Hatching responses of subsocial spitting spiders to predation risk

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The carrying of eggs often renders parents vulnerable to predators due to increased conspicuousness or decreased mobility. Nonetheless, egg-carrying parents can escape from the predators to which they are vulnerable. Previous studies have demonstrated heavy predation by spider-eating jumping spiders (*Portia labiata*) on egg-carrying spitting spider (*Scytodes pallida*) females, but little predation on eggless females. If the timing of hatching is phenotypically plastic, then both *S. pallida* females and their eggs could reduce the risk of predation by hatching early. Hence, this study examines the hatching responses of *S. pallida* to chemical cues from *P. labiata*, both in the laboratory and in the field, and addresses the following questions. (i) Do cues from predatory *P. labiata* influence the hatching traits of *S. pallida*? (ii) Are the olfactory cues from predators sufficient for predator detection by *S. pallida*? (iii) Are hatching responses to predatory *P. labiata* controlled by egg-carrying *S. pallida* females, or directly by their embryos? The study provides evidence of hatching as a life-history switch point, which shows an adaptive plasticity in response to predation risk in egg-carrying *S. pallida*. Egg-carrying *S. pallida* females, but not unattended eggs, adjust egg-hatching time (the interval between oviposition and hatching) in response to the threat of predation on both the female and her eggs by *P. labiata*. In the presence of *P. labiata*, eggs that are carried by females hatch sooner; the hatchlings of these eggs are therefore smaller than hatchlings born in the absence of *P. labiata*. Chemical cues that are released from the draglines of *P. labiata* are sufficient to elicit changes in the egg-hatching traits of *S. pallida*. Hatching early in response to this predator may benefit both females and their offspring. To my knowledge, this is the first direct experimental study to demonstrate predator-induced hatching plasticity in spiders and, in particular, in animals with parental care.

Keywords: hatching response; predation risk; chemical cues; spider; *Scytodes pallida*; *Portia labiata*

1. INTRODUCTION

It has recently become apparent that many prey animals respond to predation risk adaptively and plastically (reviewed in: Sih 1987; Lima & Dill 1990; Tollrian & Harvell 1999), in spite of the costs that are associated with phenotypic plasticity (DeWitt 1998; Relyea 2002). Numerous theoretical and empirical studies have revealed that predators influence the behaviour, morphology and body mass of prey species (reviewed in: Havel 1987; Sih 1987; Lima & Dill 1990; Chivers & Smith 1998; Tollrian & Harvell 1999). However, fewer experimental studies have directly examined the effect of predators on prey life-history switch points, such as those that are related to the timing of hatching (e.g. Sih & Moore 1993; Warkentin 1995, 2000; Chivers *et al.* 2001), although there is a much larger body of studies on metamorphosis (e.g. Werner 1986; Skelly & Werner 1990; Rowe & Ludwig 1991; Skelly 1992; DeVito *et al.* 1998; Peckarsky *et al.* 2001). Theoretically, prey animals should time life-history switch points to minimize their mortality/growth ratio across life stages (Werner & Gilliam 1984; Werner 1986, 1988; Rowe & Ludwig 1991). Niche-shift models (Werner & Gilliam 1984; Werner 1986, 1988; Rowe & Ludwig 1991) predict two possible hatching responses, based on the mortality/growth ratio. If there is high mortality among hatchlings, then whilst eggs are relatively safe, prey may respond to predator risk by delaying hatching. This response has been demonstrated in salamanders (Sih &

Moore 1993; Moore *et al.* 1996) and hypothesized in crustaceans (Blaustein 1997). By contrast, high egg mortality and enhanced post-hatching growth rates favour the acceleration of hatching. Examples of early hatching in response to egg predation risk include several species of amphibians (Warkentin 1995, 2000; Vonesh 2000; Chivers *et al.* 2001). The embryos that have been studied so far, however, do not receive parental care, so parents are presumably not involved in adjusting the timing of hatching. Rather, embryos that are isolated from adults detect and respond to predation risk by changing the time of, and their size at, hatching.

