Polarized light as a butterfly mating signal

This optical feature of some iridescent wings catches a suitor's eye in the deep forest.

Iridescent butterfly scales are visually stunning structures that reflect highly saturated colour. They also create an array of non-chromatic optical phenomena, such as polarization, polarization mixing and highly directional flashes[1,2], but the ecological purpose of these effects is unclear[3,4]. Here we show that polarized light is used in mate recognition by *Heliconius* butterflies, a genus that is known to rely on visual cues in sexual selection and speciation[5]. This terrestrial example of exploitation of polarized light may have adaptive value in dense forest, where illumination varies greatly in spectrum and intensity.

Coloured light from thin-film iridescence, as in the iridescent members of *Heliconius*, is often polarized[1] — for example, the blue iridescence of *H. cydno* is 90% polarized at certain angles of reflection (Fig. 1). To determine whether this polarization is involved in mate recognition, we carried out mate-choice experiments[5] to compare responses in *H. cydno chioneus* with those of the closely related but non-iridescent *H. melpomene malleti*[6].

We displayed female butterfly wings, which were conspecific to the males being tested, behind one of two filters: optically anisotropic, colourless, depolarizing mylar[7] (Grafix Dura-Lar 0.003, Graphic Arts Systems) or a circular polarizing screen (3M Optical Systems Division). Control filters, chosen for their similar transmission of ultraviolet and visible light, were polarization-neutral, isotropic colourless plastic and grey-tinted window glass, respectively. The depolarizing and circular polarizing filters remove polarization signals from wings while leaving colour signals intact; the control filters leave both polarization and colour signals unaffected.

Figure 1 Polarized iridescent patterning of the butterfly *Heliconius cydno* (top) compared with *H. melpomene malleti* (bottom), whose wings do not show polarized iridescence. Photographs of left wings are unmodified; images of right wings were generated by taking two photographs through a polarizing filter that was rotated by 90° between exposures, and then producing the difference of the two images in Photoshop (Adobe). *H. cydno* shows a pattern of polarized and depolarized regions, whereas *H. melpomene malleti* shows no polarization pattern. Wing spans, 9 cm.

In an outdoor insectary containing at least five conspecific males, we displayed mounted female wings beneath filters, and moved them to simulate flight. The number of male flights through a volume of radius 30 cm above the window was counted by eye over a 10-min period for the depolarized and control conditions, with the order of presentation being randomized; one pair of 10-min treatments represents a single trial. Male *H. cydno* approached the female wings significantly less often when the wings were displayed behind the depolarizing filters rather than the non-depolarizing control filters, but there was no significant difference in the response to the non-iridescent *H. melpomene* for either condition (Fig. 2).

To our knowledge, this is the first example of polarized light being used for mate recognition, or indeed for detection of any object, in a terrestrial environment. It may be particularly important in the visually complicated forest inhabited by *H. cydno* and by other iridescent *Heliconius* species, such as *H. sapho*[8]. Whereas the spectral radiance of pigmentary colour is strongly affected by the patchy light distribution in the forest, a polarized signal from iridescent wings is easily recognizable against the relatively unpolarized background[9,10].

The use of iridescence for intraspecific recognition may correlate with the radiation of *Heliconius* into deep-forest habitats. The occurrence of several species pairs with different iridescent properties, such as *H. melpomene* and *H. cydno*, suggests that the use of polarization has contributed to adaptive radiation and speciation.

Butterflies of several species are physiologically sensitive to polarization[11,12]. Unlike the eyes of other insects, such as bees, which have polarization-sensitive ommatidia only in their dorsal rims, butterflies' eyes are sensitive to polarization in all of their ommatidia[11]. Butterflies of the genus *Papilio* can also discriminate between stimuli that differ only in their angle of polarization[12]. Investigation of the effects on butterfly behaviour of the optical properties and visual ecology of structural colour should help to explain patterns of ecological diversity in different butterfly groups.

