Predation is a well-studied driver of ecological selection on prey traits, which frequently drives divergence in anti-predator performance across environments that vary in predation risk. However, predation also alters prey mortality regimes, where low predation risk often results in higher prey densities and consequently higher intensities of intraspecific resource competition. In addition, predation risk alters the foraging context, as acquiring food can be risky in the presence of predators. Thus, different predation regimes can drive divergent selection on traits associated with resource competition, such as foraging behaviours. Moreover, because sexes often differ in susceptibility to predation and limitations to their reproductive output, the intensity of the tradeoff between predator avoidance and resource competition may depend on sex. We used a laboratory experiment to assess key aspects of foraging performance in a predator-free context in Bahamas mosquitofish *Gambusia hubbsi* wild-caught from multiple populations that experience either high or low levels of predation risk. When competing for limited food resources at a common density, females from low-predation regimes showed higher foraging and food consumption rates than females from high-predation regimes. Males showed fewer differences between predation regimes, and an opposite pattern from females. We suggest these sex-specific effects result from females facing a greater tradeoff between predation risk and resource competition, combined with males from high-predation environments elevating foraging behaviours in the absence of nearby predators and females. Females of this species are larger than males, bear live young and show higher foraging rates in the wild than males. On the other hand, males spend more time pursuing females in the wild, and may exhibit greater flexibility in foraging behaviours based on the immediate context. Our results show that varying
levels of predation risk can lead to differences in behaviours associated with resource competition, but these effects can strongly differ between sexes.

Keywords: adaptive radiation, Bahamas mosquitofish, foraging, predation risk, predator–prey interactions, resource competition

Introduction

Predation can act as a strong selective agent on prey phenotypes, shaping the evolution of prey traits such as life history, morphology and behaviour (Reznick et al. 1990, Swaddle and Lockwood 1998, Bell and Sih 2007, Langerhans 2007). Major ecosystem-level impacts of predation not only derive from direct lethal effects that alter the mortality regimes of prey populations, but can also occur through indirect trait-mediated effects (Peacock and Werner 2001, Preisser et al. 2005). That is, perceived predation risk can induce changes in prey traits, irrespective of lethal effects, such as altered reproductive output, activity levels or habitat use (Valeix et al. 2009, Zanette et al. 2011, Sha et al. 2020). In the absence of predators, or in relatively low-risk environments, an increase in prey population densities can result in reduced resources per capita, which should select for individuals with high competitive potential (Palkovacs et al. 2011, Reznick et al. 2019). There is indeed support for organisms trading off predator defences for competitive ability, with the absence of predators favouring individuals with relatively high growth rates (Yoshida et al. 2003, 2004, Araujo et al. 2017) or higher survival in competitive environments (Kraaijeveld and Godfray 1997). Despite this, the majority of studies addressing how predator-mediated selection can drive adaptive shifts in prey traits have focused on traits known to confer survival benefits in high-risk environments, whereas traits associated with competitive advantage have received less attention.

The relative effects of both predation and competition can also be sex specific. For example, in many systems, females seem to experience higher predation risk as a result of either their larger body size or gestation state (Magurran and Nowak 1991, Svensson 1997, Plath et al. 2011). Additionally, as a consequence of anisogamy, males usually face stronger competition for mating opportunities, whereas female fitness tends to be more limited by resource competition (Perrin and Mazalov 2000, Lehtonen et al. 2016). In other words, if females are both more susceptible to predation and more affected by resource competition, they should face a stronger tradeoff between predator avoidance and competition.

Foraging is a key behavioural trait that can directly influence reproductive output, but is also susceptible to the tradeoff between predator avoidance and competitive ability. That is, increased foraging effort can make the individual more susceptible to predation (Cowlishaw 1997, Cooper Jr. 2000), but can also be favoured by selection via resource competition (Mitchell et al. 1990). Thus, behavioural traits associated with foraging capacity should be under divergent selection across areas with high and low predation risk. The consistent selective pressures in different predation regimes can therefore result in different phenotypes that persist even when the immediate cues (predator presence or conspecific density) change, as opposed to individuals adjusting their behaviour based on current perceived predation risk (Brown and Kotler 2004, Verdolín 2006) or population density (Davidson and Morris 2001). We still lack a strong understanding of how predation regimes shape such foraging behaviours in prey across systems (but see Fraser et al. 2004 and Elvidge et al. 2016) and whether this effect depends on prey sex.

