Heat reward for insect pollinators

Scarab beetles save on energy by making themselves at home inside a warm flower.

In neotropical forests, adults of many large scarab beetle species spend most of their time inside the floral chambers of heat-producing flowers, where they feed and mate throughout the night and rest during the following day, before briefly flying to another flower. Here we measure floral temperatures in *Philodendron solimoesense* (Araceae) in French Guiana and the respiration rates of *Cyclocephala colasi* beetles at floral and ambient temperatures, and show that the the beetles' extra energy requirements for activity are 2.0–4.8 times greater outside the flower than inside it. This finding indicates that heat produced by the flower constitutes an important energy reward to pollinators, allowing them to feed and mate at a fraction of the energy cost that would be required outside the flower.

Self-heating flowers occur in several diverse families of primitive flowering plants in which the female parts are pollinated first, after which pollen is shed[1]. Nearly all of these species are pollinated by insects, particularly beetles, which voluntarily remain in the flowers for about 24 hours between the female and male phases[2,3].

Thermogenesis by these blooms is likely to increase the dispersal of insect-attracting scents[4], but this does not explain why heating often continues throughout the period of insect residence, rather than merely during the attraction period[5]; why floral temperature is physiologically maintained in some species at the activity temperature of the insect[6]; and

Figure 1 Warm welcome: the thermogenic flower of *Philodendron solimoesense*, which is found in the neotropical forests of French Guiana, offers a heated chamber as a reward to insect pollinators such as the scarab beetle *Cyclocephala colasi*. The white spadix protrudes from an open scathe; the floral chamber is hidden at the base.

why temperature regulation occurs in the floral chamber and not in the thermogenic, scent-producing organs of some species[7].

The answers may lie in the fact that many insects require a raised body temperature for activity, which they achieve by metabolically producing their own heat (endothermy)[8]. Partly because insects are small, the required increase in metabolic rate can be enormous: for example, it increases 16-fold in terrestrially active beetles[9]. A warming floral environment may therefore be a significant energy reward, enabling the insect to reduce the energy cost of its activity.

We measured the effect of floral temperature on energy expenditure by *C. colasi* Endrödi, which is the principal pollinator of *P. solimoesense* A. C. Smith[10,11] (Fig. 1). Inflorescences showed a rapid increase in spadix temperature after dark, which was associated with strong scent production and the arrival of beetles (Fig. 2a). During the night, when the beetles were still active, the mean floral-chamber temperature was 3.4–5.0 °C warmer than the ambient temperature.

Beetles resting in the respirometer had a low metabolic rate, which increased slightly with rising temperature, whereas the metabolic rate of active beetles was greater and increased with decreasing temperature (Fig. 2b). Active beetles occasionally showed an explosive increase (150-fold) in respiration, indicating an endothermic bout. Such bursts occurred at all temperatures, but were less frequent, shorter and less intense at temperatures above 27 °C.

To estimate more accurately the difference in energy expenditure during periods of rest and of activity, we distributed test temperatures evenly and averaged the metabolic rates over uniform 40-min periods which included shorter bouts of endothermy. Using the temperature of the floral chamber and of the ambient air (Fig. 2a), and applying the energetics equations (Fig. 2b) for active and resting beetles, we calculated the difference in metabolic rate between rest and activity at the two temperatures throughout the night.

The results are expressed as an 'energy-saving factor', which is calculated as the ratio of excess energy required for activity at ambient temperature to that required at the floral temperature (Fig. 2a). This ratio is 4.8 in the evening when the beetles arrive, and decreases to 2.0 at dawn.

Even in the warm lowlands of French Guiana, beetles gain a large energy reward when the floral chamber is only marginally warmer than the air (28 °C and 24 °C, respectively; Fig. 2a). The reward must be even greater for scarab beetles that remain active inside *Philodendron* in the Brazilian highlands, where the air temperature drops to 6 °C (ref. 12). Thermogenesis by flowers pollinated by large scarab beetles is widespread in tropical forests[3], with an estimated 900 plant species in at least six families (Cyclan-
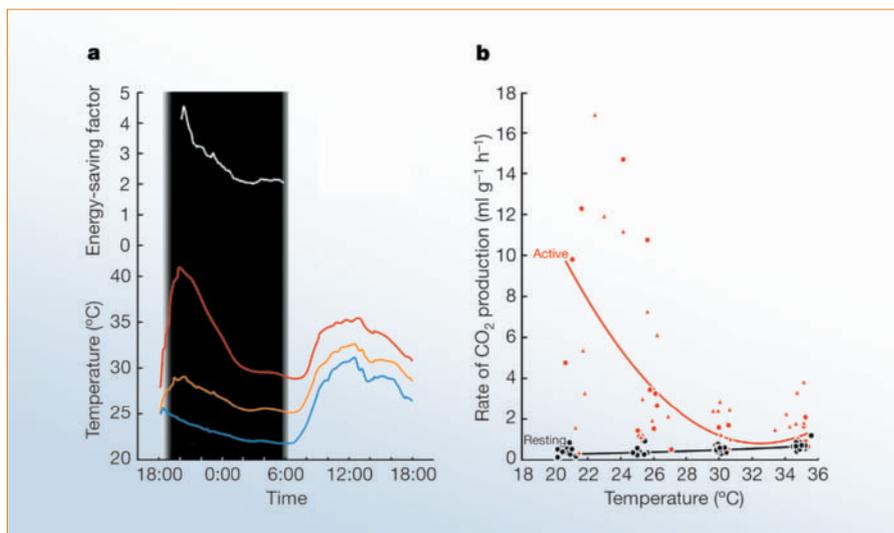
Figure 2 Energetics of *Cyclocephala colasi* beetles in relation to the temperature of *Philodendron solimoesense* flowers. **a,** Temperatures of spadix (red line), floral chamber (orange line) and ambient air (blue line) for 20 inflorescences, measured over 24 h with loggers. The energy-saving factor (white line, top) is calculated as the ratio of the extra energy required for activity at ambient temperature to that required at the temperature of the floral chamber. **b,** Energetics of beetle metabolism, measured as the rate of CO_2 production (V_{CO_2}) by using standard techniques. Results are shown from single beetles (circles) and from groups of three beetles (triangles). The corresponding equations are: resting state (black), $V_{CO_2} = 0.0769e^{0.06167}$ ($r^2 = 0.42$); active state (red), $V_{CO_2} = 0.0636T^2 - 4.14T + 68.1$ ($r^2 = 0.40$).

