



The effects of the diel cycle and the density of an invasive predator on predation risk and prey response



L. K. Lopez*, M. Y. L. Wong, A. R. Davis

School of Biological Sciences, University of Wollongong, NSW, Australia

ARTICLE INFO

Article history:

Received 12 November 2015

Initial acceptance 25 January 2016

Final acceptance 25 April 2016

MS number 15-00962

Keywords:

antipredator
density
diel cycle
invasive
predation
risk

All prey face a fundamental trade-off between avoiding predation and pursuing activities, such as foraging and mating, that enhance fitness. Therefore, the effects of predation can be both consumptive and nonconsumptive and prey need to assess and respond appropriately to predation risk which in turn varies with environmental and social contexts. We tested the effects of predator density and diel cycle on the consumption, interspecific interactions and behavioural responses of a prey species, the native Australian glass shrimp, *Paratya australiensis*, exposed to a predator, the invasive eastern mosquito fish, *Gambusia holbrooki*. In the laboratory, *P. australiensis* were exposed to low or high densities of conspecifics or predators and observed during the day and at night. While *P. australiensis* experienced more interspecific approaches and nips when exposed to a high density of *G. holbrooki* and during the day, neither predator density nor diel cycle influenced the actual number of *P. australiensis* consumed. Similarly, while *P. australiensis* engaged in significantly more shelter use and swam less, there was no difference in these behaviours in relation to predator density and diel cycle. Foraging by *P. australiensis* was not related to species composition, but instead depended on the overall number of animals present with more *P. australiensis* foraging when exposed to a high density of conspecifics and *G. holbrooki*. These results indicate that the mechanisms by which *G. holbrooki* exerts negative effects on *P. australiensis* can be multiple and wide ranging, from direct predation to a reduction in activity and competition for resources. However, as neither predator density nor diurnal variation altered predation rate, *P. australiensis* did behave in an adaptive manner, by only adjusting its behavioural responses in proportion to the direct risk of predation.

© 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

To reduce the risk of being consumed by predators, prey often exhibit substantial behavioural changes including increased vigilance, refuge use, dispersal and changes in activity patterns (Eccard, Pusenius, Sundell, Halle, & Ylönen, 2008; Lima, 1998; Lima, Valone, & Caraco, 1985; Sih, 1986; Sih et al., 2010). While frequently successful in reducing the rate of direct consumption (defined as consumptive effects, CEs), such behavioural changes may also negatively impact upon foraging and reproduction (defined as nonconsumptive effects, NCEs), thus leading to a trade-off between minimizing mortality from predation and maximizing fitness (Lima et al., 1985; Paterson et al., 2013; Sih, 1986). Therefore, as posited by Helfman's (1989) threat-sensitive predator avoidance hypothesis, prey need to maximize their overall fitness by exhibiting antipredator responses that are proportional to the level of predation

risk to which they are exposed. If the avoidance behaviours exhibited by prey are in excess of the predation risk, then the strength of NCEs on prey fitness will increase, yet if antipredator behaviours are insufficient, the strength of CEs on prey should become greater (Anholt, Werner, & Skelly, 2000; Ferrari, Sih & Chivers, 2009; Helfman, 1989; Lima et al., 1985; Sih, 1986).

One of the key factors influencing levels of perceived predation risk is predator density (Ferrari et al., 2009; Foam, Mirza, Chivers, & Brown, 2005; Vucetich, Peterson, & Schaefer, 2002). Density itself can be modulated if predators form aggregations in the environment, in turn generating a predation risk that is spatially heterogeneous (Butler, 1989; Mella, Banks, & MacArthur, 2014; Navarrete & Menge, 1996). Currently, there is mixed support as to whether predator density and CEs are positively correlated (Sih, 1986; Vance-Chalcraft, Soluk, & Ozburn, 2004). Typically, higher predator densities have been related to an increased number of encounters between predators and prey, leading to a higher per capita kill rate, as observed in wolves, *Canis lupus*, and moose, *Alces alces* (Stier, Geange, & Bolker, 2013; Vucetich et al., 2002). Even so,

* Correspondence: L.K. Lopez, School of Biological Sciences, University of Wollongong, North Fields Avenue, Wollongong, NSW 2522, Australia.