In this study, we used the model system of the post-Pleistocene radiation of Bahamas mosquitofish Gambusia hubbsi to examine how naturally contrasting predation environments have shaped foraging behaviours of prey populations. The Bahamas mosquitofish is a sexually dimorphic live-bearing fish inhabiting inland blue holes on Andros Island, The Bahamas. Some blue holes completely lack piscivorous fish (low-predation regime) whereas other populations (high-predation regime) coexist with a highly piscivorous fish, the bigmouth sleeper Gobiomorus dormitor (Langerhans et al. 2007, Björnerås et al. 2020). The elevated extrinsic mortality rates in high-predation blue holes has resulted in marked differences in Bahamas mosquitofish population density between regimes, with low-predation populations having ca five times higher density than high-predation counterparts (Heinen et al. 2013). These two contrasting predation regimes have driven adaptive phenotypic divergence in numerous traits and performance capabilities in Bahamas mosquitofish (Langerhans et al. 2007, Langerhans 2018, Riesch et al. 2020). For example, mosquitofish originating from high-predation environments have evolved a body shape more suitable for fast-start swimming bursts, whereas low-predation fish have evolved a body shape better suited for energy-efficient prolonged swimming (Langerhans et al. 2007, Langerhans 2009, Araujo et al. 2017). In low-predation populations, we expect high levels of foraging effort to be advantageous because of stronger resource competition and the absence of predation threat. In high-predation environments, on the other hand, it should be advantageous to avoid unnecessary activity in order to avoid the attention of predators, as well as to conserve energy for potential predator escapes. Unlike males, female mosquitofish grow indeterminately and their weight positively correlates with their fecundity (Riesch et al. 2013), while the larger body size and gestation may potentially make them more favourable prey. Consequently, they may simultaneously be more at risk to predation and have higher motivation for gathering resources. In the wild, Bahamas mosquitofish in low-predation populations tend to show higher foraging rates than those in high-predation populations (Heinen et al. 2013), but whether differences persist in the absence of immediate predation risk and under controlled density remains unknown.
We hypothesize that natural selection will more strongly favour high foraging effort in low-predation environments, and that a difference in foraging effort between predation regimes will persist even when fish from either regime forage in the absence of immediate predation risk. We test two predictions in this study. First, we predicted that mosquito-fish from low-predation regimes would show higher foraging rates and food consumption rates compared to individuals from high-predation regimes, while foraging efficiency (food consumption per foraging attempt) might remain similar between predation regimes. Second, owing to the stronger hypothesized tradeoff in females, we predicted that differences between predation regimes would be stronger in females.

Material and methods

Blue holes in the Bahamas are vertical water-filled caves that have been colonized by fish since the ocean levels rose after the last interglacial period ~15 000 years ago (Fairbanks 1989, Mylroie et al. 1995). Inland blue holes have a surface freshwater layer and are without inlets or outlets except for some underground tunnels filled with anoxic saline ground-water (Bottrell et al. 1991). These small but vertically deep lakes are stable environments with simple fish and plankton communities (Heinen et al. 2013, Björnerås et al. 2020). In addition to Bahamas mosquito-fish, each blue hole used in this study harbour one additional fish species (Table 1): the predatory bigmouth sleeper was always present in the high-predation sites, whereas the low-predation sites had either the sheepshead minnow Cyprinodon variegatus or the crested goby Lophogobius cyprinoides. The latter two species are similarly sized to Bahamas mosquito-fish and represent potential competitors of Gambusia hubbsi but unlikely pose any meaningful predation threat (Langerhans et al. 2007, Heinen et al. 2013, Langerhans 2018). Because the fish communities of blue holes are dominated by Bahamas mosquito-fish, intraspecific resource competition is expected to play a much greater role in their foraging levels and abilities than interspecific competition (Heinen et al. 2013). Prior analyses of population densities and age structure suggest that all age classes of Bahamas mosquito-fish suffer higher mortality in the presence of bigmouth sleepers, and thus strongly elevated mortality risk occurs for all Gambusia hubbsi in high-predation blue holes (Heinen et al. 2013, Riesch et al. 2020). Most Bahamas mosquito-fish populations in blue holes are also highly isolated from one another, and their genetic relatedness does not correlate with predation regime (Schug et al. 1998, Riesch et al. 2013). Thus, the Bahamas mosquito-fish system provides a natural experiment with multiple populations with minimal gene flow at early stages of speciation (Langerhans et al. 2007, Heinen-Kay and Langerhans 2013, Langerhans and Riesch 2013). The mosquito-fish diet is dominated by small invertebrates, such as zooplankton and insect larvae (Gluckman and Hartney 2000, Araujo et al. 2014). While foraging propensity typically depends on mosquito-fish body size (Rehage et al. 2005), the average body length and weight do not differ between predation regimes (Langerhans et al. 2007, Langerhans 2018).

