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In Focus

Featured Articles in This Month's *Animal Behaviour*

The Evolution of Paternal Care

Exclusive paternal care, in which males alone care for the eggs and young, is an uncommon form of parental care in animals and is particularly rare in arthropods. In an earlier issue of this journal, Douglas W. Tallamy proposed that exclusive paternal care evolved in arthropods 'more as a sexually selected means of attracting mates than as a naturally selected mechanism for improving offspring survival' (Tallamy 2000, page 560). In other words, the advantage of exclusive paternal care most important to its evolution is not the increased survival of the eggs and young presently under care, but rather the attraction of additional females for mating. In a paper in the present issue (pages XXX–XXX), Tais M. Nazareth and Glauco Machado of the Universidade de São Paulo provide a thorough test of this sexual selection hypothesis for a Neotropical harvestman of the genus *Pseudopucrolia*.

Harvestmen are a group of arachnids commonly known as 'daddy long-legs,' in which exclusive paternal care has evolved multiple times. In the harvestman studied by Nazareth and Machado, males defend holes in roadside banks, and females enter the holes to copulate and lay eggs. In laboratory populations of mixed sexes, the only form of parental care observed was guarding of the eggs against predators, and only males performed this behaviour (Fig. 1). In the laboratory populations, conspecifics were the only potential predators, and guarding males were usually successful in repelling conspecific intruders before they obtained any eggs. In two instances, intruders that succeeded in taking eggs were attacked by a guarding male, who was able to reclaim most or all of the stolen eggs and replace them in the nest.

The central prediction of the sexual selection hypothesis is that females should prefer males already guarding eggs to males without eggs. To test this prediction, Nazareth and Machado allowed females to choose between pairs of males, one of which had eggs in his nest from an earlier mating and the second of which did not. After the first round of females had chosen, Nazareth and Machado arranged another round of mating trials with the same pairs of males but reversing which males had eggs. When the data from both rounds were combined, males that already had eggs were chosen for mating on 25 occasions while males without eggs were chosen only three times. Females thus strongly prefer males guarding eggs to those without eggs, as predicted.

If males benefit from guarding eggs because doing so helps attract females to mate, then eggs should be valuable to them even if those eggs have been fertilized by another male. Nazareth and Machado tested this prediction by removing guarding males from nests with eggs and observing subsequent intrusions. Most intruding females ate eggs, as might be expected. Intruding males, by contrast, were much less likely to cannibalize eggs, and those that did cannibalize ate substantially fewer eggs than did their female counterparts. Remarkably, approximately one-third of the male intruders showed guarding behaviour, repelling other intruders from their adopted eggs; female intruders, by contrast, never showed guarding behaviour.

Figure 1. A male of the Neotropical harvestman *Pseudopucrolia* sp. guards eggs inside an artificial nest in the laboratory. Photo: Bruno A. Buzatto.

In the male removal experiments, unguarded clutches suffered severe reductions in number of eggs relative to guarded clutches, indicating that there is a natural selective advantage to males in guarding eggs. The mating preference results demonstrate that there is also a sexual selective advantage, and only this advantage can explain the solicitousness of males towards eggs not their own. As Nazareth and Machado point out, comparative studies can be used to test further which advantage has been more important in the evolution of exclusive paternal care.

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Alluring Adders

In Disney's cartoon version of 'Jungle Book', Kaa, the python, tries, and fails, to lure Mowgli into becoming his lunch by using his crazily hypnotic eyes. In real life, snakes are much more likely to use their tails to attract their prey, a behaviour known as caudal luring. One such snake is the death adder of Australia, which makes either slow, rippling movements with its tail, or thrashes it rapidly back and forth. These movements have been shown to facilitate the capture of prey such as mice and lizards, and previous studies suggested that lizards are attracted to lures because the movements resemble those of the lizards' own prey species, such as worms. None of these previous studies actually investigated the design of the death adder's lure in any detail, so, in this month's issue, Ximena Nelson, Daniel Garnett and Christopher Evans (pp.**–**) remedy the situation by investigating how Jacky dragon lizards (Fig. 2), one of the death adder's prey species, respond to lures, and whether the design of lures maps onto the patterns shown by the lizards' potential prey species.

To investigate the lizard's response to lures, Nelson and her colleagues made clever use of an animated 'cartoon' snake, known as 'cybersnake', to see whether they could provoke lizard attacks. The cybersnake was an accurate 3-D representation of a death adder, designed to produce the characteristics of the slow and fast luring movements in a precise and controllable way. Using cybersnake also allowed the researchers to control for any other cues that the snakes might produce, such as odour cues. The cybersnake was presented as highly conspicuous (on a background of white sand), camouflaged (on a background of leaf litter) or 'obscured' (on a background of leaf litter with some leaves on top of the snake), and it either produced luring movements or was shown lying still (as a control condition). As predicted, Jacky dragons showed a higher response to both fast and slow lure movements compared to the control, but only when the snake was conspicuous.

Nelson and her colleagues then went out to the field and collected all the potential invertebrate prey items from the territories of 13 wild Jacky dragons, so that they could film their movements in the laboratory. Analysis of the footage showed that the average speeds of the fast and slow caudal lures matched the typical speed ranges of the invertebrates that were found most commonly in the lizards' home range.

Finally, to put all the pieces of the puzzle together, Nelson and her colleagues used their invertebrate footage to generate an animated 'cybercricket' that could produce the movement characteristics of real prey. Just as with cybersnake, they used the cartoon cricket to test the Jacky dragons' response. They found that the lizards attacked cybercrickets moving at common prey speeds (matching those of lures) more often than when moving at rare invertebrate speeds.

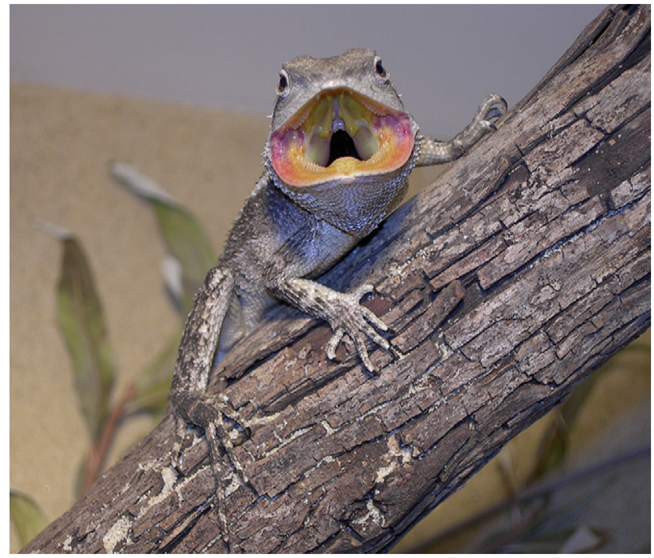

Figure 2. Death adder caudal lures exploit the perceptual processes by which Jacky dragons recognize the most common types of their prey species. Photo: Ximena Nelson.

Although Nelson and her colleagues cannot prove it to be the case conclusively, these findings suggest strongly that the death adder's particular pattern of caudal luring may have been shaped by aspects of the receiver psychology of the Jacky dragon. Specifically, the efficacy of the death adder's luring movements seems to lie in the way that they engage the lizards' prey recognition processes, which are responsive to the most common prey speeds. In other words, the death adder lure doesn't mimic a lizard's prey item as such, but rather exploits the process by which the lizards themselves tune into the prey most commonly available to them.

Louise Barrett
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Reference

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