Dynamic switching in predator attack and maternal defence of prey

SINLAN POO[1]*, THEODORE A. EVANS[2], MING KAI TAN[3] and DAVID P. BICKFORD[3]

[1]*Sakaerat Environmental Research Station, 1 Moo 9, Udom Sab Subdistrict, Wang Nam Khieo District, Nakhon Ratchasima Province, 30370, Thailand*
[2]*School of Animal Biology, The University of Western Australia, 35 Stirling Highway, Crawley, WA, 6009, Australia*
[3]*Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Block S3, 117543, Singapore*

Predator and prey relationships are dynamic and interrelated. Thus, any offensive behaviour will vary according to differing defensive behaviours, or vice versa, within each species in any predator–prey system. However, most studies are one-sided as they focus on just one behaviour, that of either the predator or prey. Here, we examine both predatory behaviour of an oophagus katydid and antipredator behaviour by a frog with egg-stage parental care. Katydid offensive behaviour and predation success was greater in females and increased with predator maturity and size. Frog defensive behaviour was sex specific, probably because only mothers provide parental care. Defensive behaviour could be active, such as charging predators, or passive, such as sheltering eggs, with greater active defence against larger predators; neither was influenced by offspring age. These results are contrary to existing theory, which argues parental investment ought to be negatively correlated with parental predation risks and affected by offspring age. This study highlights the use of antipredator behaviour to test predictions of parental investment theories in amphibians. In addition, it illustrates the need to consider factors that influence both species concurrently when examining the complex interaction between predators and parents. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **118**, 901–910.

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INTRODUCTION

Eggs are valuable prey. They are relatively easy to subdue and provide an important source of nutrition (Denoel & Demars, 2008). Oophagus species are found across many taxa (e.g. Coelho, Malaquias & Calado, 2006; de Queiroz & Rodriguez-Robles, 2006; Koedam, Aponte & Imperatriz-Fonseca, 2007; Cerwenka *et al.*, 2012). Oophagy can be obligatory, depending entirely on eggs (Kam, Chuang & Yen, 1996; Li, Fry & Kini, 2005), or opportunistic, depending on nutritional needs or availability of eggs (Ochi, Sato & Yanagisawa, 1999; Denoel & Demars, 2008).

Due to their desirability as a food source, eggs require defences to lower their vulnerability to predation. Defence can come in many forms, including safety attained in numbers (selfish herd, overwhelming predators with abundance of eggs), morphological adaptations (having hard cases or rough surfaces) (Dumont, Nandini & Sarma, 2002), and additional investment by parents. Parents can alter their behaviours in response to predators by concealing their eggs (Lemos *et al.*, 2010; Hirayama & Kasuya, 2013; McKeon & Summers, 2013), or engage in antipredation defence (Requena *et al.*, 2009; Colombelli-Negrel *et al.*, 2010; Goiran & Shine, 2015).

Defence of offspring that reduces future reproduction is a form of parental investment (Trivers, 1972; Smiseth, Kölliker & Royle, 2012). Behaviours that increase survival in current offspring can reduce energy available for future offspring production or

*Corresponding author. E-mail: sheilapoo@gmail.com

parental self-preservation (Curio & Regelmann, 1985; McLean, Smith & Stewart, 1986; Redondo, 1989). Consequently, parents should vary investment in offspring relative to level of risk (i.e. probability of occurrence and severity of impact) in conjunction with other life-history characteristics. For example, parents should decrease investment under high personal predation risks to preserve future reproduction opportunities (Dassow *et al.*, 2012; Ghalambor, Peluc & Martin, 2013). Similarly, parents are expected to increase investment in older offspring (Trivers, 1972; Winkler, 1987), due to the additive benefits of larger past investment (Coleman & Gross, 1991) or larger current benefits from more mature offspring, which have higher survival chances (Ackerman & Eadie, 2003).

