



## In Focus

Featured Articles in This Month's *Animal Behaviour**Spatial Memory in Frogs Transporting Their Tadpoles*

Spatial memory guides animals when they are searching for resources and it is particularly important in challenging environments where resources are scattered and fluctuate in quality. Studies of insects, birds and mammals have shown that animals use flexible spatial learning strategies when they search for food or new nest sites. Little is known, however, about the application of these strategies in other contexts. A study on poison frogs in the present issue (pp. 89–98 in this issue) demonstrates that amphibians are a particularly suitable group for understanding spatial learning strategies in the context of parental care. Andrius Pašukonis, Katharina Trenkwalder, Max Ringler, Eva Ringler, Rosanna Mangione, Jolanda Steininger, Ian Warrington and Walter Hödl (all affiliated with either the University of Vienna or the University of Veterinary Medicine Vienna) explore how tropical frogs use spatial learning to transport their tadpoles from terrestrial sites of oviposition to widely scattered and ephemeral aquatic sites.

Earlier studies of orientation in amphibians have focused predominantly on nocturnal temperate species and on sensory modalities as the underlying mechanism of orientation. Although laboratory experiments and field observations strongly suggest that many amphibians are able to learn cues as a guide to their local orientation, the role of spatial memory in guiding natural amphibian movements has never been addressed directly. The ability of many temperate-region amphibians to return to their stable breeding ponds or streams could be based on natal imprinting and orientation through the perception of cues, such as the odour of the natal pond, emanating from a long-distance target. However, underlying mechanisms like these are insufficient to explain orientation in tropical frogs, which often depend on small, widely scattered and ephemeral pools for their reproduction.

Pašukonis and coauthors aim to understand whether tropical frogs rely on spatial memory to perform their parental duties, given that learning about dynamic reproductive resources is less reliable and cognitively more demanding. Their study species is the diurnal brilliant-thighed poison frog, which lives in leaf litter. The tadpoles of this species are transported to distant ephemeral aquatic sites predominantly by the father (Fig. 1). Tadpole transport is costly in terms of energy expenditure, exposure to predation and the loss of mating opportunities. Earlier translocation experiments have shown this frog species is capable of very accurate experience-based homing. Hence the authors hypothesize that the brilliant-thighed poison frogs use spatial memory to navigate to potential deposition sites they have discovered earlier. To test this, the authors removed small artificially introduced pools that had been

used as the principal tadpole deposition resource by the population over several years and tracked the movements of individual males, taking advantage of the unique ventral colour patterns in this species. The tadpoles from the removed pools were collected in two large buckets which were suspended in the vicinity of the array of former pools so that the tadpoles could emerge near their original deposition sites. Pašukonis and coauthors predicted that if these frogs use spatial memory for their orientation, the males carrying tadpoles will move mainly around the location of the removed pools. In addition they expected the frogs to search for several pools based on the requirement of a flexible memory in an environment with scattered ephemeral resources.

The experiments were carried out at the CNRS Nouragues Ecological Research Station in the Nouragues Nature Reserve, French Guiana on a river island, where the frogs had been introduced only a few years earlier.

Pašukonis and coauthors found that males that travelled further away from the centre of their territory tended to transport more tadpoles. Most males were captured at least once within 1 m of a former pool site. Of the 15 tracked individuals, 13 visited the former pool sites and most males visited several of them. Within the average of 8.5 h of tracking, they travelled on average 100 m in bouts of rapid locomotion interspersed by longer pauses. Movement bearings were strongly directed along the array of former pool sites. The suspended buckets with tadpoles also attracted the males and several of them changed their direction of movement from 10 m away. Approximately half of the tracked tadpole-carrying males visited one of the suspended buckets.

These results are compatible with the spatial-memory hypothesis. Simple following of odour cues cannot explain the frogs' strong affinity for removed pool sites days and weeks after removal. The results also rule out natal imprinting, which could explain orientation behaviour in temperate-region frogs living in environments with more stable breeding sites, because most of the tracked frogs visited multiple former pool sites. This strongly suggests that the underlying learning process is flexible. It is still not known how males discover pool sites in the first place but their ability to detect tadpole odour is likely to help them find pool sites already inhabited by tadpoles. The positive relationship between the distance travelled and the number of tadpoles transported by these male poison frogs suggests that it pays to transport more tadpoles when moving to distant pools.

It remains unknown whether brilliant-thighed poison frogs have a map-like knowledge of the area and the full extent and flexibility of their spatial memory are still to be tested. Given the similar ecological requirements, it is likely that the present results



**Figure 1.** A father brilliant-thighed poison frog, *Allobates femoralis*, with a load of tadpoles on his back is finding his way through the understory of the rainforest to memorized pool sites tens to hundreds of metres away from his territory in Nourague Nature Reserve, French Guiana. Photo: Andrius Pasukonis.

could be generalized to many other species of poison frog. The interesting individual-based study by Pašukonis and coauthors illustrates the potential of amphibians for deepening our understanding of the way environmental factors shape spatiocognitive abilities.

