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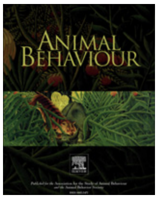

Discrimination of offspring by indirect recognition in an egg-feeding dendrobatid frog, *Oophaga pumilio*

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Offspring discrimination, the differential treatment of offspring and unrelated young, functions in numerous animal taxa to ensure that vital and costly parental care behaviours are appropriately directed. Discrimination can be facilitated either by direct (phenotypic) recognition of offspring or by indirect (nonphenotypic) recognition of offspring location. Offspring discrimination and recognition mechanisms have not been identified in an amphibian. In the strawberry poison frog, *Oophaga pumilio*, a dendrobatid frog with obligatory maternal provisioning behaviour, I tested whether mothers discriminate between offspring and unrelated young, whether they use direct or indirect recognition cues, and whether prior parental investment plays a contextual role in the differential treatment of young. Mother frogs utilized tadpole-rearing cups attached to tree trunks in wet tropical forest. After manipulating the identity, location and/or age of tadpoles in cups, I determined whether maternal provisioning behaviour was maintained by measuring tadpole growth and development. Mothers provisioned young regardless of tadpole identity, but were sensitive to location and did not provision tadpoles that were moved 2 cm to an adjacent cup. When given a choice between related and unrelated tadpoles in originally chosen or adjacent cups, mothers discriminated by location, but not by relatedness. Maternal provisioning behaviour persisted when a tadpole provisioned for 10 days was replaced with either an age-matched or newly hatched unrelated tadpole, so direct offspring recognition does not appear to be dependent on prior parental investment. Together, these results provide strong evidence that mother *O. pumilio* use indirect recognition cues to discriminate between offspring and unrelated offspring.

In species that show parental care, the ability to discriminate between offspring and unrelated young has strong and obvious implications for fitness. The success of a parent's offspring is directly related to the quality and amount of care that the offspring receive (Hepper 1986). Also, parental care behaviours are costly to parents and their future offspring, and these costs are fruitless if care is directed at unrelated young (Trivers 1972; Queller 1997; Duckworth et al. 2003). Thus, to ensure that care is beneficial, parents from diverse taxa modulate the intensity and the target of their care according to the genetic relatedness of young. For example, in bluegill sunfish, *Lepomis macrochirus*, fathers adjust the intensity of care based on the prevalence of cuckolding males and on the familiarity of offspring chemosensory cues (Neff 2003). Mother sub-Antarctic fur seals, *Arctocephalus tropicalis*, forage at sea for weeks, and return to provision their offspring after recognizing their pups' voices among hundreds of others (Charrier et al. 2002). Mother crab spiders, *Diaea ergandros*, maintain nests with both related and unrelated young, but only catch prey and produce trophic oocytes for their own offspring (Evans 1998).

For parents to discriminate based on the degree of genetic relatedness of young, a recognition mechanism must be present (Sherman et al. 1997; Tsutsui 2004). Recognition mechanisms can indicate relatedness in one of two ways. In direct recognition mechanisms, parents use a phenotypic component of the young (Waldman 1987). The phenotypic cues that are used to recognize offspring can vary widely in modality, from chemosensory (Greenberg 1979; Main & Bull 1996; Evans 1998; Yamazaki et al. 2000; Neff & Sherman 2005) to auditory (Espmark 1971; Jouventin et al. 1999; Charrier et al. 2002; Searby & Jouventin 2003; Knörnschild & Von Helversen 2008) and less often to visual (Lahti & Lahti 2002) modes. In indirect recognition mechanisms, on the other hand, parents make use of a contextual cue such as spatial location or frequency of encounters with young (Waldman 1987). Indirect mechanisms are most commonly used when offspring are not likely to move from where parents have left them, or when offspring are not likely to be confused with unrelated young in an adjacent location (Waldman 1987; Sherman et al. 1997). In these cases, parents use spatial, chemosensory or visual cues that are derived from the nest itself (Lank et al. 1991; Bonadonna et al. 2003;

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Neff 2003; Chiu & Kam 2006), or depend on temporal cues such as in several rodent species, which cease infanticidal behaviours while nursing (Elwood 1991). Both direct and indirect mechanisms can signify relatedness (Hamilton 1964), and thus both can mediate the differential treatment of young.