Although there are numerous studies on predatory and antipredator behaviour, the majority examines relationships solely from perspective of either predator or prey. Studies that examine both views, although rare, indicate the importance of concurrent information processing to understand fully these behavioural interactions (Christensen, 1996; Wcislo & Schatz, 2003; Uma & Weiss, 2012). For example, predator presence can trigger avoidance behaviour in prey and, in turn, counter-behaviour by predators (Wcislo & Schatz, 2003). Behaviour of both parties can be further affected by their respective life-history characteristics. For example, increase in prey size is associated with a switch from avoidance to defensive behaviours in prey and a decrease in approaching behaviour in predators (Uma & Weiss, 2012). A comparable, but unexplored, interaction may exist between oophagus predators and egg-caring parents. In this case, the relative costs and benefits for predators (e.g. the decision, timing, and effort of attack) and parents (similarly, the decision, timing, and effort of defence) create a dynamic relationship that requires examination of behaviour in both.

The interaction between *Hexacentrus unicolor* (Serville, 1831), an egg-eating katydid, and *Chiromantis hansenae* (Cochran, 1927), an egg-caring treefrog, provides an excellent opportunity to study predator–parent dynamics from both perspectives. *Hexacentrus unicolor* is an omnivorous species with three distinct life stages (egg, nymph, and adult stage), with the latter two stages observed to prey on *C. hansenae* frog eggs and frogs (Poo & Bickford, 2013; I. Poo, pers. observ.). *Chiromantis hansenae* is an arboreal-breeding frog that lays gelatinous egg masses that overhang ponds. Maternal care is essential to the survival of their eggs, without which over 60% of egg clutches will suffer mortality due to desiccation (Poo & Bickford, 2013). Predation is the primary source of egg mortality under natural settings (Poo & Bickford, 2013), and katydids are the main predator (Poo & Bickford, 2014). As a response to

predation pressures from katydids, eggs can accelerate hatching to escape predation, with eggs at different developmental stages responding differently to predation cues (Poo & Bickford, 2014). However, field observations indicate female frogs that attend and guard their eggs can effectively defend them against predators (Fig. 1; Poo & Bickford, 2013).

Predatory behaviour by katydids in distinct life stages (adult and nymph) and obligatory parental care in frogs allow us to examine not only the effects of prey on predator distribution and behaviour, but also the effects of predation risk on level of parental investment in prey. Little is known about katydid abundance in response to transient food resources and ontogenetic diet shifts (Pearson *et al.*, 2011). Similarly, few empirical studies show frogs adjusting parental defence behaviour in response to predation risks or other factors that influence parental investment. This situation is particularly surprising as it is often assumed that defence against predators is one of the primary functions of amphibian egg attendance (Forester, 1979; Crump, 1996). Consequently, the high diversity in amphibian reproductive behaviour and modes of parental care is juxtaposed with a paucity of studies that examine fundamental assumptions in parental care.

In this study, we record predatory behaviours by an oophagus katydid and antipredator behaviours by an egg-caring frog in a dynamic system. Specifically, we address the following questions: (1) Do katydids respond to frog egg availability? (2) Is katydid predatory behaviour affected by its life-history characteristics? (3) Do frogs respond to presence of predatory katydid? (4) Is frog antipredator behaviour correlated with their involvement in parental care? and (5) Is level of parental investment in defence influenced by offspring age?

Figure 1. Female treefrog, *Chiromantis hansenae*, guarding her eggs (white clutch under frog) against a predatory adult katydid, *Hexacentrus unicolor*.

METHODS

EXPERIMENTAL SETUP

We conducted the field research from July to October 2013 at the Sakaerat Environmental Research Station in Thailand (14°30′N, 101°55′E, elevation 250–762 m). We conducted field observations at a seasonal pond within the dry evergreen forest. We conducted laboratory experiments using animals collected from the field site. We housed frogs in glass aquaria ($40 \times 20 \times 25$ cm) that contained rocks, plants, and filled with 2 cm of aged tap water to simulate pond habitats. Aquaria had plastic mesh covers and a vertical mesh dividing the tank into two equal partitions. Only one side of each tank was used to be consistent with experimental design in a concurrent study (Poo & Bickford, 2014). We monitored frogs and eggs twice daily, and sprayed them with rain water to provide hydration. We collected katydids 24–48 h prior to the experiment and starved them to standardize and maximize predatory behaviour. We conducted observations between 2000 and 0300 h, when both frogs and katydids were active. We measured frog snout vent length (SVL) and katydid body length (BL). We returned all animals to their original locations once observations had been concluded. Methods followed the Institutional Animal Care and Use Committee approved protocol (B11/12) at the National University of Singapore.