Foraging trials were used to evaluate the feeding behaviour of individuals from six mosquito-fish populations (three high-predation (HP) and three low-predation (LP) populations, Table 1). Fish were caught in the wild using hand nets and transported to a field laboratory on the day of capture. The fish were kept in mixed-sex 45-l tanks with water from their respective blue holes, filtration pumps and artificial plant-like plastic structures. The fish were acclimated to laboratory conditions for at least one day, and all fish were tested within five days of capture. Fish were fed flake food and dried Chironomidae larvae in the evenings and starved overnight to standardize hunger levels among individuals. Because Bahamas mosquito-fish typically swim and forage in small groups in the wild, and because we explicitly wished to quantify foraging behaviour within a competitive scenario, we used two individuals in each trial. Each experimental replicate consisted of two similarly sized fish of the same sex and population of origin to avoid sexual interactions and population- and size-specific effects on behaviours. The individuals of each pair were placed together in a transparent arena (22 × 10 × 14 cm) filled with water from their own tank and left to acclimate for 15 min before the start of each trial (n=14 (HP females), 19 (HP males), 12 (LP females), 16 (LP males) (see the Supporting information for more detailed sample sizes). The sex of mature mosquito-fish is easily identified, as the male anal fin develops into a gonopodium upon maturation. At the start of the trial, we initiated video recording from a lateral view and added 15 small (2–3 mm) cut pieces of Chironomidae larvae into the centre of the tank. Trials lasted 15 min, starting when fish entered the tank. We recorded foraging behaviours from the videos using the Behavioral observation research interactive software BORIS (Friard and Gamba 2016). Two behaviours were manually recorded from the 15-min trials: 1) foraging rate: number of foraging

Table 1. Characteristics and location of the blue holes in our study. Predation regime is either high predation (HP) or low predation (LP).

| Blue hole   | Predation regime | Latitude   | Longitude     | Fish species                                      |
|-------------|------------------|------------|---------------|--------------------------------------------------|
| Cousteau's  | HP               | 24°46'35"N| 77°54'58"W   | Gambusia hubbsi, Gobiomorus dormitor              |
| Stalacite   | HP               | 24°47'08"N| 78°01'00"W   | Gambusia hubbsi, Gobiomorus dormitor              |
| West twin   | HP               | 24°45'09"N| 78°00'31"W   | Gambusia hubbsi, Gobiomorus dormitor              |
| East twin   | LP               | 24°45'05"N| 78°00'21"W   | Gambusia hubbsi, Lophogobius cyprinoides          |
| Hubcap      | LP               | 24°46'33"N| 77°51'28"W   | Gambusia hubbsi, Cyprinodon variegatus            |
| Rainbow     | LP               | 24°47'06"N| 77°51'36"W   | Gambusia hubbsi, Cyprinodon variegatus            |
Foraging rate was significantly affected by the interaction term between predation regime and sex (Table 2). Inspection of least-squares means revealed that females more strongly differed between predation regimes than males, with LP females showing higher foraging rates than HP females, while males showed only a weak trend in the opposite direction (Fig. 1a). This resulted in a pattern of sexual dimorphism in HP populations (higher foraging rate in males than females), but only weak evidence of any sex differences in LP populations. Similarly, consumption rate was also significantly affected by the interaction term between predation regime and sex (Table 2), and showed a similar pattern of group differences (Fig. 1b). LP females showed a higher consumption rate than HP females, while males again showed little evidence of differences between predation regimes (only a weak trend and in the opposite direction; Fig. 1b). This resulted in a similar pattern of sexual dimorphism for consumption rate as for foraging rate. No model terms were significant for foraging efficiency (Table 2, Fig. 1c).

