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ORIGINAL ARTICLE

Predation risk and breeding site value determine male behavior and indirectly affect survivorship of their offspring

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Abstract
Predation is one of the main drivers of behavioral adaptation in prey. In species with parental care, predation can affect survival of both adults and the offspring under their care. This effect can be further modulated by or combined with other factors that contribute to mating and reproductive success of adults, such as the quality of their breeding site. Using the nest guarding behavior of a treefrog with paternal egg attendance, *Kurixalus eiffingeri*, we quantify the effects of predation on the behavior of adult frogs and the survival of their offspring. We observed predator avoidance behavior of male frogs guarding empty breeding sites or breeding sites with eggs in response to the introduction of a predatory snake, *Dinodon rufozonatum*. We hypothesized that male nest guarding behavior would be negatively correlated with predation risk and positively correlated with their clutch sizes. Furthermore, we predicted that predator avoidance in male frog would negatively impact the survivorship of their offspring. We found that breeding site fidelity in male frogs was determined by perceived predation risk and breeding site value, with more males abandoning sites when exposed to high mortality risks (presence of a snake) and when the reproductive benefits (number of offspring) were low. In addition, we found that the willingness of males to return to their breeding sites was positively correlated with their clutch sizes. Abandoning breeding sites, however, can be costly to males, because abandoned eggs had a lower hatching rate. Our findings provide empirical evidence of how the costs and benefits of predation risk and breeding site value can determine the behavior of an amphibian with parental care.

Significance statement
When faced with predation risks, the willingness of individuals to maintain their ownership over nest sites can have significant effects on their reproductive success. For species with parental care, nest defense can also be critical for offspring survival. Using an East Asian treefrog with male egg attendance, we hypothesized that males would maximize their reproductive output by increasing investment for nest sites with low predation risks and with more offspring. We found that males are more likely to invest in nest attendance when risks are low and benefits of offspring survival are high. Moreover, we found that the willingness of males to continue parental investment resulted in an increase in survivorship of their offspring. Our results show that perceived risks and benefits to the adults are important factors in determining offspring survival in an amphibian species with parental care.

Keywords Parental care · Egg attendance · Breeding site fidelity · Predator-induced behavior · Amphibian

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Introduction

Predation pressure is an important driver of behavioral (Caro 2005; Martin and Briskie 2009) and physiological adaptations (Hawlena and Schmitz 2010; Travers et al. 2010). For species with parental care, predation can affect both adults and the offspring under their care (Smiseth et al. 2012; Basso and Richner 2015). In response, some parents can alter their behavior when they perceive predators in the vicinity (Lemos et al. 2010; Zanette et al. 2011; Lehtonen et al. 2013; McKeon and Summers 2013; Poo et al. 2016a). Changes in parental behavior can affect the fitness of current offspring and the lifetime reproductive success of the parent (Trivers 1972). For instance, increases in parental care and investment in antipredator defenses can lead to higher survivorship of current offspring (Huang and Pike 2013). Alternatively, reduced parental investment under predation threats can ensure higher survivorship of parents (Dassow et al. 2012; Ghalambor et al. 2013), thereby ensuring future opportunities for reproduction (Trivers 1972).

For species with parental care, predation risk can not only affect the behavior of adults, but can also have indirect effects that carryover onto offspring that are still dependent upon the care of their parents (Basso and Richner 2015). In other words, the level of predation threat experienced by the parents can determine the level of care that they are willing to invest (Ghalambor et al. 2013). In some cases, such as songbirds, the mere perception of predators can negatively affect the amount of care that parents invest in both their current and future offspring (Zanette et al. 2011). Another factor that is particularly important for individuals during reproduction is their breeding site. For species with breeding site competition or oviposition site selection, a good breeding site is an important resource and can lead to higher mating success before reproduction and higher offspring survival after reproduction (Lin et al. 2008; Smiseth et al. 2012). Consequently, the relative value of breeding sites should affect the willingness of individuals to maintain their ownership over these sites (Lindström and Pampoulie 2005; Valencia and Delia 2016). When threatened by predation, therefore, there is a trade-off between maintaining ownership over one's breeding site and abandoning it to ensure one's own survival and chances for future reproduction.