PART 1: FIELD SURVEY OF KATYDID ABUNDANCE AND DIET

To investigate abundance and diet of katydids, we conducted visual encounter surveys in pond and forest habitats. We walked transects along pond edges and in forest trails located more than 50 m away from ponds. Each transect was 20 m long, 1.5 m wide, and 2 m above ground. We recorded the life stage (adult or nymph) and sex, and made feeding status observations (consuming animal material, plant material, or nothing) for each individual encountered.

PART 2: ANTIPREDATOR BEHAVIOUR OF GUARDIAN FEMALE FROG

To examine the effects of predation risks and offspring age on parental investment, we made 2 h focal observations of females that were guarding young (2-day-old) or old (4-day-old) eggs in response to the presence of a katydid adult or nymph; note that eggs usually hatch after 5 days (Poo & Bickford, 2014). We placed one male and one gravid female frog into an aquarium. Frogs mated readily in aquaria and most eggs were laid between 2100 and

0300 h. Guardian female frog behaviour was recorded each minute and categorized into: active defence, passive defence, or avoidance behaviour. Active defence behaviours included: charge (leap towards or onto predator) and jerk (sharp, sudden spasmodic movement of body). Passive defence behaviours included: shield (position body over eggs and extend limbs to cover eggs) and puff up (enlarge body by filling with air). Avoidance behaviour included: retreat (leap away from predator in response to predator approach). Once observations concluded, katydids were removed while frogs were allowed to remain in aquaria and continue caring for eggs until they hatched.

PART 3: ANTIPREDATOR BEHAVIOUR OF MALE FROG

To examine the effects of predation risks on behaviour of frogs without parental care, we made 1 h focal observations of male frogs in response to the presence of a katydid adult or nymph. We placed a single male frog into an aquarium and allowed it to acclimatize for 15 min prior to the introduction of a katydid. Observations of antipredator behaviours followed that of the guardian female frogs, with the exception of shield, as males do not attend eggs.

PART 4: PREDATORY BEHAVIOUR OF KATYDID

To examine factors that affect predatory behaviour, we observed katydids concurrently with observations of guardian female frogs (part 2) and male frogs (part 3). Focal observations of katydids followed the same methods as that of frogs. For katydids that were introduced to tanks with guardian female frogs and their eggs, the following behaviours were recorded: approach eggs (move directly towards eggs), prey on eggs (consume part or entire egg clutch), and prey on female frog. For katydids introduced to tanks with single male frogs, the following behaviours were recorded: approach male (move directly towards male frog) and prey on male frog.

STATISTICAL ANALYSES

For field surveys (part 1), we compared the abundance of katydids in pond and in forest transects using Mann–Whitney U-Test. We analyzed the relationship between katydid life stage and feeding status using 2×3 Fisher's exact test for small sample sizes, with katydid life stage (adult or nymph) and feeding status (consumption of animals, plants, or none). The same procedure was done for the relationship between katydid sex and feeding status. For laboratory observations of frogs (part 2 and 3), we analyzed behaviours with GLM with underlying

quasi-Poisson distribution, used for count data and corrected for over-dispersion. For guardian female frog behaviour (part 2), we tested the explanatory variables: katydid life stage, offspring age, female frog SVL, and all interactions between the variables in a single model for each of the three behavioural categories (active defence, passive defence, and avoidance). Subsequently, we analyzed the same explanatory variables for each of the five types of female behaviour (charge, jerk, shield, puff up, and retreat). Similarly for male frogs (part 3), we tested the explanatory variables: katydid life stage, male frog SVL, and their interactions for the three categories and four types of male behaviour observed (charge, jerk, puff up, and retreat). For laboratory observations of katydids (part 4), we tested the explanatory variables: effect of katydid life stage, katydid BL, katydid sex, and all interactions in a single model with quasi-Poisson GLM for approaching behaviours (approach eggs and approach male frog) and with Bernoulli GLM for predatory behaviours (prey on eggs, prey on female frog, and prey on male frog), as predation events were quantified as present or absent per treatment. We used stepwise model simplification for all GLMs and determined the statistical significance using χ^2 test for Bernoulli GLMs and F test for quasi-Poisson GLMs. We applied Bonferroni–Holm corrections to all *P*-values to control for multiple behavioural comparisons (Holm, 1979). We performed all statistical analyses using R programming language (R Core Team, 2013). Means are presented with ± standard errors.