**Discussion**

Using controlled trials, where fish competed for a constant number of prey items under a common density and in the absence of immediate predation risk, we found that the predation regime of origin affected foraging behaviours of a live-bearing fish in a sex-specific manner. Female foraging behaviours matched our initial prediction, with female mosquitofish from low-predation regime showing higher foraging and consumption rates, as compared to females originating from high-predation environments. However, males did not exhibit this pattern, showing weak trends in the opposite direction from females. Below, we argue that these sex- and predation-specific results are likely due to natural selection on foraging behaviours (expressed through plasticity or genetically-based differences) and life-history strategies in the wild.

Long-term exposure to different predator and competition regimes has apparently shaped foraging behaviours of female Bahamas mosquitofish. In the wild, female Bahamas mosquitofish show elevated foraging rates in low-predation populations (Heinen et al. 2013). We found that in a controlled laboratory setting, with constant density and the absence of any immediate predation threat, females from low-predation populations still showed higher foraging and consumption rates than counterparts in high-predation populations. Considering that the quality and quantity of resources are not known to differ between predation regimes (Heinen et al. 2013), this means that when competing for food low-predation females likely show higher rates of energy acquisition than high-predation females. This matches our prediction.
Based on divergent selection between predation regimes: high population densities and the absence of chronic predation risk should select for higher competitive ability in low-predation blue holes.

The stronger differences in foraging behaviours between predation regimes in females compared to males support our prediction that female mosquitofish face a stronger tradeoff between predator avoidance and resource competition. In multiple systems, females and males experience different sex-specific predation risk, such as egg-carrying females being preferred as prey (Svensson 1997, Plath et al. 2011) or males with conspicuous sexual signals and ornaments being more susceptible to predators (Zuk and Kolluru 1998, Godin and McDonough 2003). In Bahamas mosquitofish, larger females may be more favourable prey for the bigmouth sleeper, and as live-bearers, their slower breeding potential may cause them to avoid risks to a greater extent than males. Female mosquitofish are indeed more risk averse than males, showing lower boldness and reduced exploration of novel environments (Heinen-Kay et al. 2016), similar to patterns observed in other taxa, such as guppies (Magurran and Nowak 1991, Magurran and Nowak 1991, Piyapong et al. 2010, Lucon-Xiccato et al. 2016). On the other hand, the indeterminate growth linked to fecundity of female mosquitofish can result in a higher motivation for gathering resources in females (Boehlert et al. 1991, Hayward and Gillooly 2011, Barneche et al. 2018).

While the female mosquitofish in our study maintained foraging patterns similar to those previously observed in the wild, the same was not true for males. When observed in blue holes, wild male mosquitofish from low-predation sites show slightly higher foraging rates than those in high-predation sites (Heinen et al. 2013). In the present study, we observed similar foraging and consumption rates for males from low- and high-predation populations, with the trend in the opposite direction as that observed in the wild. This difference between in situ observations and controlled laboratory trials may be due to sex-specific plasticity in foraging behaviours. In contrast to females, male poeciliid fishes typically allocate more time to sexual behaviour than to feeding (Magurran 2005, Heinen et al. 2013). In high-risk environments, male mosquitofish must trade off time for courting, predator avoidance and foraging. Thus, males from high-predation populations may take advantage of both the absence of predators (i.e. lower perceived risk) and the absence of females (i.e. no need for mate searching or sexual behaviours) in the experimental context to increase their foraging behaviours. Similar compensatory foraging has been observed in other poeciliid fish, where individuals from high-predation sites resume foraging faster and at elevated rates after predatory encounters in comparison to low-predation individuals (Elvidge et al. 2014). The more risk-averse females may also show behavioural plasticity in the opposite direction, reducing their foraging behaviours in the experiment following a generally elevated level of caution in an unfamiliar situation. This may explain why females did not show higher average foraging rates than males in our study.

Our study suggests that the loss of predation pressure in the low-predation blue holes may have selected for changes in foraging behaviours, and that these effects may differ between females and males. The persisting divergent foraging behaviours between wild populations can in turn have implications for population differentiation, whether they reflect phenotypic plasticity, fixed genetic differences or both. For example, similarly to how migrating or introduced predator-naïve individuals may face higher mortality in areas with high predation risk (Langerhans 2009, Ingley and Johnson 2016), individuals from high-predation areas can be outcompeted in low-predation
areas where population densities are much higher. Such immigrant inviability can act to reduce gene flow between populations. Sex-specific costs and benefits of foraging traits may also lead to different foraging strategies between males and females (Lewis et al. 2006, Pichegru et al. 2013) that can also be involved in population differentiation (Berner et al. 2008). A stronger tradeoff between resource competition and predator avoidance in females compared to males could therefore lead to females diverging more between populations, or potentially to male-biased dispersal rates if other factors do not additionally select against male immigrants.

