ORIGINAL ARTICLE

Cannibalism or congeneric predation? The African clawed frog, *Xenopus laevis* (Daudin), preferentially predates on larvae of Cape platannas, *Xenopus gilli* Rose & Hewitt

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Abstract

Predators are not limited to prey from other species as they can cannibalise vulnerable individuals within their own population. The African clawed frog, *Xenopus laevis* (Daudin), is a predator with a broad diet, known to consume multiple prey species, including congeners and conspecifics. African clawed frogs occur in sympatry with the Endangered Cape platanna, *Xenopus gilli* Rose & Hewitt, which are under threat through competition and predation from *X. laevis*. We investigated the threat of *X. laevis* predation on *X. gilli* using choice and no-choice experiments to evaluate the relative vulnerability of *X. laevis* and *X. gilli* larvae. Results showed that large *X. gilli* larvae had a significantly higher vulnerability to *X. laevis* predation compared to small *X. gilli* larvae. However, the same discrimination was not discerned when offered large and small *X. laevis* larvae, or mixed larvae of the same size. We report ontogenic shifts in behaviour of *X. gilli* larvae that may be a factor in contributing to the vulnerability of large *X. gilli* larvae to adult *X. leavis* predation. Congeneric predation likely has negative implications for the population structure of the Endangered *X. gilli*. Our study underlines the call for the removal of *X. laevis* to conserve populations of *X. gilli*.

Résumé

Les prédateurs ne se limitent pas aux proies d'autres espèces car ils peuvent cannibaliser les individus plus vulnérables de leur propre population. Le xénope lisse *Xenopus laevis* (Daudin) est un prédateur au régime alimentaire diversifié ;on sait qu'il consomme de nombreuses espèces de proies, dont des congénères et des individus conspécifiques. Les xénopes lisses sont sympatriques de *Xenopus gilli* Rose & Hewitt, espèce en danger en raison de la compétition et de la prédation de *X. laevis*. Nous avons étudié la menace de la prédation de ce dernier sur l'autre espèce au moyen d'expériences de choix – non-choix, pour évaluer la vulnérabilité relative des larves des deux espèces. Les résultats montrent que les grands têtards de *X. gilli* avaient une vulnérabilité significativement plus grande à la prédation par *X. laevis* que les petits têtards. Cependant, nous n'avons pas décelé la même discrimination en cas de présentation de petits et de grands têtards de *X. laevis*, ou de têtards mêlés de même taille. Nous rapportons des modifications ontogéniques de comportement de têtards de *X. gilli* qui peuvent être un facteur contribuant à la vulnérabilité des grands têtards de *X. gilli* face à la prédation

par les *X. laevis*. La prédation probable des congénères a des implications négatives pour la structure de la population menacée de *X. gilli*. Notre étude conforte l'appel à l'élimination de *X. laevis* dans le but de protéger les populations de *X. gilli*.

1 | INTRODUCTION

Xenopus laevis (Daudin), the African clawed frog, is a large pipid (~130 mm snout-vent length [SVL] in females), and one of the most widespread and common amphibian species found in southern Africa (Measey, 2004). Their adaptability to habitat type and diet has allowed them to move between and exploit permanent and temporary water bodies (Measey et al., 2017), traits which have also made them effective invaders around the world (Measey et al., 2012). They are known to consume other amphibians and are also notorious cannibals that consume both their own eggs and larvae for food even when resources are not limiting (Measey, 1998; Measey et al., 2015; Schoonbee, Prinsloo, & Nxiweni, 1992). A recent review of diet suggests that cannibalism occurs whenever larval conspecifics are present, apparently independent of other prey availability (Courant et al., 2017).

The Cape platanna, *Xenopus gilli* Rose & Hewitt, is a species endemic to the south-western Cape of South Africa. It is significantly smaller (~60 mm SVL in females) than *X. laevis* (Fogell, Tolley, & Measey, 2013; Picker & De Villiers, 1989), but co-occurs at all sites with synchronous breeding (Rau, 1978). Where the two species co-occur, adult *X. gilli* are outnumbered three to one, and recruitment is severely curtailed (de Villiers, Kock, & Measey, 2016). Competition for resources and predation are currently considered to be direct threats from sympatry with *X. laevis* (Vogt, Villiers, Ihlow, Rödder, & Measey, 2017), resulting in its current listing as Endangered by the IUCN (IUCN & SA-FRoG, 2017). Although predation from adult *X. laevis* on adult *X. gilli* has been observed (Vogt et al., 2017), it may be that predation of more vulnerable life-history stages is more important. However, in these temporary ponds, this impact would be increased if adult *X. laevis* could discriminate between cannibalism of their own larvae and selection of larvae of the sympatric congener, *X. gilli*.

