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Research article

The nest entrance signal of the Amazonian bees *Partamona pearsoni* – a case where insects design their own flight targets

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Abstract – *A very peculiar structure, made of white sand and resins, marks the nest entrance of the Amazonian stingless bees* Partamona pearsoni. *We present evidence and conclusions drawn from data on other species of bees to test the hypothesis that this signal is designed so as to maximize its adaptive value for detecting and identifying the nest entrance. Color vision is used to identify the location of the nest entrances in all bee species so far tested. Thus, to evaluate the bee-subjective color contrast which the nest entrance makes with its black backdrop, we recorded intracellularly from receptors of* Partamona *eyes, and measured the spectral reflectance of the nest entrance and its background.* Partamona *possess UV-, blue, and green receptors very similar to those of other species of Apoidea. Using the measured spectral sensitivity functions as inputs to color space, we show that the nest entrance provides no color contrast to its background. Intensity contrast is strong, but such contrasts are often given relatively little attention by bees in the context of identification of targets that mark either food sources or nest entrances. However, signals which differ from their background in intensity, but not in color, may become valuable if they address an entirely different neuronal channel, that of pattern perception. When color information is not available, bees can be easily trained to a target whose boundary is dissected, rather than having a closed outline (e.g. a circular shape). The greater the degree of dissectedness (length of outline of target divided by its area) the faster bees will learn the target. Possibly for this reason, the relative contour length of the nest entrance margin is increased many times over relative to a closed shape of equal area. However, we point out potential complications with this interpretation, and outline where behavioral tests are needed to resolve these difficulties.*

Keywords: *Partamona*, color vision, pattern vision, signal evolution

Introduction

The question of how biological signals and receivers influence the evolution of each other is currently subject of much debate (Chittka et al., 1993, Guilford, 1995). Selective pressures commonly accepted for shaping the evolution of biological signals are their detectability, discriminability and memorability (Endler, 1992, Guilford and Dawkins, 1993, Chittka et al., 1994), and, possibly, innate biases of the receivers (Basolo, 1990, Shaw, 1995, Giurfa et al.,

1995). To understand how well a signal is suited for these purposes, we must know the properties of the receiver systems to which the signals are directed. In the usual case, scientists have to extract properties of the visual system of an animal by designing artificial signals. The animal is then tested for innate preference towards such signals; alternatively one tests how well it can distinguish these signals from others, or how fast it can detect or memorize them (e.g. Chittka et al., 1992, Giurfa et al., 1995a, Lehrer et al., 1995). However, some animals design signals all of their own.

