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In Focus

Featured Articles in This Month's *Animal Behaviour*

The Function of White Coloration in Nocturnal Spiders

In diurnal animals, colour patterns can help avoid predators, lure prey or attract mates. In nocturnal animals, however, we find it more difficult to understand the function of colour patterns, being diurnal creatures ourselves. Many organisms living in a dark environment, such as fireflies, marine animals, fungi or bacteria, are bioluminescent; in other words, they produce and emit light themselves rather than reflect light from other sources. Bioluminescence could help attract mates, or distract or avoid predators. Nevertheless, recent studies have demonstrated that nocturnal animals can also use colour signals. For example, eagle owls and some treefrogs employ them in male–male combat, glow-worms use them in defence or prey attraction and certain fish use colour for predator avoidance. Although less is known about whether nocturnal animals use colour signals to attract mates, recent manipulative experiments showing that males from a crepuscular spider species are more attractive to females when their mouthparts are painted white suggest that colour might play a role in the mating behaviour of nocturnal animals as well.

In the present issue (pp. 25–32), Tai-Shen Lin, Shichang Zhang, Chen-Pan Liao (all from Tunghai University, Taiwan), Eileen Hebets (University of Nebraska, U.S.A.) and I-Min Tso (Tunghai University, Taiwan) test the hypothesis that the bright white patches on the bodies of male nocturnal spiders play a role in mating behaviour as well as in foraging. The fishing spiders they studied forage during the night for aquatic or semiaquatic animals and display a sexual colour dimorphism. Males have minute white hairs that form white stripes along the margins of their bodies. Females lack white body stripes but have white spots on the tips of their legs (Fig. 1).

More specifically, Lin and coauthors aimed first to measure the variation in the male colour pattern and then to test experimentally whether this pattern is dependent on nutrition. Diet is strongly related to the attractiveness of male sexual traits preferred by females in many sexually dimorphic animals, probably because it conveys information about the male's foraging history. Furthermore, the authors aimed to test whether dummies with the male white pattern would attract more prey than dummies without white colour and whether males with the white pattern would attract more mates than males with their colour pattern experimentally removed.

The authors collected the spiders from streams near the Dongshi Forest Recreation Area in Taiwan, returning them after the experiments. The effect of diet on the white colour pattern was tested with two treatments: a high- and a low-nutrition diet. To test the hypothesis that the white male stripes attract prey, Lin and coauthors compared two groups of dummies shaped like the real spiders. The control group had white stripes made of paper and the experimental group had no colour pattern. For the final experiment testing the reproductive function of the male white pattern, the authors compared two groups of real fishing spider males. Those in the experimental group had their white stripes covered with brown paint while those in the control group had the same

Figure 1. The studied fishing spiders: (a) an adult female; (b) an adult male; (c) three males courting a female. Photo: Tai-Shen Lin.

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amount of brown paint applied but to the brown part of their bodies and not on the white stripes.

Lin and coauthors found that the white stripe area is positively correlated with body size and weight. This suggests that, potentially, females could use the size of a male's white stripes as an indicator of that male's size in the context of mate choice. Furthermore, the white stripe area of males on a high-nutrition diet was larger than that of males on a low-nutrition diet, suggesting that, potentially, females could use the area of a male's white stripes as an indicator of his feeding history as well. The results from the dummy experiments suggest that the male white stripes play a role in luring prey because more prey were attracted to dummies with white stripes than to dummies without them. Last but not least, the results from the experiments in which the authors manipulated the colour of the male stripes showed that males with white stripes were more likely to be accepted by females. By contrast, males with experimentally removed white stripes were not only more likely to be rejected but also more likely to be attacked by females.

Overall, the detailed experimental study by Lin and coauthors does demonstrate that colour signals in a nocturnal animal species are used both for foraging and reproduction. Their results show that colour patterns could be visible for nocturnal animals and suggest that colour signals might be employed by animals living in a dark environment more widely than previously suspected. Future work will be required to establish whether such colour signals incur any costs. These could be difficult to assess given the complex inter-relationships suggested by the results of Lin and coauthors between the presence of the white stripes, their size, foraging success and mating success. This area of research has the potential to alter dramatically our understanding of communication in nocturnal conditions.