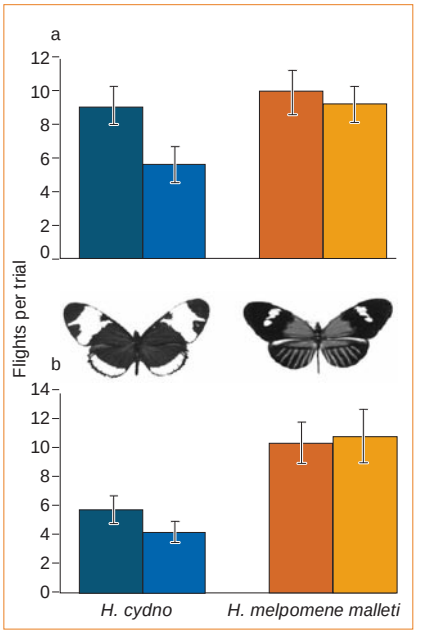

Figure 2 Response of male *Heliconius cydno* and *H. melpomene malleti* butterflies to polarized and depolarized views of female butterfly wings. **a, b,** Mean number of male approaches per 10-min trial period to a polarized (left bars) and depolarized (right bars) female stimulus. In **a**, female wings were presented through a glass window made up of either polarization-neutral grey glass (control) or a circular polarizing screen; in **b**, a plastic window consisting of polarization-neutral plastic film (control) or a mylar depolarizer was used. Error bars show standard error. For iridescent *H. cydno*, $P = 0.01$ is the combined probability value of two independent experiments: $P = 0.05$, $n = 17$ for plastic treatment; $P = 0.02$, $n = 8$ for glass treatment. For the non-iridescent *H. melpomene malleti* control group, $P = 0.88$ is the combined probability value of two independent experiments: $P = 0.83$, $n = 9$ for plastic treatement; $P = 0.66$, $n = 10$ for glass treatment. P values in a single experiment compare the total number of male flights to filters by Yates-corrected χ^2 test. The smaller response by *H. cydno* males in **b** is due to the time of day at which the experiments were done.

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Social insects

Cuticular hydrocarbons inform task decisions

Social insect colonies are organized without central control, and must not only accomplish many tasks, such as foraging and nest construction, but must also respond to changing conditions by adjusting the number of workers performing each task[1,2]. Here we use chemically treated, artificial ants to show that cuticular hydrocarbons, which differ according to task, are used by workers of the red harvester ant (*Pogonomyrmex barbatus*) to recognize the tasks of the ants that they encounter. Encounters with other ants thus inform a worker's decision on whether to perform a particular task.

A mature colony of the red harvester ant, a seed-eating desert species, consists of a single queen and 10,000–12,000 workers. We focused on two task groups: foragers, who collect food; and patrollers, who scout the foraging area each morning. If patrollers do not return safely, foragers will not leave the nest to search for seeds[3]. Nest-maintenance workers are active at the same time as patrollers and do not stimulate foraging[4]. A social-insect worker can become active or switch task as conditions are altered — depending, for example, on the number of other workers who are currently engaged in a particular task[5–7].

Communication in social insects occurs mostly by chemical and tactile means[8], with cuticular hydrocarbons often acting as recognition cues[9]. A harvester ant's task decisions depend on its interaction, by antennal contact, with ants at the nest entrance[10] — ants in different task groups differ in their cuticular hydrocarbon profiles[11]. Foragers, for example, spend more time outside the nest and so are exposed to warmer, drier conditions than nest-maintenance workers, who mostly stay inside. This causes the foragers to have higher ratios of *n*-alkanes to *n*-alkenes and branched alkanes in their cuticular hydrocarbon profiles[12].

For field experiments, we used nine mature colonies at a long-term study site near Rodeo, New Mexico, in the United States[13]. We first inhibited foraging by removing returning patrollers. After 30 min of inactivity, we mimicked the flow of returning patrollers by dropping glass beads (3 mm in diameter) that had been coated with one ant-equivalent of extract into the nest at a rate of one every 10 seconds. The coating on the beads consisted of patroller cuticular lipids, patroller hydrocarbons, nest-maintenance hydrocarbons (which acted as a control for task specificity), or plain solvent (blank control). As a positive control for forager activity, we used live patrollers that were captured and then immediately returned to the nest. Cuticular lipids were extracted in 100% pentane for 10 min[9,11] and hydrocarbons were purified from cuticular lipids by using column chromatography[9].