Many animals show parental care of eggs and/or young, thereby enhancing offspring survival (reviewed in Clutton-Brock 1991). However, parental care is costly, and predation is considered an important cost of parental care (reviewed in: Clutton-Brock 1991; Magnhagen 1991). For example, the carrying of eggs may render both parent and offspring (i.e. eggs) vulnerable to predators due to increased conspicuousness or decreased mobility (Winfield & Townsend 1983; Berglund & Rosenqvist 1986; Reguera & Gomendio 1999). In this context, parents that care for eggs may increase both their own and their offspring's chances of survival by altering the timing of egg-hatching. However, there is no direct evidence of the effect of predation risk on hatching in animal species with parental care. Moreover, whether adult animals or embryos alter the timing of hatching in response to predation risk is unknown, and there are no reported studies

of predator-induced hatching in spiders. In this work, I investigate whether the risk of predation by spider-eating jumping spiders, *Portia labiata* (Salticidae), on egg-carrying females of subsocial spitting spiders, *Scytodes pallida* (Scytodidae), alters the hatching characteristics of *S. pallida* eggs.

Like all other species of *Scytodes* (Bristowe 1958; Dablow 1958; McAlister 1960; Gilbert & Rayor 1985; Nentwig 1985), *S. pallida* attacks its prey and defends itself against predators by spitting sticky gum out of its chelicerae (Li *et al.* 1999; Whitfield 1999). *Scytodes pallida* is an especially interesting spider because, as well as its unique predatory and defence behaviour, it also performs maternal behaviour (Li *et al.* 1999); carrying its eggs with its chelicerae until hatching. After hatching, there is an extended female-offspring association, with juveniles tending to remain in their mother's web until they develop into later instars (Li *et al.* 1999). Because an egg-carrying female cannot spit without first releasing her eggs, egg-carrying is a handicap (Jackson *et al.* 2002). An egg-carrying female occasionally releases her eggs to spit at prey or predators, but appears to be reluctant and slow to do so (Li *et al.* 1999). Therefore, *S. pallida* females are less dangerous prey (i.e. more defenceless) when carrying eggs than when eggless (Jackson *et al.* 2002).

Portia labiata is sympatric with *S. pallida* in tropical South-East Asia (Jackson *et al.* 1998), including Singapore (D. Li, personal observation). It often preys on *S. pallida*, including both egg-carrying and eggless females (Jackson *et al.* 1998; Li *et al.* 1999; D. Li, unpublished data), but prefers egg-carrying females to eggless ones (Jackson *et al.* 2002). Therefore, compared with eggless *S. pallida* females, egg-carrying *S. pallida* females are subject to intense predation by *P. labiata*. If *S. pallida* females are capable of detecting the presence of *P. labiata* and appropriately adjusting egg-hatching time, then both the parents and their eggs may avoid predation, because females freed of eggs may spit to defend both themselves and their newly-hatched spiderlings. In this study, I use a series of laboratory and field experiments to test this hypothesis. I predict that the eggs of *S. pallida* will hatch faster in the presence of *P. labiata* than in the absence of *P. labiata*, and I also hypothesize that chemical cues from the draglines that are released from *P. labiata* will elicit changes in the timing of hatching and the size of eggs at hatching. Finally, I predict that *S. pallida* females, but not unattended eggs, will adjust the timing of egg hatching.