Despite growing literature on the evolution of parental care (Royle et al. 2012), few empirical studies investigate the proposed effect of predation risk and reproductive output on the behavior of amphibians with parental care. Amphibians are particularly suitable taxa to study direct effects of predator on parents performing care (e.g., Poo et al. 2016a; Valencia and Delia 2016) and indirect effects that this predator-parent interaction may have on offspring development and survivorship. Being ectotherms with relatively basal forms of parental care, amphibians serve as a comparison to the relatively well-studied endothermic species with more advance or complex forms of parental care (e.g., birds and mammals, Caro 2005).

Kurixalus eiffingeri (Rhacophoridae), a phytotelm-breeding treefrog with paternal egg attendance (Kam et al. 1996), provides a perfect opportunity to examine (1) the effects of predation risk and breeding site value on the predator avoidance and nest guarding behavior of adult frogs and (2) the effects of adult frog behavior on the survivorship of their offspring. During the breeding season (February to August), male frogs occupy bamboo stumps filled with rainwater and call to attract females (Chen et al. 2011). After amplexus, females lay eggs on the inner wall of bamboo stumps above the water line. These eggs are then attended by males who actively moisten eggs to prevent desiccation (Fig. 1, Chen et al. 2007). Males of *K. eiffingeri* are known to spend more time attending breeding sites with more eggs, and the frequency of male egg attendance is positively correlated with egg survival (Cheng and Kam 2010). Since males are territorial and occupy a fixed site before and after oviposition (Chen et al. 2011), the effects of predation risk and breeding site value on males behavior can be assessed by observing their willingness to maintain ownership over their breeding sites. Whereas an empty breeding site (hereafter, "low-value" breeding sites) may be important to a male frog because of its higher quality compared to other sites, a breeding site with eggs (hereafter, "high-value" breeding sites) is much more valuable because of the fitness benefits represented by the eggs.

Herein, we examine the effects of predation risk and breeding site value on the behavior of a frog with paternal egg attendance. We predict that male frogs will be more willing to remain at their sites when exposed to low predation risks and when guarding high-value breeding sites. Moreover, we predict that male frogs that retreat and move away from breeding sites when exposed to predation risk are more likely to return if they have high-value breeding sites. Finally, we predict that willingness of male frogs to return will be positively correlated with the number of eggs at their breeding sites and

Fig. 1 Male *Kurixalus eiffingeri* attending eggs at a breeding site (photo by Wei-Chun Cheng)

that hatching success will be higher for egg clutches that are not abandoned by male frogs.

Material and methods

Study site

We conducted field studies of *K. eiffingeri* males from July to August in 2014, 2015, and 2016 (*N* = 57, 15, and 24 individuals respectively) at Chitou, Taiwan (120° 48′ 10″ E, 23° 39′ 20″ N, elevation 1170 m, mean annual rainfall 2635 mm, mean annual temperature 16.6 °C). We conducted observations and experiments in bamboo forests between 1900 and 0000 h. At our site, the most abundant species of bamboo, *Phyllostachys edulis*, is periodically cut for commercial purposes, leaving stumps that remain for several years before collapsing. These bamboo stumps collect rainwater over time and become calling, breeding, and tadpole development sites for *K. eiffingeri* (Kam et al. 1996).

Experimental design

To test the effects of predation risk and breeding site value, we observed the behavior of male frogs under a two-by-two factorial experiment. We exposed male frogs guarding empty breeding sites (low-value sites) and breeding sites with eggs (high-value sites) to either an opaque PVC pipe that was open on both ends and cut at an angle at the opening (low-risk treatment, Fig. 2) or the same piece of pipe containing a predatory snake, *Dinodon rufozonatum* (high-risk treatment, Fig. 2). We observed a total of 96 male frogs in our four treatments, with 30 individuals exposed to low-risk treatments (*N* = 18 and 12 for those guarding low- and high-value breeding sites each) and 66 individuals exposed to high-risk treatments (*N* = 19 and 47, respectively). Male frogs were located at least 100 m apart to avoid disturbance of nontargeted individuals.