RESULTS

PART 1: KATYDID ABUNDANCE AND DIET

We conducted 16 visual encounter surveys (N = 8 for pond and forest transects each), with higher katydid abundances observed in pond transects compared with forest transects (3.50 ± 1.18 and 0.25 ± 0.16, respectively, two-sample Wilcoxon test, P = 0.03). Katydid feeding was significantly different between life stages (Fisher's exact test, N = 30, P < 0.01), with only adults observed consuming animal prey, while both adults and nymphs observed consuming plants. Feeding was not significantly different between sexes (Fisher's exact test, N = 24, P = 0.28).

PART 2: ANTIPREDATOR BEHAVIOUR OF GUARDIAN FEMALE FROG

We observed the behaviour of 53 guardian female frogs, and used the data from 51. Two frogs were not used because one frog escaped before we measured the SVL, and one frog was eaten by a katydid. These two data points were removed from further analyses. The behaviour of guardian female frogs was analyzed for 28 individuals in katydid adult treatment (N = 14 for those guarding young and old offspring each) and 23 individuals in katydid nymph treatment (N = 11 and 12, respectively). Guardian female SVL was 25.2 ± 0.2 mm.

Active defence behaviour was observed in 75% of guardian females (75% and 45% for charge and jerk, respectively). Guardian females showed higher instances of active defence behaviours towards katydid adults than towards nymphs (7.71 ± 1.28 and 2.91 ± 0.73, respectively, d.f. = 1, P = 0.01, Fig. 2A). No effect was found for offspring age, guardian female SVL, or any interactions, all of which were subsequently removed during model simplification. Passive defence behaviour was observed in 61% of guardian females (49% and 41% for shield and puff up, respectively), although behaviours did not differ in response to katydid life stage, offspring age, guardian female SVL, or their interaction (Fig. 2A). Similarly, avoidance behaviour occurred in 25% of guardian females, but did not differ in relation to the factors tested.

For the individual types of active and passive defence behaviour, only charge was significantly affected by explanatory factors (Fig. 2B), with guardian females charging towards katydid adults more frequently than towards nymphs (5.68 ± 0.96 and 2.35 ± 0.63, df = 1, P = 0.046). Although females also exhibited more frequent jerk behaviour towards katydid adults compared with nymphs, the difference was not significant after Bonferroni–Holm correction (2.54 ± 0.67 and 0.61 ± 0.26, respectively, df = 1, P = 0.07). Both types of active defence behaviours by guardian females can be successful in deterring katydids, with katydids moving away from eggs in 93% and 50% of encounters in response to charge and jerk, respectively.

Although there was no effect of egg age on guardian female behaviour, there was an effect of egg age on egg defence behaviour. Induced hatching occurred in 50% of older egg clutches that were preyed upon (N = 2 of 4), with hatchlings escaping katydid predation, while no hatching was observed in younger eggs (N = 6).

