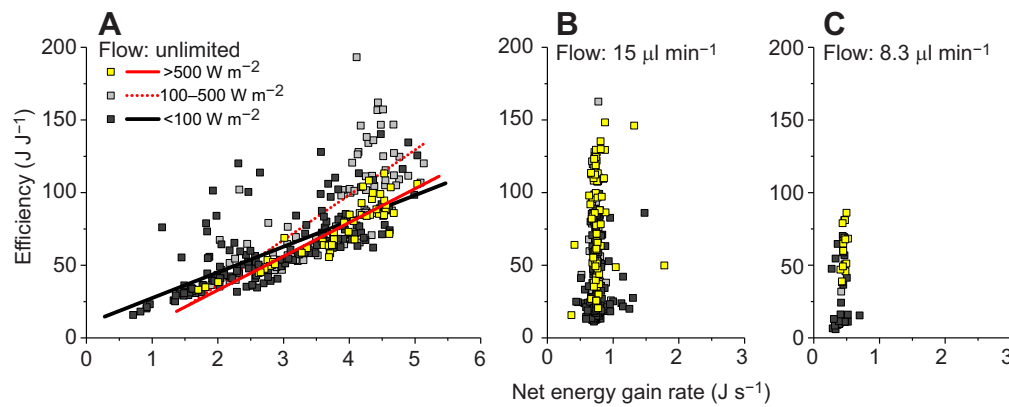
### DISCUSSION

#### Body temperature, costs and gains

Motivation is an important factor in foraging hymenopterans, modulating thermoregulatory behaviour and energetics (Stabentheiner et al., 1995; Moffatt, 2000, 2001; Kovac and Stabentheiner, 1999; Nieh et al., 2006; Sadler and Nieh, 2011; Stabentheiner and Kovac, 2014, 2016). Briefly, high-quality food



**Fig. 4. Energy efficiency and net energy gain rate of wasps foraging sucrose solution ( $0.5 \text{ mol l}^{-1}$ ) in the shade and in sunshine at different reward rates in relation to ambient air temperature near the wasps in the measurement chamber ( $T_a$ ).** Results in the shade are shown by black symbols, and in sunshine by yellow and grey symbols. (A–C) Energy efficiency [(gain–costs)/costs ( $\text{J J}^{-1}$ )]; (D–F) net energy gain rate [(gain–costs)/time ( $\text{J s}^{-1}$ )].  $N=295$  unlimited flow rate,  $N=255$  limited flow of  $15 \mu\text{L min}^{-1}$ ,  $N=48$  limited flow of  $8.3 \mu\text{L min}^{-1}$ . For constants of fit curves and statistic details see Tables S2 and S3.



**Fig. 5.** Energy efficiency of wasps foraging sucrose solution ( $0.5 \text{ mol l}^{-1}$ ) in the shade and in sunshine at different reward rates in relation to net energy gain rate. (A–C) Results in the shade are shown by black symbols, and in sunshine by yellow and grey symbols. Energy efficiency [(gain–costs)/costs ( $\text{J J}^{-1}$ )]; net energy gain rate [(gain–costs)/time ( $\text{J s}^{-1}$ )].  $N=295$  unlimited flow rate,  $N=255$  limited flow of  $15 \text{ µl min}^{-1}$ ,  $N=48$  limited flow of  $8.3 \text{ µl min}^{-1}$ . For constants of fit curves and statistic details, see Tables S2 and S3.

resources stimulate foragers to a high energetic investment. Our measurements confirm the relevance of the ‘motivation hypothesis’ in foraging wasps (Kovac and Stabentheiner, 1999). The wasps in the present study, which foraged for  $0.5 \text{ mol l}^{-1}$  sucrose at an unlimited flow, adjusted their thorax temperature to a level that was about  $1\text{--}2^\circ\text{C}$  lower than wasps foraging  $1.5 \text{ mol l}^{-1}$  sucrose under the same environmental conditions and measured with the same experimental setup (Kovac et al., 2015). This refers to both foraging in the shade as well as in sunshine (Fig. 2D–F). Under both environmental conditions, the thorax temperature increased with  $T_a$  in the shade, quite similar to as reported by Milani (1982) under laboratory conditions, but to a much lower extent than during foraging of water (Kovac et al., 2009) or during free flight (Heinrich, 1984; Coelho and Ross, 1996; Kovac and Stabentheiner, 2012).