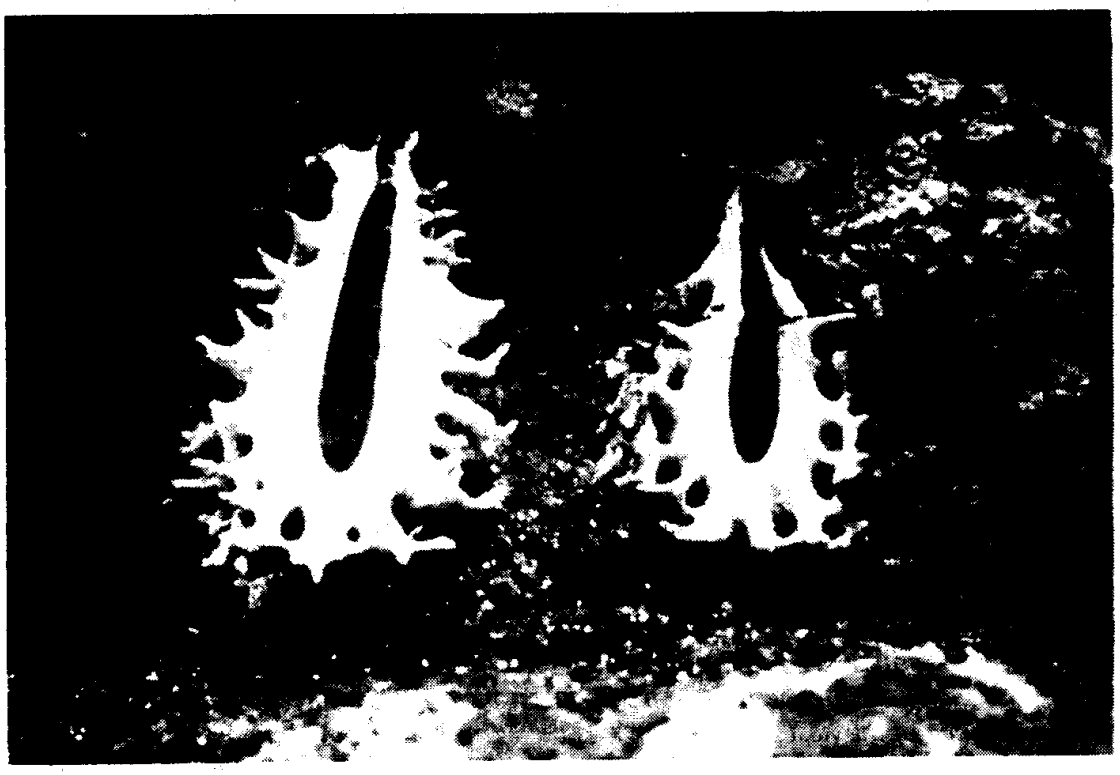

Figure 1. *The entrances of two nests of the Brazilian stingless bee* Partamona pearsoni, *from Ipixuna river, Amazonia, Brazil, 63°25' W, 6°5' S. From the bottom to the top, the larger entrance construction measures about 10 cm. The inside of the entrance is concave and assumes the shape of a funnel towards its lower end. The actual entrance hole measures 1 cm in diameter; it is hidden away under the lower margin of the entrance structure. From there, a vertical channel connects the nest entrance with the nest.*

The Brazilian stingless bees of the *Partamona pearsoni* (Meliponinae, Apidae, Hymenoptera) group live in arboreous termite nests, and often several dozens of nests, with one entrance each and very close to one another, can be found in a single termite nest (Camargo, 1980, and unpublished observations). These Amazonian bees mark their nest entrances with a bright signals, as opposed to most other bees whose nest entrances are cryptic (Camargo, 1970, 1980; Michener, 1974; Roubik, 1989). A very peculiar structure, made of white sand and resins, marks the nest entrance (Fig. 1). The bees approach this target in a straight line, in very rapid flight from > 2 m distance, and virtually collide with the concave inside of the entrance structure. The entrance has the shape of a funnel downwards, and the homecoming bees slide into a vestibule that is connected with the nest.

This visual signal is extraordinary because it is not part of the animal's body structure, but instead is *built* on a social level by the workers of a colony. This implies a considerably higher degree of plasticity than in other biological signals; the nest entrance's structure can be modified continuously to maximize its adaptive value in addressing the visual system of its receivers. The choice of signal material (and thus its color) as well as the shape are controlled by behavior rather than directly by the genes, as in many other biological signals such as flowers. Moreover,

even if the behavioral patterns to construct this signal are genetically pre-programmed, they should be less subject to evolutionary constraint and inertia than "conventional" signals. For these reasons, we expect the nest entrance signal of *Partamona* to be well matched to its visual system and/or its innate preferences.

Ultimately, this signal probably serves the following purposes: 1) to minimize time losses usually involved when homing bees slow down their flight to localize their nest entrance and land on it; 2) more importantly, to escape predators for whom a nest entrance with slowly flying (and, close to the entrance: walking) bees is a rich and reliable food source; 3) to quickly and reliably identify the correct nest entrance in a large array of different colonies. But how exactly does the signal serve these purposes? Is it a color signal that contrasts against its background in a way which is invisible to a human observer, but perceptible for bees? Or is it designed so as to address the system of pattern perception in bees in a most efficient way? If yes, are the presented patterns suitable for localization and identification by a bee's visual system?

Methods and Results

To see if the *Partamona* color receptors are comparable to those of other bee species whose vision has been extensively studied, we measured the spectral sensitivity functions of the photoreceptors in the eyes *Partamona helleri*, since *P. pearsoni* was not available in São Paulo, where we performed our measurements. Intracellular recordings from single photoreceptor cells were made by means of the peak-to-peak voltage constant response method. This method is a modification of the DC constant response method, which has been described elsewhere in much detail (Menzel et al., 1986; Peitsch et al., 1992). Thus we only describe the particulars of how this technique is modified here. The novel method maintains constant the amplitude of the response to a pulsing stimulus, obtained by a shutter, so that it measures the spectral sensitivity of the phasic (rather than the tonic) component of the response. In practice, it also has the advantage of being immune to the effects of slow baseline changes, which hamper the DC method. (de Souza et al., 1993). The spectral sensitivity curves of the UV-, blue- and green receptors are shown in Figure 2.