PART 3: ANTIPREDATOR BEHAVIOUR OF MALE FROG

We observed the behaviour of 31 male frogs in katydid adult and nymph treatments (N = 16 and 15, respectively). Male frog SVL was 21.8 ± 0.2 mm. Neither active nor passive defence behaviours were exhibited by males. Avoidance behaviour was exhibited by the majority of males (61%), but was not significantly different in response to katydid life stages, male frog SVL, or their interaction (Fig. 2).
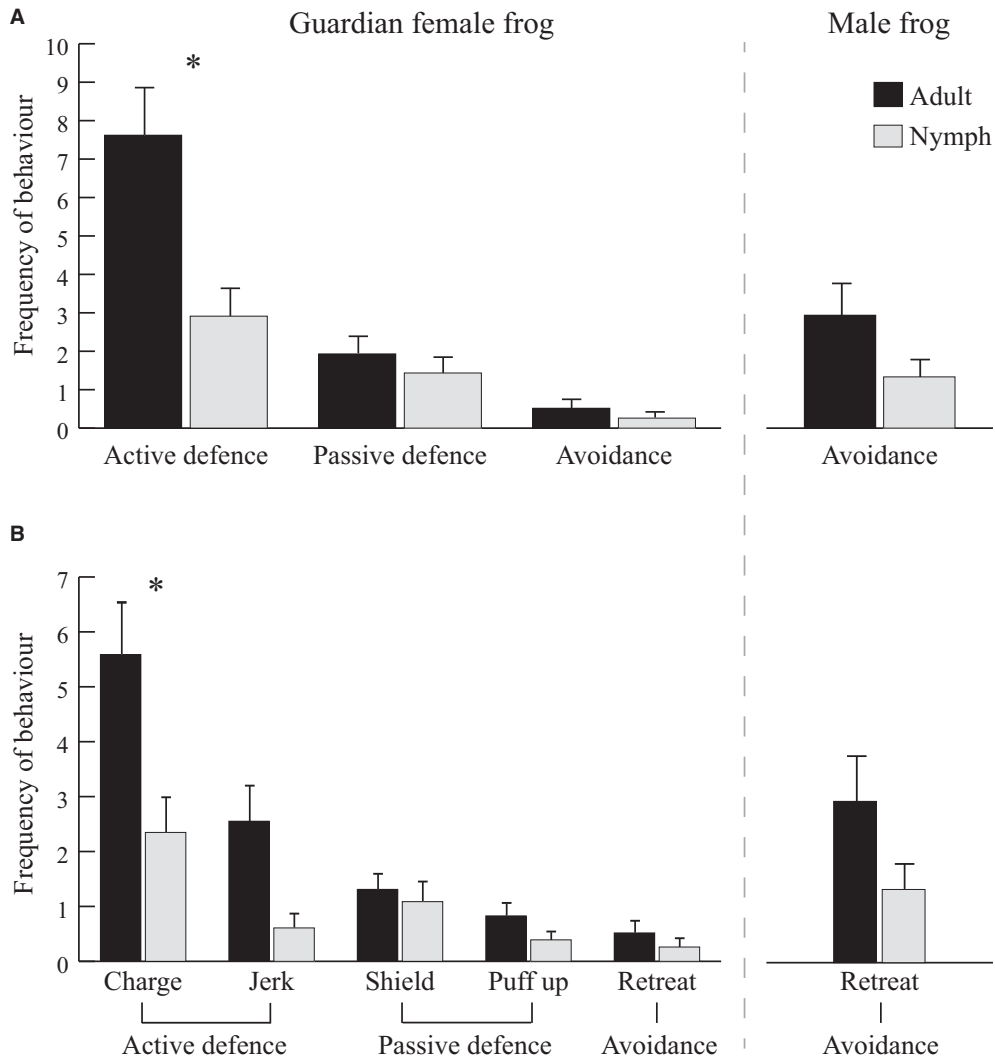
Figure 2. Behaviour of frogs in response to predatory katydid nymphs and adults. Female frogs were guarding egg clutches, whereas male frogs were alone. Response was quantified into three behavioural categories (A), that contained five types of behaviours (B). * denotes difference between bars is significant.

PART 4: PREDATORY BEHAVIOUR OF KATYDID)

We observed the behaviour of 84 katydids ($N = 53$ and 31 from part 2 and 3, respectively). Of these, one adult katydid escaped before morphological measurements were taken and was therefore removed from further analyses. Average BL for adults and nymphs was 24.2 ± 0.4 and 15.6 ± 0.5 mm, respectively ($N = 45$ and 38).

For katydids placed with guarding female frogs (part 2), all but one adult exhibited approaching behaviour towards eggs (96%), while 78% of nymphs approached eggs. Model simplification showed only katydid life stage had a significant effect on katydid approaching behaviour towards eggs, with adults approaching more often than nymphs (10.82 ± 2.29

and 5.13 ± 1.21 individuals, respectively, d.f. = 1, $P = 0.04$, Fig. 3A). No effects were found for katydid BL, katydid sex, or interaction terms on approaching behaviour.