Loss of top predators is a major current global issue (Myers and Worm 2003, Strong and Frank 2010, Estes et al. 2011, He et al. 2019), so studying the effects of predation on prey behaviour and community composition is an important task (Heithaus et al. 2008). Still, a majority of the studies estimating the effects of altered predation pressure mainly focus on prey traits that may increase survival in the presence of predators (Fowler et al. 2018), which may lead to underestimating the importance of traits that are selected for in low-risk but high-competition environments. It has been shown that after major predator loss, populations adapted to high-predation environments can start to resemble low-predation populations both morphologically and behaviourally relatively fast (Palkovacs et al. 2011). Combined with the large number of traits that consistently differ among prey populations living with or without predators (Langerhans 2018), this indicates that there may be strong selection for particular phenotypes in the absence of major predators. Considering our results, studies should therefore carefully evaluate whether the phenomenon of predator loss can be fully understood without testing competition-associated traits and, in addition, potential sex effects.

We conclude that low predation pressure, which also results in higher population densities and thus stronger within-population resource competition, seems to have strong sex-specific effects on foraging behaviour. We suggest that these differences may be caused by differences in life-history and mating strategies, which in turn can affect motivation for risk-taking and acquiring resources. Sex-specific effects should be considered more often when studying population differentiation, adaptation and predator loss.

**Data accessibility**

The data that support our findings in this study and R code used to analyse that data is available from Dryad Data Repository [http://dx-doi.org/10-5061/dryad.cc2fqz65n](http://dx-doi.org/10-5061/dryad.cc2fqz65n) (Pärssinen et al. 2021).

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References

Araujo, M. S. et al. 2014. Ecosystem fragmentation drives increased diet variation in an endemic livebearing fish of the Bahamas. – Ecol. Evol. 4: 3298–3308.

Araujo, M. S. et al. 2017. Body streamlining is related to higher growth in Bahamian mosquitofish. – Evol. Ecol. Res. 18: 383–391.

Barneche, D. R. et al. 2018. Fish reproductive-energy output increases disproportionately with body size. – Science 360: 642–645.

Bell, A. M. and Sih, A. 2007. Exposure to predation generates personality in three-spined sticklebacks Gasterosteus aculeatus. – Ecol. Lett. 10: 828–834.

Bern er, D. et al. 2008. Natural selection drives patterns of lake-stream divergence in stickleback foraging morphology. – J. Evol. Biol. 21: 1653–1665.

Björnerås, C. et al. 2020. Inland blue holes of the Bahamas – chemistry and biology in a unique aquatic environment. – Fundam. Appl. Limnol. 194: 95–106.

Boehlert, G. W. et al. 1991. Geochemistry and isotope systematics of sulphur in the mixing zone of Bahamian blue holes. – Appl. Geochem. 6: 97–103.

Brown, J. S. and Kotler, P. B. 2004. Hazardous duty pay and the foraging cost of predation. – Ecol. Lett. 7: 999–1014.

Cooper Jr., W. E. 2000. Tradeoffs between predation risk and feeding in a lizard, the broad-headed skink Eumeces laticeps. – Behaviour 137: 1175–1189.

Cowlishaw, G. 1997. Tradeoffs between foraging and predation risk determine habitat use in a desert baboon population. – Anim. Behav. 53: 667–686.

Davidson, D. L. and Morris, W. D. 2001. Density-dependent foraging effort of deer mice Peromyscus maniculatus. – Funct. Ecol. 15: 575–583.

Elvidge, C. K. et al. 2014. Compensatory foraging in Trinidadian guppies: effects of acute and chronic predation threats. – Curr. Zool. 60: 323–332.

Elvidge, C. K. et al. 2016. Local predation risk shapes spatial and foraging neophobia patterns in Trinidadian guppies. – Curr. Zool. 62: 457–462.

Estes, J. A. et al. 2011. Trophic downgrading of planet earth. – Science 333: 301–306.