For low-risk treatments, we placed one end of an empty opaque PVC pipe (length = 30 cm, diameter = 2.5 cm, thickness = 0.2 cm) at the opening of a bamboo stump with a male frog (Fig. 2). For high-risk treatments, we placed an identical PVC pipe containing a predatory snake at the opening of a bamboo stump with a male frog (Fig. 2). *D. rufozonatum* are known predators of adult *K. eiffingeri* (Shang et al. 2009) and were obtained from the same study site as the frogs. Guiding the snake through the PVC pipe, we exposed the head of the snake beyond the pipe and allowed it to move around the breeding site, while the body was encased within the pipe, and the tail was held by the observer (Fig. 2). Snakes were held by the tail to keep them firmly in place and to ensure that no frogs or snakes were harmed during observations. For all treatments, we placed PVC pipes next to male frogs for 1 min. During this time, all animals were under continuous observation. Specifically, we noted if male frogs remained at their breeding site or if they retreated away and left their breeding site during this 1-min period (as the “initial response” hereafter). After observations of initial response concluded, we weighed, recorded snout-vent length (SVL), and marked all individuals using toe clips, so that they could be identified during subsequent observations. All individuals were then returned to their original location. The measurements of weight and SVL were used to estimate an index of body condition (i.e., length-independent body mass) of the frogs (see Baker 1992). Toe clipping is a standard method for amphibian identification and causes minimal physiological distress and impact on study animals (Perry et al. 2011). If a male frog retreated away from its breeding site, we revisited the site for three consecutive nights following the treatment to see if the same individual returned (as the “subsequent response” hereafter). If a male frog did not return after three nights, we considered the breeding site to be abandoned. In addition, for breeding sites with eggs, we counted the number of eggs at the breeding site (clutch size) and quantified hatching success by checking eggs daily (between 1400 and 1700 h) until all eggs hatched or died. It was not possible to

Fig. 2 Demonstrative photos of high and low predation risk treatments. In the high-risk treatment (*left*), a PVC pipe containing a predatory snake, *Dinodon rufozonatum*, was placed next to the opening of a bamboo stump, which is the breeding site for *Kurixalus eiffingeri*. In the low-risk treatment (*right*), an empty, snake-less, PVC pipe was placed in the same position. *Kurixalus eiffingeri* eggs can be seen on the inner wall of bamboo stumps in both photos, while a male *K. eiffingeri* can be seen in the photo on the *right*

record data blind because our study involved focal animals in the field.

Statistical analyses

We analyzed male frog behavior using logistic regressions, used for binomial distributions. For initial response of all males, we tested the following explanatory variables: predation risk (high- and low-risk), breeding site value (high- and low-value), interaction between predation risk and breeding site value, male SVL, and male body condition. For subsequent response of males that retreated away, we tested the following explanatory variables: breeding site value, male SVL, and male body condition. Since all males that retreated away were in the high-risk treatment group, predation risk was not included as an explanatory variable in this test. In addition, we used a chi-squared test to compare the difference of initial response between low-value high-risk treatment and high-value high-risk treatment. Looking specifically at males in the high-value high-risk treatment (i.e., males with egg clutches that were exposed to snakes), we tested initial response of males using the following explanatory variables: clutch size, male SVL, and male body condition. The same explanatory variables were tested for subsequent response of males within this group that retreated away initially. Looking at hatching success, we categorized hatching rate of clutches into one of five groups (0–20, 21–40, 41–60, 61–80, and 81–100%) and analyzed hatching rating using ordinal logistic regressions. For hatching rate of all clutches, we tested the following explanatory variables: initial response of males, male SVL, and male body condition. For hatching rate of clutches where males retreated away initially, we tested the following explanatory variables: subsequent response of males, male SVL, and male body condition. All statistical analyses were performed in Statistica 10 (StatSoft 2011). Means are presented with ±1 SD.

