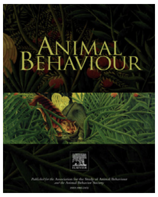
Animal Behaviour 114 (2016) 173–179

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Sex-specific offspring discrimination reflects respective risks and costs of misdirected care in a poison frog

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ARTICLE INFO

Article history:
Received 21 October 2015
Initial acceptance 24 November 2015
Final acceptance 25 January 2016
Available online
MS. number: 15-00898R

Keywords:
amphibians
offspring discrimination
parental care
sex differences
tadpole transport

The ability to differentiate between one's own and foreign offspring ensures the exclusive allocation of costly parental care to only related progeny. The selective pressure to evolve offspring discrimination strategies is largely shaped by the likelihood and costs of offspring confusion. We hypothesize that males and females with different reproductive and spatial behaviours face different risks of confusing their own with others' offspring, and this should favour differential offspring discrimination strategies in the two sexes. In the brilliant-thighed poison frog, *Allobates femoralis*, males and females are highly polygamous, terrestrial clutches are laid in male territories and females abandon the clutch after oviposition. We investigated whether males and females differentiate between their own offspring and unrelated young, whether they use direct or indirect cues and whether the concurrent presence of their own clutch is essential to elicit parental behaviours. Males transported tadpoles regardless of location or parentage, but to a lesser extent in the absence of their own clutch. Females discriminated between clutches based on exact location and transported tadpoles only in the presence of their own clutch. This sex-specific selectivity of males and females during parental care reflects the differences in their respective costs of offspring confusion, resulting from differences in their spatial and reproductive behaviours.

In species with parental care, the ability to recognize and discriminate between one's own offspring and unrelated young can have considerable fitness consequences for both the caregiving parent and its progeny (Beecher, 1991; Sherman, Reeve, & Pfennig, 1997). As parental behaviours are often very costly, parents in noncooperatively breeding species should ensure that care is directed exclusively to their own progeny (Duckworth, Badyaev, & Parlow, 2003; Queller, 1997; Trivers, 1972; but see also Larsson, Tegelström, & Forslund, 1995). Thus in several species males adjust the intensity of care according to the level of perceived paternity (bluegill sunfish, *Lepomis macrochirus*: Neff, 2003; eastern bluebirds, *Sialia sialis*: MacDougall-Shackleton & Robertson, 1998; pumpkinseed sunfish, *Lepomis gibbosus*: Rios-Cardenas & Webster, 2005; blue-footed boobies, *Sula nebouxii*: Osorio-Beristain & Drummond, 2001; but see also Kempenaers, Lanctot, & Robertson, 1998).

Substantial fitness benefits of accurate offspring discrimination abilities can be expected particularly when the risk of misdirected care is high (i.e. the likelihood of mistaking unrelated for one's own offspring, Westneat & Sherman, 1993). This is the case, for example, when offspring are highly mobile, when foreign progeny are in close spatial proximity, under polygamy or when cuckoldry is common. Several mechanisms have been proposed to explain how parents may differentiate between their own offspring and unrelated young: recognition alleles, phenotype matching, assortative learning or spatial recognition (Komdeur & Hatchwell, 1999; Sherman et al., 1997). Discrimination mechanisms are also classified regarding the use of direct or indirect cues: direct recognition refers to parents recognizing specific phenotypic characteristics of their young (chemical: Head, Doughty, Blomberg, & Keogh, 2008; Neff, 2003; Neff & Sherman, 2005; acoustic: Knörnschild & Von Helversen, 2008; visual: Lahti & Lahti, 2002; Underwood & Sealy, 2006); indirect recognition occurs if parents use contextual cues such as spatial location, frequency of encounters, larval age or external cues associated with an offspring's location (Bonadonna, Cunningham, Jouventin, Hesters, & Nevitt, 2003; Lank, Bousfield, Cooke, & Rockwell, 1991; Müller & Eggert, 1990; Waldman, 1987). Parents should follow the simplest set of rules to optimize costs and

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http://dx.doi.org/10.1016/j.anbehav.2016.02.008

benefits between two kinds of possible errors in offspring recognition: (1) caring for unrelated progeny and (2) rejecting their own offspring as recipients of care (Trivers, 1974). For example, indirect rather than direct recognition is expected to evolve when offspring are not likely to move and are deposited in spatially discrete clusters or inside a parent's territory (Sherman et al., 1997; Waldman, 1987). Sex-specific differences in spatial behaviours (e.g. territoriality versus high mobility) and/or reproductive strategies (e.g. choosing versus advertising sex, parental care versus offspring desertion) might thus favour different offspring discrimination strategies in males and females.