2. METHODS

(a) *Collection and maintenance*

I used spiders and eggs from laboratory cultures of *Scytodes pallida* (hereafter *Scytodes*) and *Portia labiata* (hereafter *Portia*), which were established from animals that were originally collected in Labrador Park, Singapore. Using these cultures, I carried out experiments in a controlled laboratory (temperature: $25 \pm 1^\circ\text{C}$; relative humidity: 60–80%; photoperiod: 12 L : 12 D, with lights turned on at 0800). *Portia* was maintained with a diet consisting of a variety of insects and web-building spiders, but not *Scytodes*, as this diet has been shown to be optimal (Li & Jackson 1997). Individual *Scytodes* were established in webs for testing by placing a leaf from cam wood, *Baphia nitida*, with a slightly concave upper surface, inside a cage. Blu Tack (Bostik,

Australia) was used to fasten the leaf with the scytodid on board to one of the top corners of a plastic cage (100 mm $\times$ 150 mm $\times$ 50 mm). *Scytodes* was maintained with a diet consisting of a variety of insect species. All of the experiments took place between 0900 and 1700. No individuals of *Portia* or *Scytodes* were used in more than one experiment, or provided data more than once for any one experiment. To control for the effects of between-sibship variation in hatching traits, I conducted my experiments on split sibships, where a 'sibship' is defined as the progeny of a particular male and female. The individuals of *Portia* and *Scytodes* that were used in each experiment were derived from at least 8 and 10 sibships, respectively, with an approximately equal number of individuals from each sibship.

All of the individuals of *Portia* that were used in the laboratory experiments were derived from laboratory rearing to the second or third generation, and all of the individuals of *Scytodes* were from laboratory rearing to the first generation. None of the individuals of *Portia* or their laboratory-reared parents had prior experience with *Scytodes*, and none of the individuals of *Scytodes* had prior experience with *Portia*. Each individual *Portia* was an adult female (body length: 10 mm) that had matured 10 days beforehand and had not mated.

(b) *Experiment 1: hatching responses of eggs that are carried by Scytodes females to chemical cues from Portia*

Three different predator cue treatments were established to examine the immediate hatching responses of eggs that were carried by *Scytodes* females to predator cues from *Portia*, and the role of proximate cues. The treatments were as follows: (i) a sterile Petri dish devoid of any *Portia* cues ('control'; without *Portia* or draglines laid down by *Portia*; $n = 30$); (ii) live *Portia* (hereafter 'predator'; $n = 30$); and (iii) freshly deposited dragline-borne chemical cues from *Portia* (hereafter 'draglines'; $n = 30$). To prepare replicates of the predator treatment, I transferred a *Portia* to a clean Petri dish (90 mm in diameter) that contained a single sheet of filter paper (80 mm in diameter). The Petri dish was then covered with a piece of fine clothing mesh (0.1 mm) so that the *Portia* could not come into direct contact with the *Scytodes*, but the non-contact chemical cues from the live *Portia* could be released into the cage. The Petri dishes that were occupied by *Portia* were then used for testing. To prepare replicates of the dragline treatment, I collected the draglines from a *Portia* in an individual sterile Petri dish (diameter: 90 mm) with a single sheet of filter paper. This was done by leaving a single *Portia* in the Petri dish for 24 h, during which it lay down draglines on the filter paper. After 24 h, the *Portia* was returned back to its original cage. Then, the Petri dishes that were previously occupied by a *Portia* were covered with a piece of fine clothing mesh (0.1 mm) and stored until they were used for testing. A different *Portia* was used for each Petri dish.

To provide egg-carrying *Scytodes* females, I randomly chose virgin *Scytodes* females from laboratory cultures that had matured 15 days beforehand. A male *Scytodes* was introduced to the leaf with a female on board in each cage, and each adult *Scytodes* female was thus allowed to mate once with a male. One hour after the female had mated, the male was removed from the cage and the mated female was kept in the cage (100 mm $\times$ 150 mm $\times$ 50 mm) until she laid eggs. One day after *Scytodes* females produced eggs, I randomly assigned the egg-carrying females to one of three treatments (either a control, predator or dragline treatment).