Results

Initial behavioral responses of male frogs during the 1-min exposure to predator risk were significantly different between high- and low-risk treatments (Table 1, Fig. 3), while no effects were found for breeding site value, interaction between predation risks and breeding site value, male SVL, or male body condition (Table 1). All males in low-risk treatments remained at their breeding sites, while less than half of those in high-risk treatments remained. Moreover, for males in high-risk treatments, a higher percentage of individuals remained at high-value breeding sites compared to low-value breeding sites (40 and 11%, respectively, $\chi^2 = 5.58$, $p = 0.018$). Males that remained at the breeding site would sometimes withdraw down into the water at the bottom of the bamboo stump for cover. No aggressive or defensive behaviors against the predation, such as moving towards the predator or covering the egg clutch (see Toledo et al. 2011; Poo et al. 2016a), were exhibited by the frogs. Subsequent response of males that retreated away initially was significantly different between breeding site value treatments (Table 1), with more males returning to high-value breeding sites to care for eggs compared to low-value breeding sites (54 and 12%, respectively), while no effects were found for male SVL or male body condition (Table 1).

Looking at male behavior in high-value high-risk treatments, we found no effect of clutch size, male SVL, or male body condition on initial response of males (Table 1). However, subsequent return of males to their breeding sites, after predation risks were alleviated, was positively correlated with larger clutch sizes (Table 1, Fig. 4). This difference in subsequent return on males in the high-value high-risk

Table 1 Logistic regression for factors associated with *Kurixalus eiffingeri* male behavior in predator risk and breeding site value treatments and ordinal logistic regression for factors associated with hatching rates of *K. eiffingeri* eggs

	df	X^2	*p* value	Coefficient
Initial response of males ($N = 96$)				
Predation risk	1	56.48	<0.001	10.24
Breeding site value	1	0.02	0.885	0.44
Predation risk × breeding site value	1	<0.01	1.000	−0.44
Male SVL	1	0.01	0.934	−0.01
Male body condition	1	0.02	0.892	−0.19
Subsequent response of males that retreated away initially ($N = 45$)				
Breeding site value	1	8.68	0.003	−1.15
Male SVL	1	0.55	0.458	0.13
Male body condition	1	0.01	0.918	−0.18
Initial response of males in high-value high-risk treatment ($N = 47$)				
Clutch size	1	1.45	0.229	0.02
Male SVL	1	0.67	0.413	−0.15
Male body condition	1	0.01	0.926	−0.51
Subsequent response of males in high-value high-risk treatment that retreated away initially ($N = 28$)				
Clutch size	1	6.57	0.010	−0.07
Male SVL	1	1.05	0.306	−0.23
Male body condition	1	0.01	0.943	2.56
Hatch rate in high value sites ($N = 47$)				
Initial response	1	0.07	0.798	0.07
Male SVL	1	<0.01	0.979	−0.01
Male body condition	1	<0.01	0.958	−0.07
Hatch rate in high value sites where males retreated away initially ($N = 28$)				
Subsequent response	1	4.81	0.028	0.96
Male SVL	1	0.04	0.838	0.06
Male body condition	1	2.62	0.105	3.15

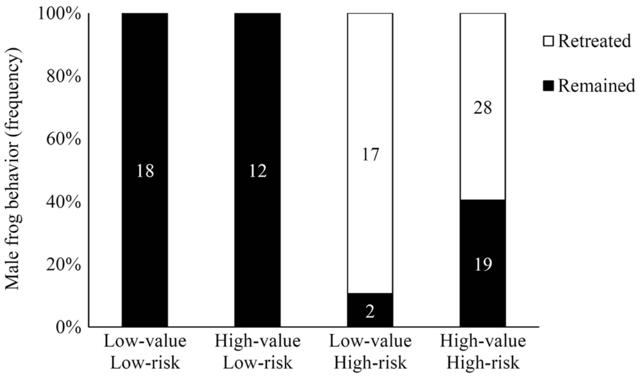

Fig. 3 Initial behavioral response of male *Kurixalus eiffingeri* at high- and low-value breeding sites (with or without eggs, respectively) when exposed to high- and low-risk treatments (with or without a predatory snake, respectively). *Numbers within bars* represent the number of individuals