E-mail address: laural@uow.edu.au (L. K. Lopez).

negative correlations between predator density and prey capture and kill rates have been reported, due to an increase in the frequency of competitive interactions among foraging predators, known as mutual interference (Abrams, 1993; Mistri, 2003; Sih, 1979).

With regard to NCEs, the relationship with predator density is also often complex. Flathead minnows, *Pimephales promelas*, show stronger antipredator responses in the form of shoaling and flee behaviours when exposed to the odour cues of 12 pike compared to just two (Ferrari, Messier, & Chivers, 2006). Similarly, exposure to a high density of predatory mites led to greater dispersal by spider mites, *Tetranychus kanzawai* (Bowler, Yano, & Amano, 2013). However, a recent review by Paterson et al. (2013) reported that crustacean prey from a number of taxa exhibited similar changes in activity levels and refuge use regardless of cue intensity or exposure time to fish predators. At this point it is unknown whether it may be advantageous for prey to display similar avoidance behaviours which may be an effective response to multiple predator densities, or whether the intensity or combination of cue types used overpowered subtle indications of predator density (Paterson et al., 2013).

Levels of predation risk can also vary with diurnal changes in predator foraging behaviour (Griffin, Griffin, Waroquiers, & Mills, 2005; Helfman, 1989), effectively providing prey with an indication of predation risk (Clark, Ruiz & Hines, 2003). Typically, prey are more active in periods of ambient light levels in which predators are less active (Benfield & Minello, 1996). For example, buffalo, *Syncerus caffer*, warthog, *Phacochoerus africanus*, and kudu, *Tragelaphus* spp., are predominantly active during the day in areas where nocturnal predators coexist; however, in their absence these prey species are also active at night (Tambling et al., 2015). There is also some evidence to suggest that the diel cycle can interact with other environmental variables such as water depth to alter predation risk and subsequently prey refuge use (Bollens & Frost, 1989; Bollens & Stearns, 1992; Clark et al., 2003). This has been observed in grass shrimp, *Palaemonetes* spp., in which mortality from predation by fish was found to be depth dependent during the day but not at night (Clark et al., 2003). Less well understood, however, is whether the diel cycle interacts with predator density to influence the magnitude of diurnal shifts in shelter use, swimming, foraging and other behaviours that have been observed in prey.

In this study, we investigated the effects of predator density and diel cycle on the consumptive and nonconsumptive effects of the invasive predator, the eastern mosquito fish, *Gambusia holbrooki*, on the native Australian glass shrimp, *Paratya australiensis*. This shrimp is widespread in coastal eastern Australia (Cook et al., 2006) and plays a key role in nutrient cycling in freshwater and estuarine ecosystems as well as being a food source for native species (March, Pringle, Townsend, & Wilson, 2002; Richardson, Grouns, & Cook, 2004; Walsh & Mitchell, 1995). The ubiquitous *G. holbrooki* has spread to eight of the 11 main drainage basins on the Australian continent since its introduction to Sydney in 1925 (Pyke, 2008). It is an opportunistic omnivore which feeds on small decapod crustaceans, including *P. australiensis* (Arthington & Marshall, 1999; Bool, Witcomb, Kydd, & Brown, 2011). *Gambusia* spp. are able to consume relatively large prey by nipping the body, tail and gills which results in immobilization and death (Komak & Crossland, 2000; Segev, Mangel, & Blaustein, 2009; Shulze & Semlitsch, 2014). For this reason, *Gambusia* spp. are not considered to be limited in their prey selectivity by their gape size (Baber & Babbitt, 2003; Drake, Anderson, Smith, Lohraff, & Semlitsch, 2014; Smith & Smith, 2015). The density of *G. holbrooki* is known to vary seasonally, with peak abundance in early autumn after the breeding season and the lowest abundance in spring (Barney & Anson, 1921;