It is noteworthy that the wasps did not save much of their own heat production at high  $T_a$  when offered an unlimited flow (Fig. 2A) but rather invested heat to actively increase their body temperature (Fig. 2D) to speed up drinking considerably (Fig. 3A). This finding is quite similar to the thermoregulatory behaviour of honeybees that forage on sucrose at an unlimited flow (Stabentheiner and Kovac, 2014, 2016). The fact that, under unlimited flow conditions, solar heat was not invested to save energy but to achieve an even higher body temperature (Fig. 2D) underlines the importance of a high body temperature for the fast uptake of liquid food. In contrast to this, in experiments with limited flow conditions, an increased body temperature could not speed up foraging during the stay at the artificial flower. Accordingly, the increase of the thorax temperature with  $T_a$  was quite moderate or non-existent in the shade (Fig. 2E,F), and the wasps were able to save much of their own heat production (Fig. 2B,C). Surprisingly, the wasps followed a mixed optimisation strategy by investing solar heat to do both: reduce their own energy investment and increase their body temperature (Fig. 2B,C,E,F).

A further surprising finding was that the metabolic rate, as a measure of the instantaneous costs (Fig. 2A–C), was, at an unlimited flow, higher in full sunshine ( $>500 \text{ W m}^{-2}$ ) than in the shade. Only at limited conditions did the wasps reduce their metabolic costs in sunshine and had mostly a lower metabolic rate than in the shade, but nevertheless maintained a high thorax temperature. We therefore conclude that a high thorax temperature seems to be the most important factor in foraging optimisation. It leads to elevated head temperatures via heat transfer by the circulatory system and this very likely improves suction speed. We suggest that in wasps, like in honeybees, the function of the musculature involved in suction

(‘suction pump’) is strongly dependent on body temperature (Kovac et al., 2010; Stabentheiner and Kovac, 2014, 2016).

An additional important parameter determining the costs of foraging is the duration of a foraging trip. Pflumm (1978) reported a decrease of the stop duration with increasing ambient temperature. These results resemble our findings (Fig. 3A). Quick foraging is accomplished by a high body temperature, which depends also on the ambient temperature (Fig. 2D–F). Fig. 3A shows that the trip duration was low at an unlimited source where the wasps could drink at full speed. However, duration and total costs of fluid intake was strongly dependent on environmental conditions and increased considerably at low temperatures. The wasps used sunny conditions to increase the suction speed by increasing body temperature. That way, they were able to reduce the total costs of foraging at our feeding station (Figs 2D and 3A,D).

Foraging under natural conditions is often characterised by limited reward from one source, e.g. conditions resembling those that wasps encounter during foraging for floral nectar or small droplets of honeydew. In any case, a low ambient temperature obviously forces a high turnover rate in order to compensate for the high heat loss. Higher ambient temperatures enable the wasps to considerably reduce both the instantaneous and the total costs (Figs 2B,C and 3E,F). Solar heat may be used quite differently, to reduce the costs (i.e. the own energy investment; Fig. 3D–F), but also to increase the thorax temperature (Fig. 2D–F). Since the increased body temperature was not used to increase load mass in sunshine (Fig. S1A–C), we suggest that it mainly prepares the wasps for a quicker and more secure take-off (Coelho, 1991).