As all other long tongued bees so far tested (Peitsch et al., 1992), *Partamona* possesses 3 spectral photoreceptor types with maximum sensitivity around 340, 440 and 520 nm. Since the color receptors in these bees are conservative (Chittka, 1996), we presume that *P. pearsoni* receptors can be adequately approximated by *P. helleri* spectral sensitivity functions. The curve shapes are typical in that halfband width increases from shorter to longer wavelengths, curves are skewed towards higher energies, and show a distinct β-peak in the UV for $\lambda max > 450$ nm.

The nest material of *P. pearsoni* was collected on the banks of Ipixuna river, a tributary of the Purus, in Amazonia, Brazil (63°25'W, 6°5'S) by Camargo, on 01-17-1986. *P. pearsoni* is possibly a polytypical species and its taxonomic structure and biology are being studied by S. R. M. Pedro and Camargo. The form described in this text is endemic to the Tefe region. To assess the bee-relevant visual properties of the nest entrance, we took spectral measurements of the background (the termite nest) and the signal material (for methods for measurement, and conversion into photoreceptor excitations and color loci in a bee color space see Chittka et al., 1994). The funnel reflects light over a broad range of the spectrum, including UV (Fig. 3a). The white material generates strong, and approximately equal, signals in the bees' UV, blue-, and green receptors. The background yields equally low excitations in all 3 color receptor types (Fig. 3b). The white and UV-reflecting funnel and the black material of the termite nest are thus both uncolored, and have practically identical color loci in the bee color space (Fig. 3c). Intensity is defined here as the sum of all three photoreceptor excitations (Chittka et al., 1992). Intensity contrast between target and background is 60% (100% contrast would be no excitation in all 3 receptors vs. maximal excitation in all receptors). Color contrast is negligible. The hexagon distance between background and signal is 0.01, where 2 is the maximum theoretical distance between two opposite corners of the hexagon, and two stimuli separated by a distance

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of 0.1 can be distinguished with 70% accuracy. This approximation holds for several species of trichromatic Hymenoptera (Chittka et al., 1992, 1993).