Morton, Beumer, & Pollock, 1988; Pyke, 2008; Zulian, Bisazza, & Marin, 1993). In addition, as it is a visual predator, the foraging behaviour of *G. holbrooki* is likely to be greater during the day than at night (Bool et al., 2011). Although it has been associated with a decline in populations of native fairy shrimp, *Linderiella occidentalis*, in California (Leyse, Lawler, & Strange, 2004), surprisingly few studies have quantified the behavioural interactions of *G. holbrooki* with native biota with the specific purpose of identifying the exact mechanisms behind its negative impacts on native species. Furthermore, native prey may be especially vulnerable as they do not share an evolutionary history with the predator, possibly rendering them less adept at detecting risk and responding accordingly (Bourdeau, Pangle, Reed, & Peacor, 2013; Heavener, Carthey, & Banks, 2014).

Specifically, we determined whether predator density and diel cycle affected the number of *P. australiensis* consumed by *G. holbrooki*. Direct behavioural interactions, in the form of approaches and nips by *G. holbrooki* to *P. australiensis*, were also recorded. Additionally, we assessed whether the behavioural responses of *P. australiensis*, namely shelter use, swimming and foraging behaviours, covaried with predator density and diel cycle. We hypothesized that (1) the number of predation events and direct interactions between *G. holbrooki* and *P. australiensis* would be greatest at the high predator density and during the day and (2) that in response to the greater predation risk, *P. australiensis* would exhibit greater behavioural changes in the presence of a high density of *G. holbrooki* and during the day.

METHODS

Animal Collection and Aquaria Set-up

Gambusia holbrooki (mean \pm SE mass = 0.19 ± 0.14 g; mean \pm SE standard length = 19.46 ± 0.46 mm; mean \pm SE total length = 24.21 ± 0.53 mm) were collected from freshwater ponds located on the University of Wollongong campus ($34^{\circ}24'19''S$, $150^{\circ}52'42''E$) using a baited hand-held landing net. Only adult females were collected so as to avoid the mating behaviours displayed by males which may have interfered with the predatory behaviours exhibited by females relevant to this study. *Paratya australiensis* (mean \pm SE mass = 0.07 ± 0.09 g; mean \pm SE carapace length = 5.77 ± 0.1 mm) were acquired from the national supplier LiveFish.com. Berried *P. australiensis* were included in the study and their condition was noted. To conduct the experiment, six recirculating aquarium systems were used at the University of Wollongong, each system containing eight aquaria (37×22 cm and 27 cm high) that were interconnected and subjected to water conditions of $23^{\circ}C$ and 5 ppt salinity. Each aquarium was lined with 2 cm of natural river gravel and contained three black plastic tubes (7×2 cm) positioned on the substratum to provide shelter for *P. australiensis*. The exterior sides of each tank were covered with black plastic to exclude visual cues from individuals in adjacent tanks. To acclimatize *G. holbrooki* and *P. australiensis* to laboratory conditions, *G. holbrooki* ($N = 72$ total fish) were placed into 12 aquaria spread equally across the six systems ($N = 12$ fish per system). *Paratya australiensis* ($N = 288$ total individuals) were placed into 36 aquaria spread equally across the six systems ($N = 48$ individuals per system) and separate from those housing *G. holbrooki*. All *G. holbrooki* and *P. australiensis* were maintained under these conditions for 7 days to ensure adequate acclimation to laboratory conditions. During this time, *G. holbrooki* were fed a commercial fish flake (New Life Spectrum Thera formula) and *P. australiensis* were fed a shrimp granule (Fluval). Water changes (<20%) were made once a fortnight and new water was supplemented with Fluval bacterial and shrimp mineral additives. Owing

Download English Version:

<https://daneshyari.com/en/article/8488959>

Download Persian Version:

<https://daneshyari.com/article/8488959>

[Daneshyari.com](https://daneshyari.com)