The experiment was started by placing a control (an empty

Petri dish with a single sheet of filter paper but without *Portia* or draglines), a predator stimulus (a Petri dish containing a live *Portia*) or a dragline stimulus (a Petri dish containing draglines that had been laid by a *Portia* but without a live *Portia*), into a cage with one egg-carrying *Scytodes* female (test spider). Throughout the course of the experiment, I fed the egg-carrying *Scytodes* females in all three groups with two houseflies once a week. The Petri dishes were removed from the cages daily and replaced with the newly collected *Portia* or dragline stimuli. I used the same individual *Portia* for the same test spider until the end of the experiment. To control for the effect of disturbance when the Petri dishes were changed, the Petri dish in the control group was also removed and the old filter paper was replaced with a clean sheet of filter paper and the dish returned to the cage.

I monitored the cages daily throughout the experiment and ended the experiment after all of the eggs had either hatched or died. To determine whether there were differences between the hatching characteristics of *Scytodes* eggs in the different treatments, three response variables were measured (embryonic period, hatching rate and hatchling size) for each cage. To determine the total number of eggs per egg-sac, which was also defined as the initial number of eggs per egg-sac, I dissected all of the egg-sacs and counted the number of hatched spiderlings and the number of eggs that had not hatched in the egg-sacs. To measure the body length (to the nearest 0.1 mm) of the hatched spiderlings, five individuals were randomly chosen from each egg-sac in each treatment, and the mean body length for each egg-sac was calculated. For each treatment, I calculated the mean embryonic period (the interval between oviposition and hatching), the mean hatching rate per egg-sac (the mean number of eggs hatched to the total number of eggs) and the mean body length of spiderlings for comparisons. All of the response variables met parametric assumptions and no data transformations were necessary. Thus, parametric statistics were used for all analyses. I performed a multivariate analysis of variance (MANOVA) first to test for treatment effects and reported the multivariate *F*-statistic (Wilks's lambda) because it does not require compound symmetry. I then conducted a univariate analysis of variance (ANOVA) on each response variable to determine which variables were responsible for significant main effects. This was followed by *post hoc* comparisons (Tukey honestly significant difference (HSD) tests), to test for significant differences between treatment means (Zar 1996).

(c) *Experiment 2: hatching responses of unattended Scytodes eggs to chemical cues from Portia*

Experiment 1 simultaneously manipulated *Scytodes* females and eggs to test their responses to the predation risk. However, it did not allow determination of whether *Scytodes* females or the eggs alone alter the hatching traits. The purpose of experiment 2 was to determine whether unattended *Scytodes* eggs would detect and respond to cues from *Portia*. Egg-carrying *Scytodes* females were obtained, as in experiment 1. The design of this experiment was similar to that of experiment 1, except that only one egg-sac was placed in the web on the leaf, without a *Scytodes* female, in each cage. The isolated egg-sacs were obtained from the females one day after oviposition by gently prodding them with a soft brush. The sacs were then checked daily until they had either hatched or died. In this experiment, I collected data on the same set of response variables as in experiment 1. As the egg-sacs were unattended by females, some of them were either

infected by mould or desiccated. At the end of the experiment, only 6, 7 and 6 out of 20 egg-sacs hatched in the control, predator and dragline treatments, respectively (see below). Thus, I calculated the mean hatching rate, the mean time until hatching and the mean body length at hatching, based on these hatched egg-sacs. When measuring the body length of the spiderlings, five individuals were randomly chosen from all of the hatched egg-sacs in each treatment. For the mean time to hatching, a non-parametric Kruskal–Wallis test was used, as the small sample size meant that parametric assumptions were not met. For the mean body length at hatching, parametric assumptions were met and ANOVA was used (Zar 1996).