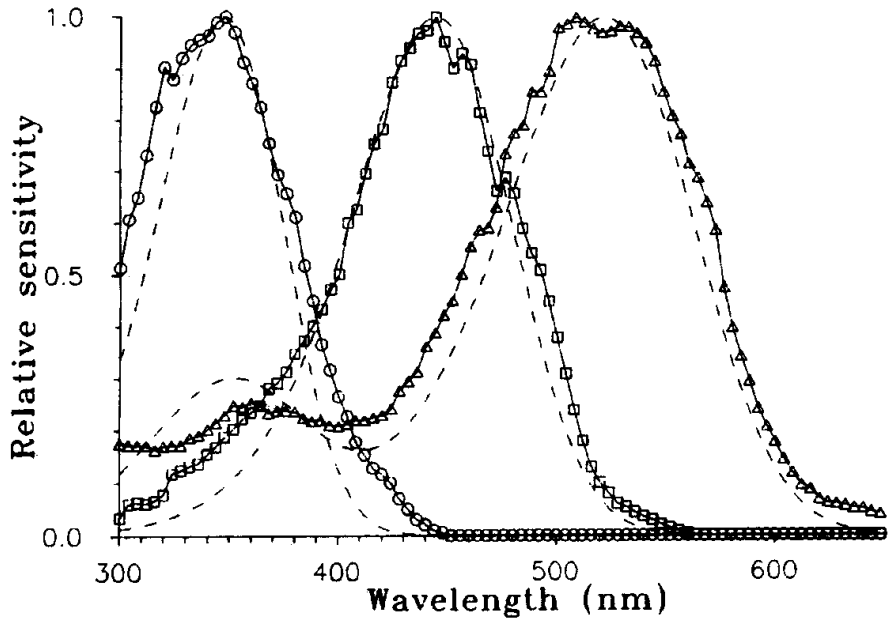


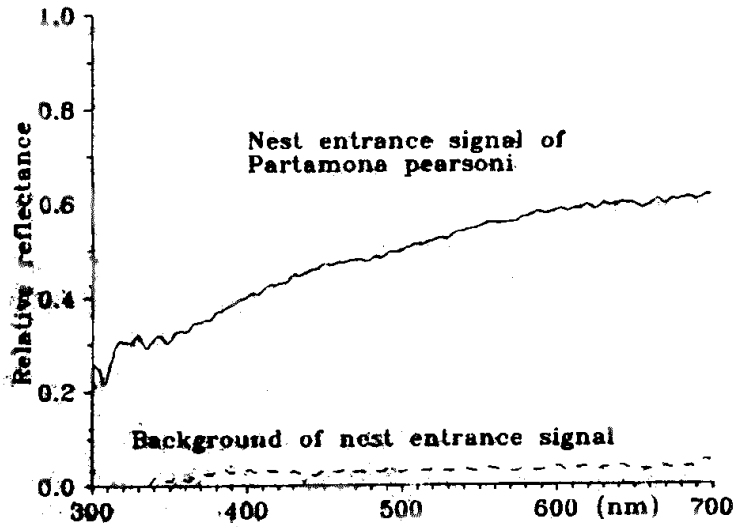
Figure 2. *The spectral sensitivity functions of* Partamona *UV-, blue, and green receptors. Each curve is averaged from intracellular recordings from several cells (UV: 39 recordings; blue: 25; green: 47), and subsequently normalized to a maximum of unity. The three curves can be best fitted by rhodopsin template functions (dashed lines) with λmax = 347, 444 and 521 nm, calculated according to Stavenga et al. (1993). For this purpose, templates were calculated for each wavelength value from 330 to 550 nm in 1 nm steps. We determined the wavelength positions of templates for which the sum of all squared residues was minimal when compared with the measured curves (least square fit method).*

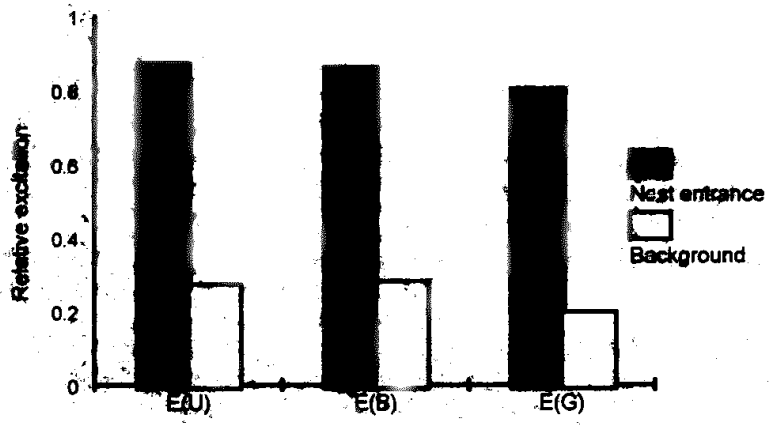
Since the relative contour length (length of contour divided by the area of the signal) is an important parameter in bee pattern vision (see discussion) we measured the outline and area of the nest entrance signal (with Bioscan Optimas 3.01). The relative contour length is 2.5 in the larger (3 in the smaller) entrance structure in Figure 1. A shape with an undisrupted boundary covering the entire entrance would have a relative contour length of 0.5 in the larger (1 in the smaller) signal of Figure 1. Therefore, the relative contour length is greatly enlarged relative to regular ellipses.

Discussion

1) Is the nest entrance construction a color signal? If not, what is the problem?

The wavelength positions of *Partamona* color receptors lie well within the scatter of the UV-, blue- and green receptors of other bee species (Peitsch et al., 1992; Chittka, 1996); thus we presume that color vision does not differ substantially from that of other bee species. Color discrimination of bees at the nest entrance seems to follow essentially the same rules as at a food source (Chittka et al., 1992); the color space is two-dimensional and lacks a brightness dimension (Daumer, 1956, Helversen, 1972). This has been shown to be valid for several species of trichromatic wasps and bees, including Meliponines (Chittka et al., 1992). This implies that objects whose reflectance differs merely in intensity, but not in chromaticity, are difficult to distinguish for bees.