The morphology of *X. laevis* and *X. gilli* larvae is very similar, with minor pigmentation differences at the later stages (Rau, 1978), whereas eggs and newly hatched larvae are indistinguishable (Rau, 1978; personal observation). Although adult *X. laevis* rely on visual cues to detect some terrestrial prey (e.g. Measey, 1998), aquatic prey are thought to be detected by the lateral line organs situated along the trunk and head (Elepfandt, 1996). These organs are extremely sensitive and can be used to detect movement in water. Therefore, differences in activity between *X. laevis* and *X. gilli* larvae may influence their relative vulnerability to predation from *X. laevis* predators. *Xenopus laevis* also use olfactory receptors to detect water-soluble odorants from carrion, but little is known on their ability to detect aquatic prey by means of chemical cues (Freitag, Krieger, Strotmann, & Breer, 1995).

In this study, we investigated whether *X. laevis* would select cannibalism (on larval *X. laevis*) or predation (on larval *X. gilli*) in a system where these two were the only available prey resource. This was tested by analysing the survival rate of *X. gilli* and *X. laevis* larvae in the presence or absence of an *X. laevis* predator. Behaviour was observed and analysed in order to determine whether larval activity plays a role in vulnerability to *X. laevis* predation.

2 | MATERIALS AND METHODS

Anecdotal evidence suggests that *X. laevis* larvae are able to reach metamorphosis twice as fast as *X. gilli* (Rau, 1978) and lay considerably more eggs: 2,700–17,000 eggs for *X. laevis* compared to 270–400 for *X. gilli* (de Villiers, 2004; McCoid & Fritts, 1989; Rau, 1978). Consequently, this may lead to different larvae of each species having different stages of development and/or size at the same age.

2.1 | Rearing larval prey

Xenopus laevis adults were captured in the Jonkershoek fish hatchery (−33.9631°S; 18.9252°E), and *X. gilli* adults were captured in Kleinmond (−34.3330°S; 19.0851°E) using funnel traps baited with chicken liver. Five adult males and females of each species were brought to Stellenbosch University and held in a temperature controlled room set at 16°C. Passive Integrated Transponder tags (APR 350, Agrident, Barsinghausen Germany) were injected into adults to allow for identification in order to avoid using the same individuals for breeding in subsequent experiments (de Villiers et al., 2016).

Adults were kept in aquaria (300 × 240 × 240 mm) and were maintained on a diet of chicken livers *ad libitum*. Frogs not in their reproductive cycle were injected subcutaneously in the dorsal lymph sac with human chorionic gonadotropin (pregnyl) 3 days prior to induced spawning. Once injected, males and females of the same species were placed together as pairs into (300 × 240 × 240 mm) aquaria with a (15 mm) mesh fitted inside in order to protect the eggs from being eaten by the adults. *Xenopus* prefer mating when there is minimal disturbance, and spawning took place overnight. Adults were then removed the following morning from the aquaria, leaving the eggs to hatch at a later stage. The resulting larvae were then monitored and fed on Sera Micron (Heinsberg, Germany) daily until the experiment began approximately 14 days after spawning.

In order to rear larvae to different sizes, different adults were induced at 2-week intervals. Prior to each experiment, larvae were photographed and snout to tail length was measured using ImageJ (Rasband, 2012). Larvae are readily identified to species based on their dorsal pigmentation (Rau, 1978). Adults used for breeding were not used as predators in any experiments. Collection and field work permits were obtained from Cape Nature (AAA007-00159-0056), and ethical clearance was obtained by Stellenbosch University (SU-ACUD15-00011).