Behavioural differences between males and females are common features across most species and across social/environmental contexts. For example, several studies have demonstrated sex differences in species recognition abilities, probably resulting from the differential costs of mismating and hybridization or sex-specific risks of predation (Saetre, Král, & Bureš, 1997; Svensson, Karlsson, Friberg, & Eroukhmanoff, 2007). Regarding offspring discrimination, sex differences have been shown in the razorbill, *Alca torda*, in which care by each parent takes place at different stages of offspring development (Insley, Paredes, & Jones, 2003). Studies on offspring discrimination have mostly focused on highly social vertebrate species with prolonged and complex parental care (Komdeur & Hatchwell, 1999; Krause & Caspers, 2012), which at the same time are considered to possess high cognitive abilities and learning capacities (Byrne & Whiten, 1988; Kummer, Daston, Gigerenzer, & Silk, 1997; but see also Holekamp, 2007). Little is known about offspring discrimination abilities in less social vertebrates, such as amphibians (but see Poelman & Dicke, 2007; Stynoski, 2009). While general kin discrimination and recognition mechanisms have been demonstrated for several amphibian species (Blaustein & Waldman, 1992; Waldman, 2005), the majority of studies have focused on differential behavioural responses towards kin and nonkin among amphibian larvae. In many animals, including amphibians, spatial and reproductive behaviours differ considerably between the sexes. In species with parental care, differential likelihood and costs of misdirected care might thus drive different offspring discrimination strategies in males and females.

We tested this hypothesis in *Allobates femoralis*, a Neotropical poison frog with sex-specific reproductive strategies and spatial behaviour. Males defend territories of about 150 m^2 (M. Ringler, Ringler, Magaña-Mendoza, & Hödl, 2011) and announce territory ownership by a prominent advertisement call (Hödl, Amézquita, & Narins, 2004; M. Ringler et al., 2011; M. Ringler, Ursprung, & Hödl, 2009). Females occupy perches which are interspersed between male territories (E. Ringler, Ringler, Jehle, & Hödl, 2012). Both sexes are iteroparous and highly polygamous throughout the prolonged reproductive season (Ursprung, Ringler, Jehle, & Hödl, 2011). Under optimal conditions in captivity females can produce a clutch every 8 days (Weygoldt, 1980). Courtship and mating occur in male territories where terrestrial clutches are laid and fertilized in the leaf litter (Montanarin, Kaefer, & Lima, 2011; E. Ringler et al., 2012; M. Ringler et al., 2009; Roithmair, 1992). Females abandon the clutch and return to their perches immediately after oviposition; males neither remain close to the clutches (i.e. egg guarding) nor provide any further care such as egg moistening or active predator defence. After 3 weeks of larval development the tadpoles are generally transported by the father to nearby water bodies (E. Ringler, Pašukonis, Hödl, & Ringler, 2013; Weygoldt, 1980). However, it has been shown that the mother takes over parental duties when the father disappears (E. Ringler, Pašukonis, Fitch, Huber, Hödl, & Ringler, 2015). As soon as the parent positions itself on the clutch the larvae wiggle onto the parent's back and are subsequently transported to widely dispersed water bodies up to a distance of 200 m (E. Ringler et al., 2013).

Considering the differential reproductive strategies and the unequal frequency of parental care in male and female *A. femoralis*, differences in offspring discrimination strategies between the sexes can be expected. As clutches are deposited in male territories, males can generally assume that all clutches inside their territory are their own offspring, and might therefore use a simple discrimination rule such as ‘all clutches inside my territory are mine’. In contrast, females have their clutches dispersed across multiple male territories, which, in general, will also contain clutches of other females. Thus, if females transfer tadpoles when the male disappears, they should be much more selective than males. Tadpole transport is likely to be costly for the carrying individual in terms of energy investment, predation risk and lost potential mating opportunities. During times of absence other males might also try to take over the territory, resulting in serious fights as soon as the former territory owner returns (E. Ringler, M. Ringler & A. Pašukonis, personal observation). Transport of unrelated offspring would impose these costs on either sex, but without yielding any benefits, and thus should be avoided. Specifically, we asked whether males and females discriminate between their own offspring and unrelated young and whether they use direct or indirect cues when transporting tadpoles. Furthermore, we tested whether parental behaviours are only elicited when an individual is predisposed to perform parental care by the presence of its own clutch.

METHODS

We performed a behavioural experiment under controlled laboratory conditions from August 2014 to March 2015 in the animal care facilities at the University of Vienna. Both wild-caught frogs ($N = 19$) from French Guiana and our own captive-bred individuals ($N = 29$) were used for the experiments (see Table A1). All tested individuals were adult and had successfully produced/sired a clutch previously.

Ethical Note and Housing

All frogs used in this study are part of the ex situ laboratory population of the animal care facilities at the University of Vienna. Permissions for sampling and export of wild-caught frogs were obtained from the responsible French authorities (DIREN: Arrete n° 82 du 10.08.2012 and Arrete n° 4 du 14.01.2013). All experimental procedures were in strict accordance with current Austrian law, approved by the Ethics Committee of the University of Vienna, and followed the ASAB/ABS guidelines for the treatment of animals in behavioural research and teaching. The experiments were noninvasive as they were based on behavioural observations alone and therefore do not fall under the Austrian Animal Experiments Act (§ 2, Federal Law Gazette No. 114/2012).

All experiments were performed in standard glass terraria of equal size (60 × 40 cm and 40 cm high) with identical equipment and furnishing. The floor was covered with pebbles of expanded clay, the back and side walls were covered with xaxim (plates made of dried tree fern stems) and cork mats, and the front was covered with fabric to prevent visual contact between neighbouring terraria and disturbances during maintenance. All terraria contained half a coconut shell, a small plant and a branch as suitable shelters and calling positions. We provided oak leaves as a substrate for oviposition, and a small glass bowl of 12 cm diameter filled with approximately 35 ml of water for tadpole deposition. An automatic raining, heating and lighting system ensured standardized climatic conditions with similar