Katydid predation of eggs occurred in 19% of treatments ($N = 10$) and was positively correlated with BL and more frequent in female katydids compared with males, with an interaction between BL and sex (d.f. = 1 for all, $P = 0.17$, 1.00, and 1.00 for BL, sex, and their interaction, respectively, Fig. 3B). Although explanatory variables in model were not significant, this model was the minimal model after simplification. The predation of eggs was more frequent in katydid adults, however the difference between adults and nymphs was not significant
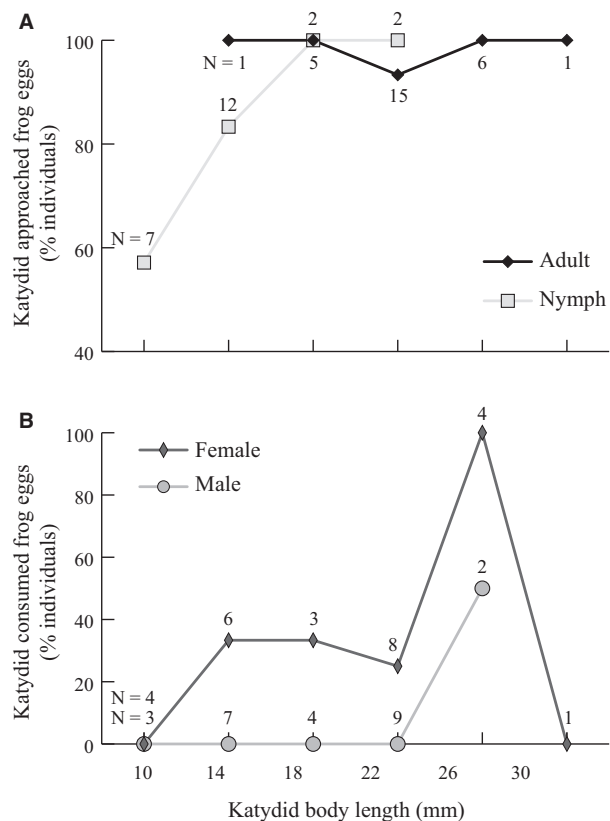
Figure 3. Predatory behaviour of katydids towards frog egg clutches. (A), Approaching behaviour of katydid adults and nymphs. (B), Egg predation by male and female katydids. The number listed beside the points represent the total number of individuals.

(N = 7 and 3, respectively). Predation of guardian female frog occurred in only one treatment by an adult female katydid; the entire frog was eaten by the katydid.

For katydids placed in aquaria with male frogs (part 3), a higher percentage of adults approached frogs compared with nymphs (50% and 33%, respectively), however, this difference was not significant. Moreover, no effects of BL, sex, or interaction terms on approaching behaviour were found. No instance of predation of male frogs was observed.

DISCUSSION

This study found a dynamic relationship between predatory behaviour of an oophagus species and antipredator parental care of an egg-caring species. Specifically, katydid abundance is higher in pond areas where frog eggs are available than in surrounding forest areas. Predatory behaviour differed between life stages of katydids, with higher instances of animal consumption by katydid adults. Katydid adults increased approaching behaviour towards desirable prey (frog eggs) and larger, female katydids were more successful predators. The presence of antipredator behaviour and differentiation between predation risks in frogs was sex-specific and depended on their role in providing parental care. Furthermore, level of parental investment was affected by predation risk to offspring, regardless of risk to parents or offspring age.