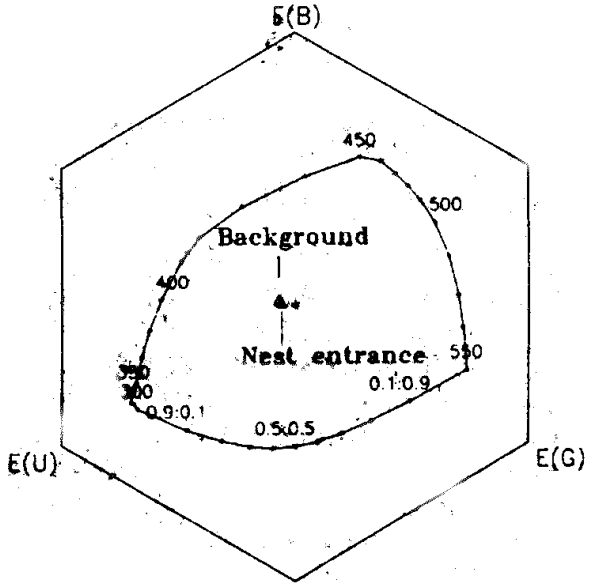


Figure 3. *The spectral reflectance functions of the white funnel-shaped entrance of* Partamona, *as well as the black background material of this funnel (the outer surface of the termite nest) are shown (Fig. 3a). Receptor excitations are calculated for* Partamona *UV-, blue, and green receptors (Fig. 3b see Chittka et al., 1992 for methods) and converted into color loci in the hexagon (Fig. 3c). Both materials have practically identical color loci for bees. The asterisk in the hexagon marks the uncolored point. The continuous line indicates the spectrum locus from 300 to 550 nm in 10 nm steps. Its curved bottom segment is the UV-green mixture line, connecting the short and long wavelength ends of the spectrum locus in 9 mixture ratios.*

Several workers found that a white target on a black background can only be detected and learnt with great difficulty, or not at all (Hertz, 1933, 1937, Schnetter, 1968, Giurfa et al., 1996). Bees judge two signals as equal if they differ strongly in intensity, but not in color. However, they easily distinguish two stimuli that differ by only a few nanometers (Daumer, 1956, Helversen, 1972). Lehrer and Bischof (1995) found that when intensity contrast is as high as 60% (as in the case of our nest entrance) detectability of a target is substantially poorer than when color contrast with no intensity contrast is provided. This peculiarity of bee color perception has long been implicated in the phenomenon that UV-reflecting white flowers are extremely rare in nature, because such flowers stand out from the green foliage background only in terms of intensity, not in color (Hertz, 1937, Chittka et al, 1994).

Recent work by Giurfa et al. (1996) has rigorously examined the role of receptor-specific contrasts and color contrast for detectability of visual targets by honeybees. They showed that both color contrast and "green contrast" (the specific excitation difference between background and target generated by the green receptor of the bee) are important. While color contrast is essential for detectability, green contrast is optional: Giurfa and his collegues found that when color contrast is provided, green contrast may further enhance detectability. However, objects with green contrast and no color contrast were not detected. The nest entrance of *Partamona* is an object that fits this description exactly: while the contrast in each single color receptor - including the green receptor - is strong, color contrast is negligible. If the *Partamona* visual system works at all like that of *Apis mellifera*, we may thus assume that the nest entrance is indistinguishable from the background. Is this the case?

2) The signal may be addressed to the bees' pattern perception system, but there are more problems.

As mentioned, Hertz (1937) did not succeed in training bees to white circular targets on a black background, while colored targets of the same shape could be easily learned. However, when Hertz used the same white material to present star shaped patterns on a black background, bees became suddenly interested in the target. In fact, the more disrupted the boundary of the target was, the more readily would bees learn to accept it as a predictor of food.

