



Diets and decisions: the potential use of food protein cues in dietary, sexual and social decisions by mosquitofish

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There is growing appreciation that successful foraging is not simply about the quantity of food consumed, but also about food quality, as animals seek to attain species-specific macronutrient intake targets. Of the various macronutrients, protein is of primary importance, and its acquisition is central to the foraging strategies of many animals. To forage effectively, animals may use cues arising directly from a food source or indirectly from conspecifics relating to their recent foraging experience. In this latter case, successful foragers may be attractive both in a sexual context, as a high-quality mate, and in a social context, since they may hold information about foraging resources that others may be able to exploit. We tested the mate choice preference of male mosquitofish, *Gambusia holbrooki*, for female conspecifics that had been fed for 72 h on a high-protein, low-carbohydrate (Pc) diet versus females that had been fed on an alternative, isocaloric diet with high-carbohydrate, low-protein content (pC). We found that males expressed a significant preference for mating with Pc females. Additionally, we tested the preference of mosquitofish for cues derived directly from each of the two diets, and indirectly from conspecifics that had been fed on the two diet treatments. We found that mosquitofish preferred both direct cues from Pc foods and cues of conspecifics from the Pc diet treatment. We discuss the role of dietary proteins in the chemical signatures of organisms and the adaptive significance of the preference for conspecifics with high protein intake in both social and sexual contexts.

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The question of how animals maximize their foraging efficiency and how in turn this relates to their social and sexual behaviour lies at the heart of behavioural ecology. Foraging success has often been considered to be represented by a single currency, the rate of energy gain, but recently the emphasis in nutritional ecology has switched to recognizing the importance of balancing nutrient intake to achieve a specific intake target (Raubenheimer et al. 2009; Simpson et al. 2010). Among the energy-yielding macronutrients (protein, fat and carbohydrate), intake of protein is strongly regulated by many organisms, from slime moulds to humans (Dussutour et al. 2010; Simpson & Raubenheimer 2011). Indeed, the dominance of regulatory mechanisms for protein intake, as compared to those for carbohydrate and fat, is thought to be a contributor to the development of obesity on low-protein diets in humans and domesticated animals (Simpson & Raubenheimer 2005). The reason why dietary protein, in optimal balance with other nutrients, assumes such importance in regulatory terms presumably relates to the fact that protein provides a source of

essential nitrogen for growth, reproduction, immune function and tissue maintenance.

To forage effectively, and regulate protein intake, animals may use direct cues (cues that are derived directly from an item of food) and indirect cues (cues that are produced by other individuals, usually conspecifics, and relate to recent protein intake). The availability of direct cues, in conjunction with fine-tuned sensory discrimination ability, allows a foraging individual to use this information on food location and quality and to use this information to make informed foraging decisions (Rozin 1976; Schaefer et al. 2003). Indirect cues yield social information, but although such cues may be less immediate, they are known to play a vital role in promoting foraging success in social animals (Galef & Wigmore 1983; Bijleveld et al. 2010). It may be advantageous to associate socially with successful foragers either because they hold valuable information about the location of food patches, or because over time they may act as a net provider to the social group (i.e. a producer rather than a scrounger, sensu Barnard & Sibly 1981). Of course, the net benefit of associating with successful foragers in this way will also depend on the competitive ability of the individual and the extent to which the food resource can be monopolized (Ward et al. 2006). Animals are likely to use both indirect and direct cues while foraging; indeed the

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simultaneous use of both direct and indirect cues allows rats, *Rattus norvegicus*, to regulate their protein intake optimally (Beck & Galef 1989).

Cues relating to a conspecific's diet, and specifically the quality of that diet, are likely to play a key role not only in social association decisions, but also in many mate choice decisions. There are good adaptive reasons for this: successful foragers will be better able to provision their offspring. Beyond this, the qualities that made them good foragers may be passed to their offspring. But how might animals make such mate choice or social group choice decisions? In the case of mate choice, research has often focused on morphological characters of suitors. Beyond morphology, behaviour patterns, including courtship rituals, often play an important role in mate choice (Johnstone 1996; Wachtmeister & Enquist 2000), while the genetic traits underlying these may also be assessed (Brooks & Endler 2001; Penn 2002; Aeschlimann et al. 2003). Similarly, when choosing whether to join or to remain with a conspecific social group, animals may discriminate between conspecifics based on their morphological characteristics, such as size or colour (Ward & Krause 2001; Ledesma & McRobert 2008). But while phenotypic characteristics can offer a direct means of assessment in sexual or social contexts, they are not the only (nor necessarily the best) means of achieving an accurate and rapid measure of quality. Another approach may be based on the detection of cues that are produced by an individual and relate to dietary quality, either visually, for example through the expression of carotenoid-based colour displays (Hill et al. 2002), or chemically, for example as a by-product of metabolism (Wyatt 2003). Making a decision on these bases may be advantageous since such cues are intrinsically honest and provide a direct measure of quality linked to the ability of an individual to locate, compete for and sequester scarce resources. Such cues may themselves form the entire basis for discrimination, or they may comprise part of a multimodal signal complex (Hill & Montgomerie 1994; Hebets & Papaj 2005).