**Ana Sendova-Franks**  
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#### *The Mysterious Nature of Female Mate Choice*

Females often exhibit strong mating preferences for particular male phenotypes, whereas males often exhibit less mating discrimination. In general, the reason for this is that, in many species, males provide little investment in offspring other than their genes, and thus can benefit by mating with many females. In contrast, females typically invest more in individual offspring than do males through direct provisioning of the egg or embryo, and they may more often provide substantial care for offspring after hatching or birth. Thus, females benefit from selecting the highest-quality males, and males with traits preferred by females can experience much higher mating success than nonpreferred males.

Often, female preferences for particular male phenotypes are clear and well established experimentally. They may, for example, include reasonably consistent preferences for large body size, bright coloration or vigorous courtship behaviour, all aspects of phenotype that could provide information on male quality. However, females may assess multiple male characteristics, including multiple components of male displays, and much of this assessment may be passive, in that females exhibit little behavioural evidence of the display components being evaluated. Both the multicomponent nature of female mate assessment and the often passive nature of evaluation create difficulty for understanding the degree to which females attend to particular male characteristics and display elements, and for understanding the degree of reliance females place upon specific display elements or male characteristics.

In an article in this issue (pp. 131–137, in this issue) Jason Keagy, Linda Cendes Hosler and Gerald Borgia (University of Maryland, College Park) argue that a focus upon elements of male displays that are actively explored by females can offer insight into the degree to which females attend to specific cues, and they also demonstrate that it is possible to evaluate the degree of female uncertainty

in mate selection by evaluating female attention to such cues. They achieve this by examining female behaviour in satin bowerbirds, *Ptilonorhynchus violaceus*, as they visit bowers of multiple males. Bowerbirds are among a fascinating set of species in which males are evaluated not only upon their personal attributes and displays (both visual and vocal), but also upon the structures they construct to attract females (extended phenotypes).

These structures, known as bowers, are complex and remarkable in form (Fig. 2), are decorated, and, somewhat inexplicably in the case of the satin bowerbird, are ‘painted’ with a paste of dried hoop pine needles that the males chew and apply to the interior of the bower. When females visit bowers, they sample the paint by nipping, and appear to swallow bits of the paint. The reason for this is not understood. However, male satin bowerbirds spend about the same amount of time painting the bower as they do building it, and the painting rate is correlated with mating success. As female bowerbirds actively sample the paint on the bower walls, this sampling can be used to evaluate the degree to which individual females use this feature of the bower in mate assessment. Keagy, Hosler and Borgia further suggest that the degree of sampling could serve as an indicator of female uncertainty in mate choice, a very valuable, measurable metric for interpreting other elements of female mating behaviour.

As part of a long-term study of satin bowerbirds at Wallaby Creek, New South Wales, Australia, most females have been uniquely banded, and motion-triggered video recording has made it possible to examine female mate-searching behaviour by observing interactions at bowers. In this study, Keagy and co-workers assigned females to one of three categories: (1) those that mated with the same male as in the previous year; (2) those that mated with a single male, but not the same male as in the previous year; and (3) those that mated with multiple males. Assessing categories 1–3 as indicative of declining certainty in female mate choice, the authors predicted that females in group 1 would sample painted walls of the bowers least and those in group 3 most often.

These expectations were supported in that females that mated multiply were more likely to sample the paint, suggesting that females uncertain in their choice of males were more engaged in male assessment than were those with more information and, thus, certainty of mate choice from previous breeding seasons. The interpretation that females that sampled the paint often were less certain in their choice of mates was further supported in that these females also switched more frequently among males they



**Figure 2.** Satin bowerbirds, *Ptilonorhynchus violaceus*: a paint-sampling female (left) and painting male (right). Paint is masticated hoop pine needles applied to bower walls. Photo: Linda Cendes Hosler and Gerald Borgia.

visited, and made more frequent visits to bowers. Additionally, females sampled the paint less in visits that ended in copulation than in those that did not, and females sampled it less during second visits to a bower than during first visits, suggesting that sampling could serve as an indicator of female uncertainty of male quality during bower visits.

In combination, the results of this study suggest that indices of uncertainty can be developed using female behavioural responses to specific cues provided by males that require active sampling by

females. These may not be available in all taxa, but when they are, they can provide valuable information concerning female mate assessment that can be used to interpret other aspects of mate choice behaviour, an exceptionally valuable insight. Now the intriguing question remains: why in the world do female satin bowerbirds care about masticated dried hoop pine paint?

**Susan A. Foster**  
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