#### Optimisation of foraging: rate or efficiency?

A basic question in foraging optimisation of social central place foragers like wasps and honeybees is whether they primarily maximise the intake rate or the energetic efficiency (Waddington and Holden, 1979; Schmid-Hempel and Schmid-Hempel, 1987; Balderama et al., 1992; Varjú and Núñez, 1993; Seeley, 1994; Ydenberg et al., 1994; Moffatt and Núñez, 1997; De Vries and Biesmeijer, 1998; Dornhaus et al., 2006; Higginson and Houston, 2015; Kovac et al., 2015; Stabentheiner and Kovac, 2014, 2016). In honeybees, it was recently shown that they do both: maximise the intake rate (minimise foraging time) whenever possible, but nevertheless minimise costs if necessary and of benefit, and this way they optimise the energetic efficiency (Stabentheiner and Kovac, 2014, 2016). If the food source is limiting the intake rate,

energetic optimisation becomes important for the foragers. Our direct measurement of both parameters in wasps not only provides empirical support for this finding, but shows that these regulatory principles are of general biological importance. Like honeybees, wasps are able to perform a flexible and gradual transition between maximisation of food intake rate and efficiency optimisation.

However, environmental factors have a much greater and more complex effect on optimisation of foraging than previously suggested. The energetic efficiency of foraging [defined as (gain–costs)/costs ( $\text{J J}^{-1}$ ); e.g. Pyke et al., 1977; Waddington and Holden, 1979; Schmid-Hempel et al., 1985; Seeley, 1986, 1994; Schmid-Hempel, 1987; Schmid-Hempel and Schmid-Hempel, 1987] is mainly determined by environmental parameters, and to some extent by the reward rate. Low ambient temperatures not only limit the achievable rate of food ingestion during unlimited flow (Fig. 4D) but also reduce efficiency regardless of foraging conditions (Fig. 4A–C). These observations are in good accordance with results of our previous study on wasps foraging from an unlimited food source of high quality ( $1.5 \text{ mol l}^{-1}$  sucrose; Kovac et al., 2015), and also with honeybees foraging under the same conditions as the wasps in the current study ( $0.5 \text{ mol l}^{-1}$  sucrose; Stabentheiner and Kovac, 2016). The highest foraging efficiency can be achieved at high ambient temperatures and high levels of radiative heat gain. Limited flow rates remarkably reduce efficiency during foraging in the shade, but to a lesser extent in sunshine (Fig. 4A–C). The present results confirm findings in honeybees that a clear correlation between energy efficiency and net gain rate only exists under unlimited flow conditions (Fig. 5). Like in honeybees, a limited sucrose flow promotes a switch from an investment-guided ('investing') strategy that promises increased returns to a more economising behaviour that allows for a considerable reduction of costs (Stabentheiner and Kovac, 2016).

### General principles of optimisation

The results of this study raise the question of whether the foraging strategies found in wasps represent main principles of optimisation in endothermic central-place foraging insects. Although wasps differ considerably from honeybees in their protein foraging behaviour, they show astonishing similarities with honeybees concerning the general regulatory principles at liquid carbohydrate sources. In the way that optimisation is accomplished, however, we found striking differences.

Both vespine wasps and bees are heterothermic insects that strongly rely on consistent endothermy during foraging to guarantee foraging success (Heinrich, 1984, 1993; Coelho and Ross, 1996; Kovac and Stabentheiner, 1999, 2011, 2012; Kovac et al., 2009, 2010, 2015; Schmaranzer, 2000; Stabentheiner et al., 1995; Stabentheiner and Kovac, 2014, 2016). However, they obviously differ in their optimal temperature range. The wasps' thorax temperature was, on average, several degrees lower. The bees' thoracic temperature often exceeds  $40^{\circ}\text{C}$ , but wasps try to avoid such high thorax temperatures. In our measurement chamber they were very restless when foraging at ambient temperatures higher than about  $30^{\circ}\text{C}$ . This different thermal preference results from a considerable difference in the thermal tolerance of bees and wasps. The short-term critical thermal maximum (activity  $\text{CT}_{\text{max}}$ ) of wasps is  $4.1^{\circ}\text{C}$  below that of honeybees (Käfer et al., 2012).