2.2 | Behavioural observation

Behavioural observations of *Xenopus* larvae were made for 5 min per mesocosm, 24 hr prior to each experiment. *Xenopus laevis* larvae are known to swim continuously in midwater by undulating the posterior portion of their tail at a constant frequency, known as sculling (Hoff & Wassersug, 1986). Rau (1978) mentioned differences in the behaviour of larvae of *X. laevis* and *X. gilli*, where the latter remain at the bottom of the tank at elevated temperatures. We documented larval movement, as the number of times within 5 min that larvae increased their swimming velocity by using the majority of their tail so as to displace themselves, as opposed to sculling. Position was defined as the proportion of larvae situated within 10 cm of the bottom and sides of the mesocosm.

2.3 | Experimental design

To account for both age and size of the different larval species, the experimental design for this study tested predation from *X. laevis* adults in three different experiments where the prey exposed were (a) same aged larvae of *X. laevis* and *X. gilli*; (b) different sized larvae of same species (*X. laevis*); and (c) same size larvae of both species. Each treatment was replicated 4 times (*n* = 4) following the review of Skelly and Kiesecker (2001). We chose to use only female *X. laevis* as predators in all experiments as we found their appetite to be more consistent than males.

2.3.1 | Experiment 1: cannibalism and predation of intracohort larvae of *Xenopus laevis* and *Xenopus gilli*

A 2 × 3 factorial experimental design was used to examine the effect of *X. laevis* predation on *Xenopus* larvae in which predator presence (one *X. laevis* adult female) and prey species (*X. laevis* and *X. gilli* larvae) were manipulated. Treatments were either presented or withheld from a single *X. laevis* predator during the experiment. Single treatments contained either *X. laevis* or *X. gilli* larvae, whereas mixed treatments contained both *X. laevis* and *X. gilli* larvae in the same mesocosm. Experiments were conducted in individual ±500 L mesocosms covered with shade cloth (see Thorp, Alexander, Vonesh, & Measey, 2018). No refuge inside the tanks was provided as *Xenopus* larvae are all presumed to be midwater suspension feeders (Wassersug, 1996). Mean SVL of adult female *X. laevis* (predators) used in this experiment was 92.3 mm (*SE* = ±0.55). Predators and treatments were randomly assigned to

different mesocosms. Single treatments had 24 larvae of each species, whereas mixed treatments contained densities of 12 for each prey species. Upon rearing, we found that larvae of each species reached a different size at the same age (see Results). Larvae were placed into mesocosms 48 hr prior to experimental trials in order to acclimatise. Predator hunger levels were standardised by starving individuals 48 hr prior to the mesocosm experiment.

The experiment was initiated when predators were introduced into their assigned mesocosms. The experiment proceeded overnight for minimal disturbance (from 18:00 to 08:00 hours) and was completed once the predators were removed 14 hr later. Remaining prey were counted in order to generate data to determine the percentage of surviving larvae for each species.

2.3.2 | Experiment 2: cannibalism of intercohort larvae of *Xenopus laevis*

A second experiment was conducted in order to test whether vulnerability from *X. laevis* predation could be attributed to size. This experiment followed the same procedure as the previous experiments with the exception of using the same larval species at different ages. Therefore, single treatments contained either large or small *X. laevis* larvae, whereas mixed treatments contained both sizes in the same mesocosm. One group of *X. laevis* larvae were reared 4 weeks prior to another group of *X. laevis* larvae. This allowed us to compare the survival of small and large *X. laevis* larvae to *X. laevis* predation. This experiment was not conducted with *X. gilli* as this species is Endangered constraining the number of *X. gilli* adults that we were able to use. Mean length of large *X. laevis* larvae was 26 mm (*SE* = ±0.15), whereas mean length of small *X. laevis* was 7.5 mm (*SE* = ±0.04). Mean SVL of predators used in this experiment was 94.8 mm (*SE* = ±0.57).

2.3.3 | Experiment 3: cannibalism and predation of intercohort larvae of *Xenopus laevis* and *Xenopus gilli*

A third experiment was conducted to standardise size of the different prey species. This experiment followed the same procedure as Experiment 1 with the exception of rearing *X. laevis* larvae 2 weeks prior to *X. gilli* larvae. This allowed for both larval species to be of the same size once the experiment was conducted. Therefore, single treatments contained either *X. laevis* or *X. gilli* larvae, whereas mixed treatments contained both *X. laevis* and *X. gilli* larvae in the same mesocosm. Survival of both larval species was measured and compared at the end of the experiment. *Xenopus laevis* larvae were 2 weeks older than the *X. gilli* larvae. Mean length of *X. laevis* larvae was 20.2 mm (*SE* = ±0.12), whereas mean length of *X. gilli* was 19.5 mm (*SE* = ±0.10). Mean SVL of predators used in this experiment was 94.4 mm (*SE* = ±0.42).