The number of beads added to a nest was roughly equal to the number of patrollers collected. We then measured foraging activity by counting the number of active foragers outside the nest within 1 m of the entrance, every 10 min for 60 min. All colonies received each treatment in a random order; for each colony, we carried out one trial per day for five consecutive days. We normalized for variation among colonies in absolute forager number by dividing each mean number foraging per trial by the largest number of foragers ever observed for that colony.

Task-specific cuticular hydrocarbons from patrollers were sufficient to rescue foraging activity (Fig. 1). However, the behaviour is not a simple response to patroller extract alone. Our results, including preliminary data (not shown), indicate that in this patroller-mimic assay, all of the following are necessary to stimulate foraging activity: a one-ant equivalent concentration of hydrocarbon extract, location just inside the nest entrance, sequential presentation, and the time of day at which the colony is ready to begin foraging.

A brief encounter with a nestmate influences an ant's task decision because the encounter identifies the task of the other worker, cued by subtle features of other ants' hydrocarbon profiles. Encounters between ants thus provide information used for task allocation. These encounters in the aggregate produce a dynamic network that regulates the colony's behaviour.

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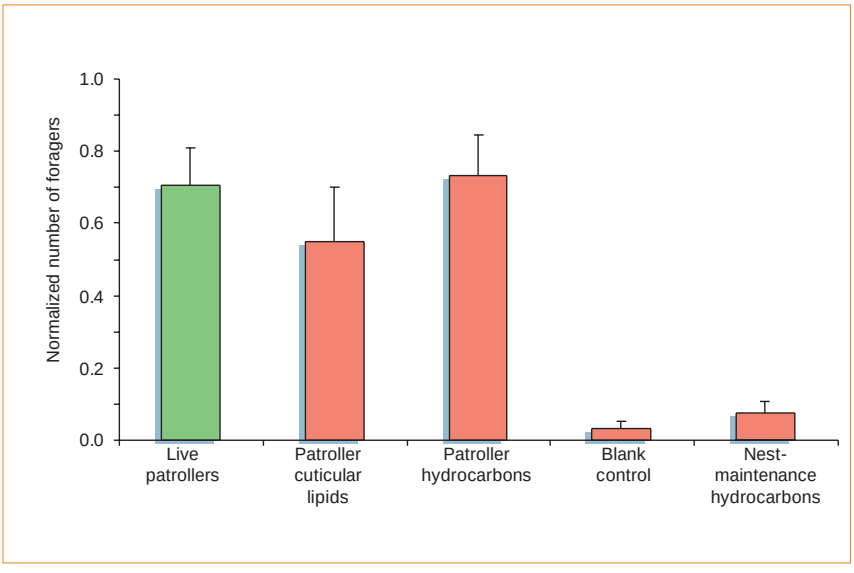

Figure 1 Task-specific cuticular hydrocarbons from patrollers are sufficient to rescue foraging activity in red harvester ants. The number of foraging ants (normalized; see text) leaving the nest is shown in response to live patrollers returning to the nest (green bars) or to different hydrocarbon-coated glass-bead ant mimics (red bars). Significantly more foragers emerged in response to live patrollers and to ant mimics treated with patroller cuticular lipids or patroller hydrocarbons than to mimics coated with blank control or nest-maintenance-worker hydrocarbons (repeated-measures analysis of variance: $F_{4,28} = 11.88$, $P < 0.0001$; $n = 9$). There was no significant difference in foraging-ant numbers among the returned live patrollers, patroller cuticular lipid and patroller hydrocarbon treatments, or between the blank and nest-maintenance hydrocarbon treatments (Tukey's post-hoc analysis). Data were transformed with an angular transformation (square-root of arcsine) for analysis.

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