DISTRIBUTION, DIET, AND BEHAVIOUR OF PREDATORY KATYDIDS

Katydid abundance was higher in pond areas where frog breeding occurs, which agrees with suggestions of increased density in response to availability or concentration of desirable food resources in other insects (Eubanks & Denno, 1999). In addition to frogs and frog eggs, distribution of katydids may also be affected by availability of other prey resources near ponds, such as terrestrial invertebrates and emerging dragonfly nymphs. However, arboreal *C. hansenae* eggs may be a high quality resource that is relatively easy for katydids to obtain, as frog eggs lack inedible structures, such as exoskeletons of insects, which would increase energy needed for intake (Denoel & Demars, 2008). Katydid adults were bolder in their approach towards eggs (Fig. 3A) and preyed on eggs more frequently, even though nymphs were also able to prey on eggs successfully despite defence efforts of frogs. As egg predation was only observed by katydid adults and larger (late instar) nymphs, there may be a gradual change from the plant-based diet of nymphs to the animal-based diet of adults, commensurate with increased nutritional needs. Similarly, nutritional needs could account for higher instances of egg predation in female katydids (Fig. 3B). Thus far, active regulation of nutrient intake by choice of food items in katydids has only been reported by one other study (Pearson *et al.*, 2011) and little information is known about the relationship between age, sex, and the diet or predatory behaviour of katydids. In omnivorous insects, the change from a plant-based diet to an animal-based diet can be important in the survival of later instars (Eubanks & Denno, 1999), as nutrition provided by animal prey is more beneficial (Xu, Held & Hu, 2013).

Although similar trends of behaviour were observed for katydids placed with male frogs, the difference in predatory behaviour was not significant and no predation of male frogs occurred. Higher mobility of male frogs and their avoidance of katydids could

account for the lack of successful predation, making frogs less desirable prey compared with eggs and again highlighting the relative value of eggs as a food source. Consequently, dietary needs by katydids combined with the relative value of prey items may be driving increased predatory behaviour in larger katydids and, subsequently, antipredator defence or avoidance behaviour in frogs. As such, the effect of frog egg consumption on reproductive output of female katydids would be of further research interest.

ANTIPREDATOR BEHAVIOUR IN FROGS

Active defence behaviours by frogs were successful in deterring predators, most of the time. Guardian females showed higher levels of active defence when exposed to katydid adults, the most successful predators, indicating behavioural plasticity in response to level of predation risk. Male frogs showed no defensive behaviours toward katydids. This situation is perhaps because females provide care to immobile eggs. Consequently, females may need to differentiate levels of risk and modify their responses, thereby minimizing their own energy expenditure and mortality risks. In comparison, males are not bound to one location and so can reduce predation risk by fleeing. If the costs or energetical disadvantages of behavioural plasticity in response to risk level outweigh the reproductive benefits, male frogs may not have evolved the ability to differentiate risks or modify their responses. In other words, the trade-off between gaining more information about predators and simply retreating regardless of predator type may have led to a 'rule of thumb' reaction in male frogs, in which individuals exhibit a constant cautious behaviour towards all predators (Welton, McNamara & Houston, 2003). A similar example can be seen in California ground squirrels, in which females providing parental care are more sensitive to variations in predation risks compared with non-caring females and males (Swaisgood, Rowe & Owings, 2003). Interestingly, a recent study in glassfrogs with maternal egg attendance showed females that are caring for eggs are more reluctant to move away from their location when disturbed compared with non-caring females (Valencia & Delia, 2016). Likewise, studies in Italian wall lizards and funnel-web spiders indicate that antipredator behaviour can differ depending on reproductive status (Downes & Bauwens, 2002; Pruitt & Troupe, 2010). As such, both sexual differences and differences in reproductive status may play a significant role in determining the antipredator behaviour exhibited by an individual.

FACTORS INFLUENCING INVESTMENT IN PARENTAL CARE

Increased care in current offspring can come at a direct cost to future offspring production (Trivers, 1972). Consequently, parental investment should vary according to the costs and benefits, which are represented by predation risks and offspring maturity in our study. While caring for eggs, guardian female frogs showed more active defence behaviour towards katydid adults, thereby increasing their investment in situations of higher risk both to themselves and their offspring. This finding is contrary to that of the majority of studies, which show parents decrease their investment in care (Morosinotto, Thomson & Korpimaki, 2013) and, specifically, antipredator behaviour (Dassow et al., 2012; Ghalambor et al., 2013) when exposed to higher predation risks. For instance, salamanders that are guarding eggs are more defensive towards smaller and less threatening intruders, which pose lower risks to parent survival (Hom, Willits & Clark, 1990). Accordingly, when parents are faced with predators that pose a direct threat to their survival, as in the case of C. hansenae, predation risks should lead iteroparous parents to prioritize self-preservation and ensure future reproduction. However, results indicated that guardian females actually increased investment in antipredator behaviour against larger predators, despite the higher threat to their own survival.