2.4 | Data analyses

All experimental and behavioural data were analysed with a Shapiro–Wilk's test in order to test the normality of the residuals. Experimental

data were analysed with a factorial ANOVA in order to compare overall differences vulnerability to *X. laevis* predation. If differences were found, a Tukey HSD posthoc analysis was used to determine where the differences lie. Behavioural data were also analysed using a factorial ANOVA and followed with a Tukey HSD in order to test whether there were differences in movement and position between species and/or size. All analyses were conducted using R v3.3.1 (R Core team, 2016).

3 | RESULTS AND DISCUSSION

3.1 | Experiment 1

The first experiment showed that large *X. gilli* larvae were more vulnerable to predation than smaller *X. laevis* larvae of the same age. Contrary to expectation, *X. gilli* larvae grew faster than *X. laevis* and

were larger at the beginning of the experiment, even though the adult size is eventually larger in *X. laevis*. Mean length of *X. gilli* larvae was 25 mm (*SE* = ±0.13), whereas mean length of *X. laevis* was 9 mm (*SE* = ±0.05). Survival rates of large *X. gilli* larvae (single = 30.2%, *SE* = ±0.15; mixed = 31.2%, *SE* = ±0.20) were significantly lower than small *X. laevis* larvae (single = 62.5%, *SE* = ±11.79; mixed = 72.9%, *SE* = ±9.24) for both treatments ($F_{1,8}$ = 6.51, *p* < 0.05; Figure 1a). No mortality was observed in the control treatment.

Xenopus gilli's faster larval development was in contrast to our expectations. Rau (1978) had observed *X. gilli* larvae to have much slower growth rates than *X. laevis* larvae. This may have been due to Rau (1978) comparing the growth rates of *X. gilli* larvae found in temporary ponds, with fluctuating temperatures, to the growth rates of *X. laevis* larvae reared in a laboratory. Faster larval growth is expected in the temporary water bodies in which in *X. gilli* lives
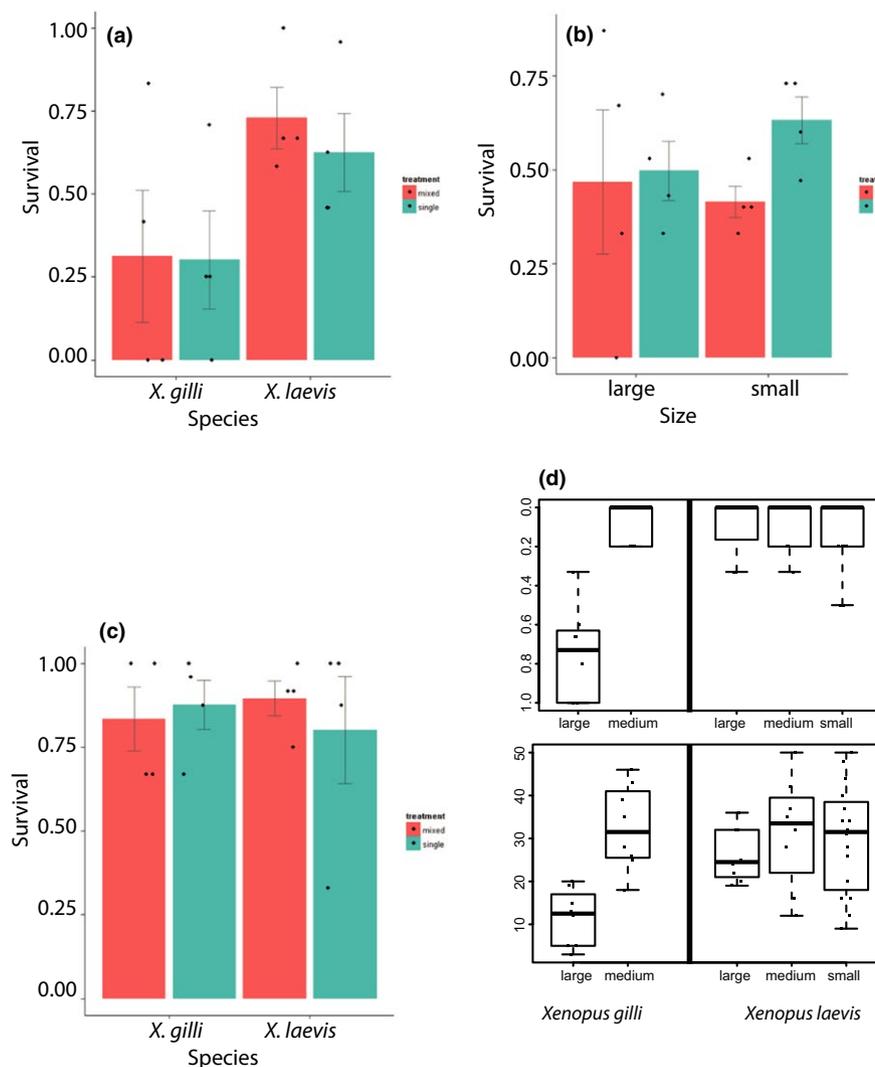