(d) *Experiment 3: field experiment to test the hatching responses of egg-carrying Scytodes to dragline-borne chemical cues from Portia*

The aim of the field experiment was to confirm the findings from the laboratory experiments, paying particular attention to the hypothesis that *Scytodes* females are able to detect non-contact dragline-borne cues that are released from *Portia*. I conducted the field experiment between 15 February and 20 May 1999 in Labrador Park, Singapore. Adult *Scytodes* females frequently built their webs on a single, green leaf of cam wood (*B. nitida*). Occasionally, a few individuals were found on the same plant, but on different leaves. The females began laying eggs in early March, and many were carrying egg-sacs by the middle of March.

In February 1999, I marked 87 adult *Scytodes* females that were not carrying eggs (their reproductive status was unknown), by fastening orange flagging tape on their leaves. I then monitored the *Scytodes* females once daily, between 1300 and 1500, and recorded the egg-laying date of each marked female. A total of 59 marked *Scytodes* females that laid eggs between 15 February and 6 March were used in the field experiment. Shortly after the females produced eggs, I randomly assigned them to one of two treatment conditions: (i) a control ($n = 30$); and (ii) a dragline-borne chemical cue treatment ($n = 29$). These two treatment conditions were the same as in experiment 1. However, in this experiment, a single sheet of filter paper (cut as a leaf shape) that bore the fresh draglines laid by a *Portia* female, was fastened with Blu Tack to the underside of the leaf with a marked egg-carrying *Scytodes* female on board (generally on the upper side). In the control treatment, a sheet of leaf-shaped filter paper without draglines from predators was attached to the underside of the leaf with a marked egg-carrying *Scytodes* female. The old filter papers were replaced with new filter papers every day. As not all 59 females laid eggs on the same day, they were assigned to the treatment groups on different occasions from 15 February to 6 March. At each site, an equal number of egg-carrying females were assigned to either the experimental or the control treatment on the same day. However, the egg-carrying females that were assigned to the experimental and the control groups were not from the same plant, although there might have been more than one egg-carrying female in either treatment condition from the same plant. This minimized the possibility of olfactory cues from the experimental treatment affecting the *Scytodes* females in the control treatment, as olfactory cues can spread over a certain distance (Foelix 1996). Furthermore, the egg-carrying *Scytodes* females in the control treatment were at least 100 m away from those in the experimental treatment. The monitoring of these egg-carrying *Scytodes* females was carried out once (between 1300 and 1500) every day, until all of the eggs had either hatched or died.

Figure 1. Mean ($\pm$ s.e.) duration of (a) embryonic period and (b) body length at hatching for egg-carrying *Scytodes pallida* females that were exposed to live (non-contact) *Portia labiata*, draglines of *P. labiata* and nothing (control). Different letters within bars indicate significant differences at $p < 0.05$ based on HSD Tukey tests.

Data were collected on the same set of response variables (time to, and size at, hatching) as in experiment 1. However, in this field experiment, I collected the leaf with the female and the hatchlings immediately after the eggs hatched. In the laboratory, the egg-sacs were dissected to count the number of hatched spiderlings and eggs that had not hatched. I randomly chose five spiderlings from each egg-sac in either treatment and then measured the mean body length of the chosen spiderlings. For both treatments, the mean embryonic period, the mean hatching success and the mean body length of spiderlings were calculated for comparisons. For the rate of hatching, because parametric assumptions were not met even after data transformation, I used a non-parametric Mann–Whitney *U*-test to compare the difference in hatching rate between treatments. For the response variables (time to, and size at, hatching), the parametric assumptions were met and no data transformations were necessary. Thus, independent *t*-tests were used to compare differences in the hatching characteristics (time to, and size at, hatching) between the two treatments (Zar 1996).