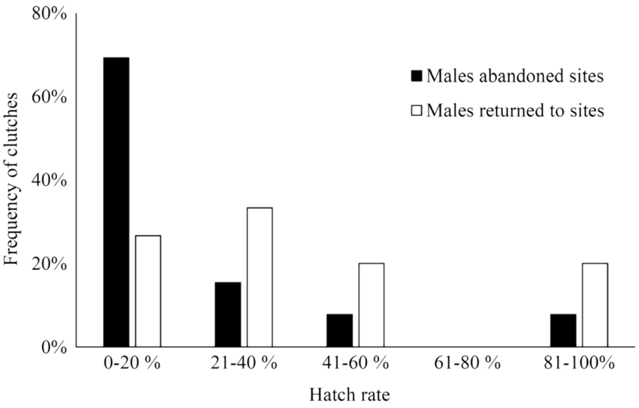

Fig. 5 Frequency distribution of hatch rate at breeding sites that were abandoned by male *Kurixalus eiffingeri* compared to breeding sites where male frogs returned to continue their egg attendance behavior after threats of predation were alleviated

treatments was not correlated with male SVL or male body condition (Table 1). Hatching rate was not correlated with initial response of males, male SVL, or male body condition (Table 1). However, hatching rate was significantly higher at breeding sites where males subsequently returned to continue caring for their clutches compared to abandoned sites where males did not return (Table 1, Fig. 5). Here again, no effects were found for male SVL or male body condition (Table 1).

Discussion

In this study, we investigated the trade-offs between self-preservation and parental investment in a frog with egg attendance. Results showed that male frogs were able to recognize predators as possible risks and were capable of adjusting their behavior accordingly. Furthermore, male frog behavior reflected the relative value of their breeding sites, as represented by both the presence and the number of eggs. Finally, we found that predator avoidance in male frogs had a negative effect on the survivorship of their dependent offspring.

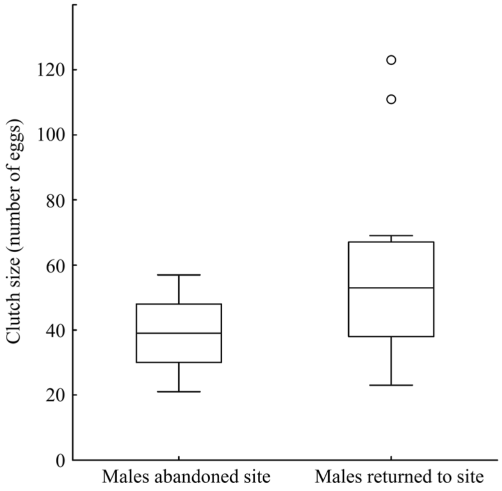

Fig. 4 Number of eggs (clutch size) at breeding sites that were abandoned by male *Kurixalus eiffingeri* compared to breeding sites where male frogs returned to continue their egg attendance behavior after threats of predation were alleviated (medians, first and third quartiles, extreme ranges, and outliers are indicated in the boxplot)

When exposed to a predatory snake, most male frogs retreated away from the predator and left their breeding site regardless of whether they were guarding breeding sites with or without eggs (Fig. 3). In comparison, all male frogs that were exposed to low level disturbances caused by a snake-less PVC pipe remained at their breeding site. Similar to other amphibians, *K. eiffingeri* likely use visual cues to detect the presence or appearance of predators (e.g., Stancher et al. 2014; Kundey et al. 2016). Since most frogs are limited in their ability to deter predatory snakes (reviewed in Wells 2007), a logical response to the presence of such predators would be to avoid or minimize direct encounters by retreating away, such as in the case of the Hansen's bush frog, *Feihyla hansenae* (Poo et al. 2016b). For species with parental care, however, there is a trade-off between self-preservation and protection or provisioning of offspring. Since parental investment is often costly for adults (Dugas et al. 2016), adults of iteroparous species should be more willing to abandon current offspring in order to preserve their energy, lower their risks of mortality, and increase their chances of future reproduction. For example, rocky shore frogs, *Thoropa taophora*, have been shown to decrease their parental care activities in response to harsh environmental condition (Consolmagno et al. 2016), while nuthatches, *Sitta carolinensis* and *Sitta canadensis*, have been shown to alter their predator avoidance behavior according to their chances of survival and their fecundity (Ghalambor and Martin 2000). Similarly, we found a tendency of male frogs to abandon their breeding sites in the presence of predatory snakes in favor of self-preservation.