FIGURE 1 (a) Mean survival rates (±*SE*) of large *Xenopus gilli* and small *Xenopus laevis* larvae in each treatment exposed to adult *X. laevis* predation. (b) Mean survival rates (±*SE*) of large *X. laevis* and small *X. laevis* larvae in each treatment exposed to adult *X. laevis* predation. (c) Mean survival rates (±*SE*) of same sized *X. laevis* and *X. gilli* larvae in each treatment exposed to adult *X. laevis* predation. (d) Behaviour of *Xenopus* tadpoles in mesocosms prior to the start of the experiment. (a) The position of different sized *Xenopus* tadpoles within the mesocosm is presented as a percentage of tadpoles that are more than 10 cm away from the bottom and sides. (b) The total number of movements made by *Xenopus* tadpoles within a 5-min period

and has been observed elsewhere (Wilbur, 1980; Woodward, 1983). Smaller *X. laevis* predators would be expected to select smaller *Xenopus* larvae due to gape limitation. Thus, faster growth rates in *X. gilli* larvae may reduce vulnerability to predation from smaller *X. laevis* predators. It is suggested that predators will select the more dominant prey species in an environment (Wilbur, 1988), and with larger clutch sizes, this may make *X. laevis* more vulnerable than *X. gilli*.

3.2 | Experiment 2

In the second experiment, size was not a factor in larval vulnerability, as large and small *X. laevis* larvae had no differences in survival. Large *X. laevis* larvae were 4 weeks older than the small larvae. Survival rate from *X. laevis* predation was not found to be dependent on larval size. There was no significant difference between the survival rates of large *X. laevis* larvae (single = 49.8%, *SE* = ±0.08; mixed = 46.8%, *SE* = ±0.19) and small *X. laevis* larvae (single = 63.25%, *SE* = ±0.06; mixed = 41.5%, *SE* = ±0.04) for both treatments ($F_{1,8}$ = 0.14, *p* > 0.05; Figure 1b). No mortality was observed for large larvae, while small larvae had 86.7% survival in the control treatment.

3.3 | Experiment 3

The final experiment found that *X. laevis* predators showed no preference or selection towards either species when they were the same size, with no difference in survival between *X. gilli* and *X. laevis* larvae. Survival rate from *X. laevis* predation was not dependent on species alone. There was no significant difference between the survival rates of *X. laevis* larvae (single = 80.1%, *SE* = ±0.16; mixed = 89.6%, *SE* = ±0.05) and *X. gilli* (single = 87.6%, *SE* = ±0.07; mixed = 83.5%, *SE* = ±0.10) for either treatments ($F_{1,8}$ = 0.01, *p* > 0.05; Figure 1c). No mortality was observed in the control treatment.