3. RESULTS

(a) *Hatching responses of eggs that are carried by Scytodes females to chemical cues from Portia*

There was no significant difference in the initial number of eggs among the treatments (mean $\pm$ s.e. = 21.0 ± 0.5 , 22.4 ± 0.4 and 20.8 ± 0.5 for the control, predator and dragline treatments, respectively; ANOVA: $F_{2,87} = 2.552$, $p = 0.084$). A MANOVA revealed that the treatment condition had a significant effect on the egg hatching traits of *Scytodes* (Wilks's lambda: $F_{6,170} = 14.901$, $p = 0.0001$; figure 1). The hatching rate (%) of the eggs was high in

all three treatments ($89.2 \pm 1.5\%$, $86.2 \pm 1.7\%$ and $91.5 \pm 1.6\%$ for the control, predator and dragline treatments, respectively), and there was no significant difference between the three treatments ($F_{2,87} = 2.295$, $p = 0.107$). ANOVA showed that the treatment condition significantly influenced the embryonic period ($F_{2,87} = 9.775$, $p = 0.001$) and spiderling size at hatching (ANOVA: $F_{2,87} = 46.556$, $p = 0.0001$). Embryos hatched earlier (Tukey HSD for embryonic period between the predator treatment and the control: $p = 0.0001$; between the dragline treatment and the control: $p = 0.001$; figure 1a) and at a smaller size in the live predator (*Portia* female) and the dragline-borne pheromone treatment than in the control treatment (Tukey HSD for body length of spiderlings at hatching between the predator treatment and the control: $p = 0.0001$; between the dragline treatment and the control: $p = 0.0001$; figure 1b). However, there were no significant differences in either embryonic period (Tukey HSD: $p = 0.396$) or spiderling size between the live predator and the dragline-borne pheromone treatments (Tukey HSD, $p = 0.593$; figure 1).

(b) *Hatching responses of unattended Scytodes eggs to chemical cues from Portia*

There was no significant difference in the initial number of eggs per egg-sac among the treatments (mean $\pm$ s.e. = 20.9 ± 0.8 , 19.9 ± 0.6 and 21.4 ± 0.7 for the control, predator and dragline treatments, respectively; ANOVA: $F_{2,57} = 1.222$, $p = 0.302$). In this experiment, only 30% (6 out of 20), 35% (7 out of 20) and 30% (6 out of 20) of isolated (unattended) egg-sacs hatched in the control, predator and dragline treatment conditions, respectively. Among the hatched egg-sacs, the treatment condition had no significant effect on the mean embryonic period (Kruskal–Wallis test: $\chi^2_2 = 1.329$, $p = 0.515$), the mean hatching rate (Kruskal–Wallis test: $\chi^2_2 = 0.985$, $p = 0.611$) or the mean body length of spiderlings at hatching (ANOVA: $F_{2,92} = 1.306$, $p = 0.737$; figure 2). Of the 41 egg-sacs that failed to hatch, 30 (73%) were infested with mould and 11 (27%) were desiccated (but without mould).

(c) *Field experiment*

There was no significant difference between the initial number of eggs per sac in the experimental and the control treatments (mean $\pm$ s.e. = 20.1 ± 0.7 and 21.7 ± 0.6 for the control and dragline treatments, respectively; $t_{50} = -1.811$, $n = 52$, $p = 0.76$). At the end of the experiment, 52 out of the 59 egg-sacs that were carried by the females had hatched. *Portia* were seen feeding on two (29%) of the seven egg-sacs that failed to hatch; the other five (71%) disappeared, presumably having been taken by *Portia* or other predators. Among the hatched egg-sacs, the rate of hatching was high in both the control and the experimental treatments ($83.5 \pm 2.1\%$ and $82.2 \pm 3.0\%$ for the control and the experimental treatments, respectively), and there was no significant difference between treatments (Mann–Whitney *U*-test: $z = -0.635$, $n_1 = 30$, $n_2 = 29$, $p = 0.525$). However, the treatment condition had a significant effect on the hatching characteristics of *Scytodes*. Embryos hatched significantly earlier in the presence of draglines of *Portia* than in the absence of draglines ($t_{50} = 2.581$, $p = 0.013$; figure 3a). The hatched spiderlings

Figure 2. Mean (± s.e.) duration of (a) embryonic period and (b) body length at hatching for isolated (unattended by *Scytodes pallida* females) eggs that were exposed to live (non-contact) *Portia labiata*, draglines of *P. labiata* and nothing (control). Different letters within bars indicate significant differences at $p < 0.05$ based on HSD Tukey tests.