Pattern and color perception in bees are disjunctive in a way which is rather contra-intuitive for humans. Bees will sometimes ignore pattern cues such as angular orientation, so long as color information is provided (Giurfa et al., 1995b, but see Menzel and Lieke, 1983, Chittka et al., 1988), or they will ignore white targets on black backgrounds so long as their boundary is undisrupted. When black and white patterns are horizontally presented, bees spontaneously prefer patterns with large relative lengths of contour (Hertz, 1929, 1933, 1937) and learn such patterns faster (Cruse, 1972, Anderson, 1977, Wehner, 1981). This preference is widespread not only in Hymenoptera (see also Tinbergen and Kruyt, 1938), but insects in general (butterflies: Ilse, 1932; locusts: Wallace, 1958; Diptera: Sippell and Brown, 1953, Vogel, 1954, Kugler, 1956), and it effects numerous behavioral contexts. Even though other parameters certainly play a role (Wehner, 1981, Zhang and Srinivasan, 1994), relative contour length is certainly correlated with spontaneous bee choices. Indeed, the relative contour length is increased 3-5 fold relative to a theoretical target of the same size, but with an undisrupted boundary. This may increase spontaneous preference by a factor of 5 relative to an object with a closed margin (Anderson, 1977). Hertz (1929, 1933) speculated that the parameter used by the insects is the flicker produced as the bee moves over the pattern. It was proposed that a target can be more easily detected when it generates a strong flickering perception in the insect eye. In this sense, the disrupted boundary of the nest entrance signal may be a strategy to enhance detectability from a large distance, and facilitate learning the features of the target. It is also possible that the "arms" of the ornamentation are used to center the bees rapid flight towards the entrance of the nest.

If the *Partamona* visual system is comparable to that of honeybees, the *Partamona* nest entrance would fit in well with the system of pattern perception just described. The *Partamona* nest entrance may be useless as a signal if it did not have the disrupted margin, given that it

provides no color contrast. This means that the bees, given white sand as a building material, *must* furnish their entrance signal with an intricate boundary, if the signal is to be of any adaptive value. However, there are several complications with this interpretation. The results for pattern attractiveness, detectability, and memorability described above were often obtained for targets presented on a horizontal surface. When honeybees choose between *vertical* stimuli, they prefer patterns with radiating elements (as in the *Partamona* nest entrance) over those with circular structures, but those with *lower* spatial frequencies are apparently most attractive (Lehrer et al., 1995). Clearly, there are open questions. Behavioral tests with Partamona bees involving manipulations of the nest entrance's structure are needed to resolve these difficulties.

3) Is the nest entrance used to identify home? Yet more problems!

No two of the *Partamona* nest entrance signals are similar to each other for the human observer. It is thus possible that they serve as cues for identification of individual nests. Evidence for this hypothesis comes from the observation that when one colony dies and another moves in, a new entrance is constructed, sometimes over the old structure. Occasionally the nest entrance is repaired, modified and restructured. Thus, the bees "care" about the appearance of their nest entrance; not any arbitrary structure will do the job, and it is apparently not just the size, but also the shape, that matters. Moreover, the "ornamentations" of the nest entrance structures are clearly more elaborate in the bottom part, and most spatial detail is thus presented in the lower visual field of an approaching bee. This is interesting because honeybees give special weight to spatial detail in the ventral visual field in pattern discrimination tests (Wehner, 1981, Chittka et al., 1988, Giurfa et al., 1995b).

However, the higher visual acuity in the ventral visual field has been associated with a matching strategy, in which, through horizontal scanning, the bees try to achieve a pixel-by-pixel match between a memorized image of the target and the visual scene currently evaluated (Wehner and Flatt, 1977, Srinivasan, 1994). Clearly, this is not what *Partamona* is doing on its straight and rapid approach flight to the nest. Thus, the hypothesis that bees use differences in temporal cues as they approach the target (Hertz, 1933) is more likely to account for nest entrance pattern discrimination.

It is also clear that at least the experienced, fast-flying bees must have made their decision for a particular nest entrance before the pattern information is actually available for them. In honey bees, the minimum detectable angle subtended by a reflecting target presented against a reflecting background (as opposed to selfluminant targets or backgrounds) is 5° (Giurfa et al., 1996). Of course it is possible that the visual acuity of Partamona is somewhat better than in the honeybee, and the rapid flight from a large distance provides a hint that it is: at 2 m distance, a target of 10 cm height subtends less than 3°. However, it is unlikely that the bees can actually discriminate between different nest entrance patterns from that distance; Zhang et al. (1992) showed that even at a distance of 30 cm from the target, when the pattern cues involved could still be resolved, only global spatial parameters played a role in honeybees discrimination performance. Even if *Partamona* visual resolution is better, but it is unlikely that it differs so drastically that a nest entrance pattern can be identified from such a large distance. Moreover, research on *Osmia* spp. has shown that bees can identify their nest by using as a cue its position relative to other nest entrances, and also external landmarks (Steinmann, 1973). Thus, the nest "ornamentations" are not necessarily essential for nest identification.