The mosquitofish, *Gambusia holbrooki*, is a livebearing Poeciliid fish, which is native to the southeastern United States. Females reach up to ca. 4 cm in length, while males reach up to ca. 3 cm. The species exhibits sexual dimorphism and operates a coercive mating system, wherein females are harassed and coerced into mating by the males (Dadda et al. 2005). While males are promiscuous and may mate with many females, they are known to mate selectively, choosing female characteristics that relate to brood size and quality (Hoysak & Godin 2007). Females and, to a lesser extent, males are social and aggregate to form shoals. Mosquitofish are generalist foragers and have a broad diet, consuming zooplankton, algae, benthic invertebrates and larval fish (Pyke 2005, 2008).

We tested four main hypotheses. First, when presented with odour cues arising from high-protein and low-protein food sources, mosquitofish would orient towards the high-protein one. Second, when presented with odour cues arising from both conspecifics that had recently eaten a high-protein food and conspecifics that had recently eaten a low-protein food, mosquitofish would orient towards the former. Third, we hypothesized that in both the direct and the indirect food odour cue treatments, the response of the focal mosquitofish would be condition dependent, specifically that focal mosquitofish that had recently eaten a low-protein diet would show a stronger positive response to high-protein cues than focal mosquitofish that had recently eaten a high-protein diet themselves. Finally, male mosquitofish presented with both females that had recently eaten a high-protein diet and females that had recently eaten a low-protein diet would attempt to mate more frequently with the former.

METHODS

Study Animals

We collected mosquitofish for use in this study during late 2009 from Lake Northam, Australia (33°53'6.31'S, 151°11'35.71'E). Fish were transported from the lake to the University, a journey of approximately 400 m, in buckets. Following this, the fish were introduced to their new holding conditions in the aquarium facilities of the University of Sydney and were monitored frequently for any signs of distress. No signs of distress were observed and there were no signs of injury or illness in the fish during their time in captivity. Fish were kept at a stocking density of no more than 100 fish per 180-litre vat and were fed daily ad libitum with Wardley tropical fish flakes prior to the experiment. Each vat was provided with environmental enrichment in the form of a gravel substrate and aquatic plants. Water in each vat was filtered and aerated continuously by an Aquaclear 600 external filter. The fish were kept at 22–24 °C under a 12:12 h light:dark photoregime. The fish were maintained in these conditions for 4–6 weeks prior to experiments. Including the experimental period, the fish were maintained in captivity for between 5 and 7 weeks. Mosquitofish are not endemic to Australia and have been declared a 'noxious' species in Australia because of their ecological impact on native species (Pyke 2008). For this reason, mosquitofish are not permitted to be released following capture. Therefore, after the experiment, the fish were humanely euthanized using an aqueous solution of the anaesthetic MS222 at a dose rate of 250 mg/litre, buffered to a pH of 7 using calcium carbonate. The fish were noted to decrease activity gradually and finally to cease breathing over a period of approximately 90 s. We left the fish in the solution for a further 10 min to ensure that the fish had been euthanized before they were netted out and placed into a freezer prior to disposal. In line with recommended animal ethics procedures, we designed our experiments carefully to minimize the number of animals that would be used. To assist with this we carried out power tests to determine the number of replicates a priori, based on expected effect sizes.

Diet and Conditioning

After the fish had been in captivity for between 4 and 6 weeks, we transferred them in groups of 12 to a conditioning tank, measuring 140 × 40 cm and 30 cm high. This was divided into seven sections of 20 cm along its longest axis using opaque plastic sheets that were fixed in place using silicone sealant. A pump circulated water throughout the tank at a rate of 2 litres/min and water flow was facilitated using holes of 5 cm diameter covered with fine mesh to prevent fish escaping. The purpose of this water circulation was to ensure that each batch of fish was exposed to the same water chemistry and hence that the chemical cues expressed by the fish would relate only to their diet (sensu Ward et al. 2009). We conditioned four batches of fish at a time. Each batch of fish was randomly allocated to one of two dietary treatments (see Table 1 for details). Diet Pc comprised 80% protein, 10% fat and 10% carbohydrate on a dry mass basis; Diet pC comprised 10% protein, 80%

Table 1
Components of each of the diets (g)

	High-protein diet (Pc)	Low-protein diet (pC)
Protein	27.2	3.4
Carbohydrate	3.4	27.2
Fat	3.4	3.4
Agar	11	11
Cellulose	28	28
Water	340	340

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