Figure 3. Mean (± s.e.) duration of (a) embryonic period and (b) body length at hatching for egg-carrying *Scytodes pallida* females exposed to draglines of *Portia labiata* and nothing (control) in the field.

were also significantly smaller in the presence of draglines than in the absence of draglines ($t_{50} = 2.564$, $p = 0.013$; figure 3b).

4. DISCUSSION

(a) Adaptive, plastic egg hatching response to predator risk

This study clearly demonstrates that egg-carrying *Scytodes* females detect and respond to predation risk from *Portia*. As predicted, predation risk caused *Scytodes* to alter the hatching traits of eggs: compared with the controls, eggs hatched sooner and at a smaller spiderling size in the presence of predator cues. Predator-induced adaptive plasticity in egg hatching has also been reported for some amphibians. In red-eyed tree frogs (*Agalychnis callidryas*) (Warkentin 1995, 2000), Pacific tree frogs (*Hyla regilla*) and cascade frogs (*Rana cascadae*) (Chivers *et al.* 2001), eggs hatch faster in response to the risk from potential predators. Sih & Moore (1993) and Moore *et al.* (1996) reported that salamander (*Ambystoma barbouri*) eggs delayed hatching in response to predator risk. The findings from this study are also consistent with the prediction of niche-shift models; that if the risk of egg mortality is increased, then prey animals will respond by accelerating hatching (Werner & Gilliam 1984; Werner 1986, 1988; Rowe & Ludwig 1991). However, unlike previous studies of egg hatching responses to predation risk, *Scytodes* is a species that exhibits parental care of eggs, whereas the amphibians that have been studied so far do not perform parental care of eggs. To my knowledge, this is the first direct experimental documentation of a probable adaptive, plastic, egg hatching response to enhanced predation risk in invertebrates, and most importantly, in animals with parental care.

It can be argued that pronounced effects of predation risk on hatching traits were easily documented for the caged *Scytodes*, because of the continuous supply of predator cues and limited space. However, this appears not to be the case. The patterns in hatching traits that were found in the laboratory were also observed in the field: eggs hatched faster and spiderlings were smaller at hatching in the presence of predator cues than in their absence.

Although it is obvious that by hatching early in response to predation risk, both *Scytodes* females and their eggs may reduce the likelihood of being eaten, there may be substantial costs associated with smaller hatchlings in response to predation risk. This is apparent in some prey species that do not provide parental care after hatching or birth. For example, in red-eyed tree frogs (*A. callidryas*), mortality among early hatching arboreal embryos, caused by snake predation, can be reduced by their falling into the water. Early hatching is, however, costly because the unattended smaller hatchlings (tadpoles) are more vulnerable to aquatic predatory shrimp and fish (Warkentin 1995). For a species such as *Scytodes*, with extended parental care after hatching, the costs to smaller offspring may be offset by the parental provisioning and guarding. In addition, life-history theory predicts that trade-offs exist between the components of parental care. That is, increased investment at one stage will reduce the investment at other stages (Stearns 1992). In spite of being smaller at hatching, the offspring that are produced in the

presence of predators might be better cared for, for instance with the provision of a greater supply of captured or partly digested prey or a longer period of care by *Scytodes* females as compared with the larger offspring that are hatched in the absence of predators. However, this hypothesis needs to be tested.