Clearly, we need behavioral tests to examine the possibility that the nest entrance is used to identify the correct colony. Will bees fly into the wrong colony when the entrance constructions of two nests are exchanged? Are flights towards a target aborted when it has been manipulated during the bee's absence? From which distance can contour density be used as a parameter to identify the nests? It will also be interesting to test quantitatively whether or not the nest entrance design is influenced by those of neighboring nests.

Conclusion

The basic design principles of how Partamona nest entrances are to be built are certainly inherited. However, in the case of this particular signal, selection does not act on the animal's morphology and physiology, but rather on the behavioral patterns used to produce that signal. The signal must be shaped so that it best addresses the animal's visual perception, which, in turn, has been evolutionarily optimized for visual tasks other than detection of signals at the nest entrance.

How, and why, did the behavior to construct these intricate signals evolve? All known species of the genus *Partamona*, regardless of whether they mark their entrance with a conspicuous signal or not, have a very efficient defense system. Closely adjacent to the entrance is a vestibule that precedes the principal nest chamber (with the brood combs and storage pots) which contains rods, lamellas made of cerumen, and "honey pots" which are either empty or filled with diluted honey (Kerr, 1969, Camargo, 1970, 1980, and unpublished observations; Michener, 1979, Roubik, 1989). These chambers have been interpreted as false nests to deceive predators (literature op. cit.). Moreover, these chambers always shelter a large number of individuals that constitute the defense force of the nest. These bees are extremely aggressive, they attack in mass, bite and pursue intruders. The cleptobiotic Meliponine species *Lestrimelitta limao* (cf. revision in Roubik, 1989) has been observed twice attacking *Partamona* nests (Camargo, unpublished observations). It did not penetrate further than the initial (false) "nests".

With the exception of *P. pearsoni* group and a second species of the group *P. cupira* (see below), all species of *Partamona* use soil obtained from their own substrate (termite nest) and only rarely transported from other places. In all of these species, the nest entrances are of the same coloration as the light background and lack any sort of ornamentation. Only *P. pearsoni*, and *P. cupira* from Northeastern Brazil, nest in black substrates of termite nests. These two species are the only ones with brightly colored nest entrances and a disrupted boundary. For this purpose, *P. pearsoni* transports white sand to the nest, which is available on the banks of black water rivers in Amazonia, whereas *P. cupira* uses light amber clay.

Thus we can envisage the following evolutionary scenario. Since using bright material for the nest entrance is exclusively associated with black substrates, the usage of this material probably evolved to offset the dark entrance hole against its surroundings. This may not have been necessary in species whose nest entrance hole contrasts against a light background. Obviously, having a conspicuous nest entrance constitutes a potential disadvantage with regard to predators. The bees' rapid flight into the nest helps them escape from predators lacking the means of penetrating the nest, such as birds, and insect predators such as Mantispidae, Aspilidae and Mantidae, which often ambush social Hymenoptera in their final and slow approach to their nests (N. Williams, personal communication). But the nest entrance might attract the unwelcome attention of vertebrate predators interested in the contents of the nest. However, the behavioral patterns for constructing the *P. pearsoni* nest entrance clearly evolved only subsequent to the elaborate defense strategy that is present in the entire genus of *Partamona*., so these bees might be well adapted to cope with such visitors.

P. pearsoni is the only known Meliponinae that approaches the nest practically without slowing down its flight, in a straight flight path from 2-3 m distance. Thus, the ornamented entrance structure clearly serves an extraordinary quick localization of the nest. Further research may show how the assembly of these intricate structures is organized on a social level: who "minds" when the nest entrance is experimentally altered? Is it the foragers who discover on their way home that the signal is no longer optimal for detection ore recognition, or is it a special caste of workers? Is the entrance reconstructed from memory or according to a genetically programmed image?

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