One of the ways that the particular case of *K. eiffingeri* differs from other cases of predator avoidance by parents is that the predatory snake, *D. rufozonatum*, only consumes adult frogs and poses minimal threat to frog eggs (Shang et al. 2009). Therefore, eggs that are left by male frogs remain unharmed by snakes, giving males the opportunity to return to their breeding site and continue their care after the snakes leave. This willingness to retain or reclaim ownership over a breeding site lies in the fitness value that it represents to the male. For example, sand gobies, *Pomatoschistus minutus*, guarding larger nests are less likely to give up their tenure (Lindström and Pampoulie 2005). Similarly, blackbirds, *Agelaius phoeniceus*, will consider the potential benefits of a breeding site before making its selection (Beletsky and Orians 1987). For *K. eiffingeri* males guarding breeding sites without eggs, the site represents potential mating opportunities that can lead to future offspring (Chen et al. 2011). However, these empty breeding sites should be less important to males compared to breeding sites with eggs, where the current offspring contribute directly to the overall fitness of the male. As we hypothesized, this difference in breeding site value is reflected in the level of predator risk that males are willing to tolerate; with males being more reluctant to leave breeding sites when there are eggs present (Fig. 3) and more willing to return to these sites after risks of predation were alleviated.

Another key factor that determines the value of a breeding site is the number of offspring present. According to the life history theory, the more offspring present within a clutch, the higher the value for the parent (Stearns 1992). Therefore, parents should be more willing to invest in care of offspring when there are more offspring present. Increased parental investment for larger clutch sizes has been found in many taxa, such as belostomatids (Kight et al. 2011), cichlids (Wisenden et al. 2008), and stitchbirds (Low et al. 2012), but similar findings have been generally lacking in amphibians. Although larger clutch sizes have been associated with increased attendance time by *K. eiffingeri* (Cheng and Kam 2010), the present study provides the first concrete evidence of both the effects of clutch size on the willingness of males to increase their care by returning to their breeding sites (Fig. 4) and the benefits of higher hatching success as a result of the male's decision to invest in such care (Fig. 5).

The lower hatching success in abandoned breeding sites indicates that threats posed by predators not only affect the behavior of male frogs, but also indirectly affect the offspring under their care. A similar case can be seen in great tits, *Parus major*, where the presence of predators affects the behavior of adult birds, leading to alternations in the frequency and duration of their incubation sessions (Basso and Richner 2015). This change in adult behavior then has a negative carryover effect onto the offspring, resulting in lighter weight in eggs and nestlings. In anurans, egg attendance can lower egg mortality by preventing predation, pathogen infection, and desiccation (Bourne 1998; Vockenhuber et al. 2009; Delia et al. 2013; Poo and Bickford 2013; Poo et al. 2016a; Valencia and Delia 2016). Egg attendance by *K. eiffingeri* males, in particular, functions to maintain hydration of eggs and to reduce potential predation by small invertebrates (Kam et al. 1996; Chen et al. 2007; Cheng and Kam 2010). In our study, we found that the presence of a predatory snake, even if it is only a predator of adult frogs, can negatively affect the survival of frog eggs via a decrease in parental investment by the males. Although there may be compensatory growth that reduces long-term effects of early development (Basso and Richner 2015), studies have shown that for species with multiple life stages, disadvantages accrued in early life stages can negatively affect fitness in subsequent stages and adulthood (Semlitsch et al. 1988; Pechenik et al. 1998). Hence, there may be carryover, or predator-induced, effects on *K. eiffingeri* eggs extending into the tadpole, juvenile, or adult stages, which require further observation and exploration.

In conclusion, we provide empirical evidence that predation risk can affect the behavior of male frogs and have a subsequent indirect effect on hatching success of their eggs. Our results illustrate how factors of adult and offspring survival contribute to the decisions that a parent makes during the mating period and the subsequent period of parental care. These findings provide us with insights into parental behavior of amphibians and broaden our understanding of the effects of predation risk and breeding site value on parental care and offspring survivorship.

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Compliance with ethical standards

Ethical approval All research presented in this manuscript was conducted in accordance with ethical standards of Tunghai University and was approved by the Institutional Animal Care and Use Committee of Tunghai University (No. 100-19). Experiments at Chitou were approved by the College of Bio-Resources and Agriculture, National Taiwan University (Document No. 1030006132).

Conflict of interest The authors declare that they have no conflict of interest.

Data availability All data generated and analyzed during this study are included in the supplementary information file of this published article (Supplementary File 1).

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