No differences in vulnerability between medium *X. gilli* and *X. laevis* larvae suggest that predators were not able to distinguish between prey species. The observed larval activity and position were similar in both species for medium-sized tadpoles. *Xenopus laevis* and *X. gilli* larvae were active and swimming in the middle of the water column. This is in contrast to findings in our first experiment where large *X. gilli* larvae were found sculling at the bottom and sides of the mesocosms. Although our results might be a false-negative, they might also be explained by ontogenic behavioural and microhabitat change in *X. gilli* that alter expected predator-prey outcomes, as has been seen in other species (e.g. Alford & Crump, 1982; Touchon, Jiménez, Abinette, Vonesh, & Warkentin, 2013). Temporary water bodies might offer a refuge for larvae as they were observed to have a larger density of benthic vegetation and were shallower in comparison with the permanent water bodies in the area.

3.4 | Behavioural observations

Across all experiments, large *X. gilli* larvae were significantly different from all other *X. gilli* and *X. laevis* larvae in displacement ($F_{5,42}$ = 5.55, *p* < 0.05) and position ($F_{5,42}$ = 25.57, *p* < 0.05). *Xenopus laevis* larvae across all experiments showed similar activity (Figure 1d). No change in behaviour was noted for tadpoles of either species in response to the addition of a predator. The proportion of *X. laevis* larvae found at the bottom and sides of the mesocosms were not significantly different between larvae of different sizes: large (0.089, *SE* = 0.07); medium: (0.092, *SE* = 0.05); small (0.12, *SE* = 0.05; *p* > 0.05). Movement of *X. laevis* larvae was not significantly different between sizes across all experiments: large ($\bar{x}$ = 26.2, *SE* = 2.2); medium ($\bar{x}$ = 31.5, *SE* = 4.5); small: ($\bar{x}$ = 29.8, *SE* = 3.2; *p* > 0.05). *Xenopus gilli* larvae showed differences in locality and activity (Figure 1d). The proportion of *X. gilli* larvae found at the bottom and sides of the mesocosms were significantly different between different sized larvae: large (0.75, *SE* = 0.08); medium: (0.08, *SE* = 0.04; *p* < 0.05). Large *X. gilli* larvae had significantly less movements compared to their medium-sized conspecifics: large ($\bar{x}$ = 11.5, *SE* = 2.3); medium ($\bar{x}$ = 32.5, *SE* = 33.4; *p* < 0.05).

Prey behaviour may have influenced the choice made by adult *X. gilli* predators. Large larvae of *X. gilli* were lower in the water and with reduced movement when compared to all *X. laevis* larvae. Most *X. gilli* larvae were found to be sculling, an antipredatory behaviour that involves the movement of only the posterior portion of the tail to minimise movement (Hoff & Wassersug, 1986). They were also observed to be situated in the same position as the predators, at the bottom and sides of each mesocosm. This would likely lead to an increase in encounter rate and therefore increase in vulnerability to predation. It has been suggested that larval movement is one of the main factors contributing to vulnerability as movement makes prey more detectable to predators (Caldwell, Thorp, & Jervey, 1980; Woodward, 1983). *Xenopus laevis* detect prey in water through movement, via their lateral line organs; therefore, it might be expected that moving larvae should be under increased threat of predation. However, *X. laevis* larvae were observed to show more movement than *X. gilli* larvae, indicating that adult *X. laevis* may be using the behaviour of the *X. gilli* larvae to distinguish them from *X. laevis* larvae. Our observations on behaviour of large *X. gilli* larvae suggest that they may swim at the bottom of these ponds among the vegetation, without the schooling typically seen in *X. laevis* (Katz, Potel, & Wassersug, 1981).

4 | CONCLUSION

We found some evidence for the ability of *X. laevis* predators to discern between tadpoles of different species (Experiment 1), but not size-matched tadpoles of different species (Experiment 3). Overall, our findings have important implications for the conservation of *X. gilli*. High densities of predators can drastically reduce recruitment success in amphibian prey species (Muedeking & Heyer, 1976). *Xenopus gilli* has a limited distribution and therefore cannot escape predation pressure from *X. laevis* in these temporary ponds. In *X. gilli* larvae, fast growth rate to a size that acts as a refuge towards relatively smaller predators; sculling, which reduces

the chance of detection, and positioning are all mechanisms that may reduce vulnerability to aquatic predators. In addition, the vegetation present in temporary water bodies, together with sculling and positioning, may help protect *X. gilli* larvae from some predation. However, these antipredatory mechanisms were not effective against relatively large *X. laevis* predators in our mesocosms or in field studies (Vogt et al., 2017).

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