thaceae, Annonaceae, Araceae, Arecaceae, Magnoliaceae and Nymphaeaceae) being visited by more than 220 species of *Cyclocephala* alone[13]. Heat reward may have been even more important during the early evolution of the flowering plants.

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Figure 1 Keeping an eye on the ball. **a,** Angles of gaze from fielder to ball: α is the angle of gaze elevation; δ is the angle of horizontal gaze rotation relative to starting direction. **b,** Movement of a fielder to adjust α. As indicated by the arrow, a fielder at position F_3 must move to a position on the red arc bounding the shaded region in the ensuing time interval to ensure that $d\alpha/dt$ decreases at a particular rate. **c,** Aerial view of ball and fielder; the red line shows the locus of points to which the fielder at position F_3 must move in the ensuing time interval to ensure that $d\delta/dt$ remains constant. **d,** Paths of real (light triangles) and simulated (dark triangles) fielders for ten catches. Initially, the simulated fielder was moved to the same positions as the real fielder; after the point marked by the arrow, it moved under the constraints for α and δ described in the text.

Psychophysics

How fielders arrive in time to catch the ball

Tracking an object moving in three dimensions, whether as an insect pursuing a mate on the wing[1] or as a batsman aiming to hit an approaching ball[2], provides the spatial and temporal information needed to intercept it. Here we show how fielders use such tracking signals to arrive at the right place in time to catch a ball — they run so that their angle of gaze elevation to the ball increases at a decreasing rate while their horizontal gaze angle to the ball increases at a constant rate (unless the distance to be run is small). Allowing the horizontal angle to increase minimizes the acceleration that the fielder must achieve to reach the interception point at the same time as the ball[3].

Figure 1a shows two sources of information that the fielder receives from tracking the ball: the angle of elevation of gaze (α) and the horizontal angle through which the gaze system has rotated relative to the initial direction from fielder to ball (δ). Fielders run so that α increases at a decreasing rate[4] — in principle, this guarantees interception. The locus of points from which α has increased by the appropriate amount in the ensuing time interval lie on a circle centred on the vertical projection of the ball to the ground. As the

ball falls, the circles decrease in diameter and the fielder, moving through successive circles, homes in on the interception point (Fig. 1b).

However, running so that α increases at a decreasing rate would not in itself be an effective strategy. Early in the ball's flight, there is little constraint on the direction in which the fielder must run, as the circle of points that satisfies the α constraint is large. If the fielder does not initially move towards the interception point, he may not be able to run fast enough to implement the strategy as the flight nears its end. Efficient interception requires the fielder to select a point in the circle that is towards the interception point[5].

We have found that fielders usually run so that δ increases at a constant rate[3]. This requires them to move at successive time intervals to a point from which δ would have an appropriate value, given the position of the ball at the end of the time interval. These points lie on a straight line (Fig. 1c). To satisfy both constraints, the fielder must move to the point at which the line and circle intersect, thereby ensuring that the fielder is moving towards the interception point throughout the ball's flight.

We simulated a fielder moving under these constraints to catch balls on the same trajectories as those caught by real fielders. The simulated fielder was moved to the same positions as the real fielder for the first 600 ms to give the same initial visual experience

as the fielder, and then moved so that α increased at the average declining rate and δ increased at the average rate experienced by the real fielder up to that point. The similarity between the real and simulated fielders' running paths can be seen in Fig. 1d.

According to our theory, fielders do not explicitly select their direction or speed when running. They move in way that satisfies the constraints for the changes in α and δ. This view of the fielder's strategy as based on repeated local constraint satisfaction, rather than on a calculation of where the ball will ultimately fall, is consistent with the subjective sensation of running to catch a ball. You do not know exactly where the ball will land, but you do know whether or not you will be able to intercept it. This presumably reflects the knowledge that you have been able to satisfy the constraints (or not).

The origin of the strategy may be that a child watching objects that hit him or her will experience α increasing at a decreasing rate, whereas watching balls that pass by will produce a declining α and an accelerating δ (ref. 3). When the child tries to catch the ball, he or she will run in a way that reproduces previous experiences with objects that hit and avoids those from objects that missed.

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