In contrast to taxa with relatively well known antipredator behaviour, such as mammals, birds, and fishes, there is little empirical evidence on factors that influence plasticity in antipredator defence during parental care in amphibians. Although predator defence is often assumed to be one of the main functions of amphibian parental care (Forester, 1979; Crump, 1996), defensive behaviours by parents are rarely tested (Carreño & Harris, 1998). We speculate that increases in parental investment observed in C. hansenae may be because, although katydids pose a severe threat to frogs, predation of guardian females occurrences relatively infrequently (< 2% of observations), resulting in a low level of actual risk to guardian females. Alternatively, since predation risk to frog eggs outweighs risk to adult frogs, katydids may be perceived as more of an offspring predator. In species that are able to differentiate predators of adults from predators that only pose a threat to offspring, parents exhibit stronger defensive behaviours in response to offspring predators (Dale, Gustavsen & Slagsvold, 1996; Ellis-Felege et al., 2013). Accordingly, defensive behaviour by guardian females could be driven by threat to offspring, rather than threat to themselves.

Antipredator parental behaviour in *C. hansenae* was not affected by offspring age. Plasticity in parental investment in relation to offspring age is generally categorized into 'offspring value hypothesis' and 'offspring vulnerability hypothesis'. The former proposes that parents should invest more in older offspring, due to the higher value they represent in past investment and chances of survival (Trivers, 1972; Winkler, 1987; Coleman & Gross, 1991; Ackerman & Eadie, 2003). In contrast, the 'offspring vulnerability hypothesis' suggests parental investment should depend on offspring need, which is greater when offspring are younger and more vulnerable (Dale *et al.*, 1996; Koskela *et al.*, 2000). Observations of *C. hansenae*, however, did not support either hypothesis as guardian females showed no difference in behaviour when caring for young and old eggs. Similarly, a recent study in glassfrogs showed paternal egg attendance was not affected by offspring age (Lehtinen, Green & Pringle, 2014).

While there are many studies that support the 'offspring value hypothesis' by showing a positive correlation between parental investment and offspring age (Lavery, 1995; Forester *et al.*, 2005; Svagelj, Trivellini & Quintana, 2012), this was not found in *C. hansenae*. The difference may be due to a relatively small amount of past investment in *C. hansenae*. Because of their relatively short embryonic period (5 days), old and young eggs differed in age by only 2 days. Therefore, additional effort invested in older eggs might be too small to have a significant effect on future fecundity, and consequently parental behaviour, of guardian female frogs. Alternatively, benefits of investing in older offspring may be mitigated by a decrease in need for care by offspring as they mature, as proposed by 'offspring vulnerability hypothesis'. For instance, parental investment in defensive behaviours is higher for younger offspring in bank voles and California ground squirrels (Swaisgood *et al.*, 2003) due to their higher vulnerability. Changes in offspring vulnerability in *C. hansenae* are particularly interesting, as older eggs are capable of hatching prematurely to escape katydid predation, whereas younger ones are not (Poo & Bickford, 2014). While there is evidence of parental care influencing hatching plasticity of eggs (Delia, Ramírez-Bautista & Summers, 2014), possible effects of hatching plasticity on chronological differences in parental care is as yet unknown.

This study demonstrates ontogenetic dietary shifts combined with relative values of prey items can influence predatory behaviour in an omnivorous katydid. Results reveal the effects of katydid life-history characteristics on their predatory behaviour, and consequently parental behaviour of prey. These findings provide evidence of sex-specific responses to predators, and suggest the ability to differentiate predation risk levels is present only in female frogs due to their role in protecting and providing care for eggs. Although katydids are predators of both frogs and frog eggs, behaviour of guardian female frogs appears to be driven primarily by threat to offspring. Contrary to existing theories, offspring age did not have an effect on parental investment. Our results illustrate a need for further theoretical and empirical studies on dynamics between predators and parents, particularly in taxa that are less-represented in the literature. In addition, this study highlights the value of studies that consider factors that influence both species concurrently when examining an interspecies interaction.

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