Kin discrimination and recognition mechanisms are known to occur in amphibian species (Blaustein & Waldman 1992), but have not been demonstrated in the context of posthatching parental care (Gibbons et al. 2003). Amphibian discrimination and recognition have been examined almost exclusively in the contexts of sibling grouping of tadpoles (Blaustein & Waldman 1992), cannibalism of larval nonsiblings over siblings and first cousins (Pfennig et al. 1993, 1994), and cannibalism of unrelated young over offspring (Forester et al. 1983; Gabor 1996; Peterson 2000; Gibbons et al. 2003). Poelman & Dicke (2007) examined but did not find evidence of an ability to discriminate offspring from unrelated young in a poison frog, *Dendrobates ventrimaculatus*. However, another poison frog, *Oophaga pumilio* (formerly *Dendrobates pumilio*; Grant et al. 2006) may be more likely than *D. ventrimaculatus* to discriminate between offspring and unrelated young because it shows more extreme parental investment that includes provisioning of offspring (Brust 1993). In addition, male *D. ventrimaculatus* defend the territories in which they rear their tadpoles (Poelman & Dicke 2007), whereas female *O. pumilio* rear tadpoles in a social environment with a greater overlap of home ranges and they compete with other females for the same tadpole-rearing sites (Pröhl & Hödl 1999; Pröhl & Berke 2001; Haase & Pröhl 2002). For these reasons I decided to investigate whether female *O. pumilio* are able to discriminate between offspring and unrelated young, whether they use direct or indirect recognition cues, and whether prior parental investment plays a role in differential treatment of young.

Moreover, kin recognition is often context dependent, such that its expression varies with the costs and benefits of discrimination (Sherman et al. 1997). Thus, kin recognition is often expected to vary with environmental conditions (Blaustein & Waldman 1992; Holmes & Mateo 2007). Therefore, I studied offspring recognition in a free-living population of *O. pumilio* at La Selva Biological Station in Costa Rica, where the natural environment might be more variable than a laboratory setting.

In *O. pumilio*, eggs are fertilized in leaf litter on the forest floor, and egg clutches are guarded and hydrated by fathers for 7–12 days (Weygoldt 1980; Brust 1993; Haase & Pröhl 2002). Once eggs develop into tadpoles, mothers return to the clutch to transport each tadpole individually to its own water-filled axil in a bromeliad or other water-holding plant, depositing only one tadpole in each axil (Donnelly 1989; Brust 1993; Maple 2002). Then, mothers return to each tadpole every 1–8 days for approximately 6 weeks to provision them by laying unfertilized eggs into the water (Brust 1993). Even though mothers do not maintain more than one concurrent clutch of offspring (Weygoldt 1980; Brust 1993; Haase & Pröhl 2002; Pröhl 2005), tadpoles of vastly different sizes and stages are found in different axils of the same bromeliads (Weygoldt 1980; J.L.S., personal observation), and different mothers are seen caring for offspring in the same plants (Haase & Pröhl 2002; J.L.S., personal observation). Together these observations suggest that mother *O. pumilio* need to discriminate regularly between offspring and unrelated young. Indeed, mothers spend a significant amount of time searching bromeliads, and always do some searching before depositing nutritive eggs (Brust 1990). Searching behaviour may allow mothers to distinguish between axils or between tadpoles.

In the present field study, I tested whether and how mother *O. pumilio* discriminate between offspring and unrelated young when provisioning. In a series of three experiments, I determined whether mothers use either tadpole phenotypic cues or spatial location to recognize their young (recognition experiment), the relative importance of indirect and direct recognition cues in offspring discrimination during provisioning (paired discrimination experiment), and whether size and/or age contribute to offspring recognition (postparental investment recognition experiment). The postparental investment recognition experiment was necessary because offspring recognition may not occur until after parents have made some investment in their offspring (Lefevre et al. 1998; Mateo 2006).

Figure 1. Field set-up of tadpole-rearing cups, which mimicked two adjacent natural bromeliad axils, and thus required that mothers had to make the same choices they would have made in a natural bromeliad. (a) Pair of cups tied to a tree with a bathing male *Oophaga pumilio*. (b) Mother *O. pumilio* with a recently deposited tadpole below her forelimb.