Ana Sendova-Franks
Executive Editor

Strategic Plasticity in Burying Beetles

Males of many species, in a diverse array of taxa, exhibit alternative reproductive tactics, the expression of which is determined by environmental conditions. Although in some cases there may be a switchpoint at which a transition from one tactic to another occurs irreversibly, most often the tactics are rapidly reversible and responsive to environmental conditions. These alternative tactics can take many forms, including, for example, males switching between territorial behaviour, sneaking and female mimicry. Transitions between tactics are usually triggered by environmental conditions (e.g. density, food availability, female availability) or by the male's assessment of his status relative to others. Often, the transitions are thought to be influenced primarily by immediate environmental contexts, given the high degree of plasticity and the rapidity with which transitions between behavioural tactics can be accomplished.

In their article in this issue (pp. 175–182), Tess Mulrey, whose master's research this was, Anne Eggert and Scott Sakaluk (Illinois State University, U.S.A.) explore the possibility that transitions among tactics are not simply responses to current conditions but that they also reflect the past experience of the males. To do this they conducted experiments on burying beetles of the genus *Nicrophorus*, which are unusual among insects in that they typically provide biparental care. Both males and females search for carcasses of small vertebrates essential for rearing their young. When a male locates a carcass, he emits a sex pheromone to attract a mate (Fig. 2), unless one is already present, and both then bury the carcass, subsequently guarding it against other burying beetles until the larvae hatch and leave the brood chamber. This searching tactic, if successful, usually results in very high paternity for the holder of the carcass. When males are unable to locate a carcass, they may simply release the sex pheromone to attract females (signalling tactic). A female attracted to the signalling male often allows a single copulation before leaving, thus ensuring that she can produce embryos if she finds a carcass at which no male is present. All males are capable of exhibiting both searching and signalling tactics, and they can switch between them rapidly.

Figure 2. Male burying beetle, *Nicrophorus orbicollis*, in classic pheromone-emitting posture. Photo: Anne Eggert and Josef Müller.

To evaluate the effect of a male's past experience regarding the availability of females and carcasses on his choice of tactics, the authors used second-generation laboratory-reared beetles and exposed males to four different treatments: (1) multiple females but no carcasses; (2) multiple females and multiple carcasses; (3) multiple carcasses but no females; or (4) no carcasses or females. They scored male reproductive tactics before and after the treatment for all males. The authors predicted that previous experience would influence the mate-finding tactics of the males, and, specifically, that males that had encountered both carcasses and females would increase searching, whereas in other treatments signalling might be elevated because carcasses had no value (females absent) or mating opportunities were perceived as common (females present).

This very elegant experimental design eliminated the possibility of maternal effects and also made it possible to discriminate the influence of previous mating experience and resource (carcass) availability upon subsequent behaviour. The research demonstrated that males exposed to multiple carcasses during the treatment phase maintained pretreatment signalling efforts after the treatment, whereas males not exposed to carcasses during the treatment period increased pheromonal signalling afterwards. Overall, males in the control and female-only groups, those not exposed to carcasses, signalled more than did those that had been exposed to carcasses. Males in the female plus carcass group maintained searching levels post-treatment, whereas those in the other three groups reduced time spent searching after treatment.

These results offer insight into the influence of specific cues on mate-searching tactics employed by male burying beetles. In particular, they indicate that males do not respond to the availability of receptive females with increased signalling. Instead, perceived access to carcasses seems to be the primary influence upon shifts among tactics. In particular, increases in signalling and decreases in searching seem to be triggered by the perception of low carcass availability, presumably leading to the expectation of low payoffs for searching. However, female abundance does make a difference when carcasses are available: when both carcasses and females are perceived as abundant, searching time is maintained, declining only when females are rare.

This research demonstrated, unequivocally, that the alternative mate-finding tactics of burying beetles are phenotypically plastic, and that expression is conditional not only upon immediate environmental context, but also upon the recent experience of the male with respect to the abundance of receptive females in the environment and the abundance of carcasses available for raising young. This study joins an increasingly large and important body of work designed to understand the adaptive value of phenotypically plastic traits, and ultimately to explore the influence of development (experience) upon the expression of plastic traits and their subsequent evolution.

Susan A. Foster
Executive Editor