(b) *The role of Scytodes females*

Interestingly, *Scytodes* eggs cannot detect and respond to predator cues. Rather, egg-carrying *Scytodes* females actively alter the hatching characteristics of their eggs. In experiment 2, the majority (60–70%) of egg-sacs that were unattended by *Scytodes* females could not hatch because of heavy mould infection or desiccation, which indicates that the parental care of eggs by *Scytodes* females is crucial for egg survival. Among the hatched egg-sacs, there were no differences in embryonic period or spiderling size at hatching between the presence and absence of *Portia* or dragline chemical cues. In this context, the present study also differs from previous studies of animals without parental care. In amphibians without parental care, the changes in egg hatching are largely outside of the female's control (Sih & Moore 1993; Warkentin 1995, 2000; Moore *et al.* 1996; Chivers *et al.* 2001), whereas, in *Scytodes* the female controls changes in hatching. It makes sense that a *Scytodes* female, at risk of a high level of predation because of egg carrying (Jackson *et al.* 2002), times the hatching of her eggs. If eggs hatch earlier, then a *Scytodes* female can free her mouth (which is used in defensive spitting) from carrying the egg-sac, so that she can defend herself and her offspring.

However, the manner in which an egg-carrying *Scytodes* female controls the timing of hatching and the stimuli that induce the hatching process is unclear. Female crabs carry their eggs, and the control of hatching appears to be partly under maternal control and partly under embryo control (De Vries & Forward 1991; Saigusa 1992, 1993). Different hatching mechanisms have been proposed, including simple osmotic hatching: osmotic hatching that is aided by movements of the embryos and osmotic hatching that is aided by the female through mechanical or chemical stimuli. De Vries & Forward (1991) found a hatching enzyme that was released by crab embryos, and suggested that the timing of its release was controlled either by the embryo itself or by the female. It would be interesting to investigate whether a hatching enzyme exists in the eggs of *Scytodes* and whether the timing of its release is controlled by the egg itself or by the female.

(c) *The role of chemical cues*

The results of this study provide evidence that *Scytodes* females use non-contact chemicals, which emanate either from live *Portia* or from draglines, as proximate cues to induce changes in the hatching traits of their eggs, and the dragline-borne chemical cues from *Portia* are apparently sufficient to elicit such changes. Some amphibians have been documented to alter their egg hatching traits in response to predation risk through chemical cues (Sih & Moore 1993; Moore *et al.* 1996; Chivers *et al.* 2001).

It may be argued that visual, vibrational or chemical cues, such as chemotactile sensory modalities, are used by *Scytodes* to assess the potential risk from predators. Like many spiders (Foelix 1996), *Scytodes* has poor eyesight, so

it is unlikely to be able to detect and respond to predators using vision alone. *Scytodes* uses the vibrations that are produced by jumping spiders when walking on the substrate (e.g. leaves) as cues for prey capturing (Li *et al.* 1999), and this may be the stimulus for predator detection. However, it is unlikely that mechanical cues, such as vibrations from *Portia*, could have been transmitted through the mesh screen to the egg-carrying *Scytodes* females in this study, because the experimental set-up was not designed to allow the *Portia* to walk on the leaves in the test cage, or to allow direct contact with the *Scytodes* female or its eggs. Chemotactile cues may be the primary trigger for the hatching response. Unfortunately, the present study was not designed to test the specific chemotactile cues that are used to elicit hatching responses, and thus the interpretation of the mechanism for detection remains unclear.

(d) *Concluding remarks*

This study has demonstrated a female-controlled, adaptive, plastic egg hatching response to predation risk in *Scytodes* with parental care. Egg-carrying *Scytodes* females, but not their eggs, are capable of detecting and responding to the risk of predation from their predators, *Portia*, by shortening the embryonic period. The responses that were observed in this species of subsocial spiders need to be tested in other spiders, as well as other taxa with parental care of eggs, to determine whether the conclusions that are reached in this current study are generally applicable to other systems. In addition, comparative studies of adaptive, plastic egg hatching between prey species with and without parental care, as well as within a species with parental care, may provide insight not only into the interaction of hatching plasticity with parental care, but also its ecological and evolutionary consequences.

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