A comparison with honeybees (hereafter referring to Stabentheiner and Kovac, 2016) reveals that during foraging at low temperatures and low solar radiation ( $T_{\text{a}}=15^{\circ}\text{C}$ , shade), efficiency is similar in wasps and bees. However, when foraging at  $T_{\text{a}}=25^{\circ}\text{C}$  (shade), the wasps' energetic efficiency is about 19% higher at an unlimited flow and 35% higher at a limited flow. At  $T_{\text{a}}=30^{\circ}\text{C}$ , the

efficiency is higher in wasps only at a limited flow (45%) but similar to bees at unlimited flow. This higher efficiency is a result of the wasps' lower thorax temperature (see above) and therefore lower metabolic costs due to lower heat loss. Both foraging insects use the energy gain from solar radiation to enhance energetic efficiency.

The second parameter, the net gain rate ( $\text{J s}^{-1}$ ), remained constant at the predetermined limited flow levels as expected but increased almost linearly with ambient temperature at an unlimited flow rate both in wasps (Fig. 4D–F) and in bees. Solar heat gain enabled bees and wasps to significantly enhance their gain rate at unlimited flow ( $P<0.0001$ , ANOVA). For both insects, the duration of stay tended towards a minimum at high ambient temperatures ( $>27^{\circ}\text{C}$ ; Fig. 3A), which shows that the fluid ingestion rate was maximised. The net energy gain rate, however, continued to rise (Fig. 4D). This was possible because they reduced their energetic effort (instantaneous costs; Fig. 2A), which in turn increased energetic efficiency (Fig. 4A). Relating the efficiency with the gain rate revealed that, in both species, the efficiency correlates with the gain rate only at unlimited flow rate but not at a limited flow rate (Fig. 5A–C; Stabentheiner and Kovac, 2014, 2016). This leads to the conclusion that experiments carried out with unlimited flow rates cannot uncover the whole truth about energetic optimisation in foraging social insects (Moffatt and Núñez, 1997; Moffatt, 2000, 2001; Stabentheiner and Kovac, 2014, 2016).

Our investigations on wasps show that the regulatory principles found in honeybees (Stabentheiner and Kovac, 2014, 2016) are of general validity for the individual optimisation of foraging. How does this fit into the optimisation strategy of a whole colony? Ydenberg et al. (1994) pointed out that maximising the individual intake rate and minimising costs are the main parameters to optimise the total net daily (energy) gain of a colony. Although wasps do not have a highly specialised recruiting system like honeybees, the income of much food in short intervals to the nest is suggested to stimulate other wasps of the colony to perform foraging flights (e.g. Overmyer and Jeanne, 1998; Jandt and Jeanne, 2005; Schueller et al., 2010; Schueller and Jeanne, 2012; Taylor et al., 2010; Taylor et al., 2012a,b; Taylor and Jeanne, 2018; Wilson-Rankin, 2014; Santoro et al., 2015; Lozada et al., 2016).

Our investigations reveal how energetic optimisation in foraging endothermic insects like vespine wasps works. It is a combination of fine-tuned behavioural and physiological responses to varying ecological conditions. The main rules are simple: to fasten intake rate whenever possible and to save energy if necessary.

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### Competing interests

The authors declare no competing or financial interests.

### Author contributions

Conceptualization: H.K., A.S.; Methodology: H.K., A.S.; Investigation: H.K., A.S., R.B.; Resources: H.K., A.S.; Data curation: H.K., A.S., R.B.; Writing - original draft: H.K., A.S., R.B.; Supervision: A.S.; Project administration: H.K.; Funding acquisition: H.K.

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### Supplementary information

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