Fairbanks, R. G. 1989. A 17 000-year glacio-eustatic sea level record: influence of glacial melting rates on the younger dryas event and deep-ocean circulation. – Nature 342: 637–642.

Fowler, A. E. et al. 2018. Predator loss leads to reduced antipredator behaviours in Bahamian mosquitofish. – Evol. Ecol. Res. 19: 387–405.

Fraser, D. F. et al. 2004. Night feeding by guppies under predator release: effects on growth and daytime courtship. – Ecology 85: 312–319.

Friard, O. and Gamba, M. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. – Methods Ecol. Evol. 7: 1325–1330.

Gluckman, T. L. and Hartney, B. K. 2000. A trophic analysis of mosquitofish, Gambusia hubbsi Breder, inhabiting blue holes on Andros Island, Bahamas. – Caribb. J. Sci. 36: 104–111.

Godin, J. G. J. and McDonough, H. E. 2003. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. – Behav. Ecol. 14: 194–200.

Hayward, A. and Gillooly, F. J. 2011. The cost of sex: quantifying energetic investment in gamete production by males and females. – PLoS One 6: e16557.

He, F. et al. 2019. The global decline of freshwater megafauna. – Global Change Biol. 25: 3883–3892.

Heinen, J. L. et al. 2013. Environmental drivers of demographics, habitat use and behavior during a post-Pleistocene radiation of Bahamas mosquitofish Gambusia hubbsi. – Evol. Ecol. 27: 971–991.

Heinen-Kay, J. L. and Langerhans, B. R. 2013. Predation-associated divergence of male genital morphology in a livebearing fish. – J. Evol. Biol. 26: 2135–2146.

Heinen-Kay, J. L. et al. 2016. Predicting multifarious behavioural divergence in the wild. – Anim. Behav. 121: 3–10.

Heithaus, M. R. et al. 2008. Predicting ecological consequences of marine top predator declines. – Trends Ecol. Evol. 23: 202–210.

Hilbe, J. M. 2014. Modeling count data. – Cambridge Univ. Press.

Ingley, S. J. and Johnson, B. J. 2016. Divergent natural selection promotes immigrant inviability at early and late stages of evolutionary divergence. – Evolution 70: 600–616.

Kraaijeveld, A. R. and Godfray, J. C. H. 1997. Tradeoff between parasitoid resistance and larval competitive ability in Drosophila melanogaster. – Nature 389: 278–280.

Langerhans, R. B. 2007. Evolutionary consequences of predation: avoidance, escape, reproduction and diversification. – Springer.

Langerhans, R. B. 2009. Morphology, performance, fitness: functional insight into a post-Pleistocene radiation of mosquitofish. – Biol. Lett. 5: 488–491.

Langerhans, R. B. 2018. Predictability and parallelism of multitrait adaptation. – J. Hered. 109: 59–70.

Langerhans, R. B. and Riesch, R. 2013. Speciation by selection: a framework for understanding ecology’s role in speciation. – Curr. Zool. 59: 31–52.

Langerhans, R. B. et al. 2007. Ecological speciation in Gambusia fishes. – Evolution 61: 2056–2074.

Lehtonen, J. et al. 2016. Why anisogamy drives ancestral sex roles. – Evolution 70: 1129–1135.

Lewis, R. et al. 2006. Sex-specific foraging strategies and resource partitioning in the southern elephant seal Mirounga leonina. – Proc. R. Soc. B 273: 2901–2907.

Lucon-Xiccato, T. et al. 2016. Sex differences in discrimination of shool size in the guppy Poecilia reticulata. – Evolution 71: 844–854.

Magurran, A. E. 2005. Evolutionary ecology: the Trinidadian guppy. – Oxford Univ. Press.

Magurran, A. E. and Nowak, A. M. 1991. Another battle of the sexes: the consequences of sexual asymmetry in mating costs and predation risk in the guppy, Poecilia reticulata. – Proc. R. Soc. B 246: 31–38.

Mitchell, W. A. et al. 1990. The effect of competition on foraging activity in desert rodents: theory and experiments. – Ecology 71: 481–491.

Myers, R. A. and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. – Nature 423: 280–283.

Mylto, A. E. et al. 1995. Blue holes: definition and genesis. – Carbon. Evap. 10: 225–233.
Palkovacs, E. P. et al. 2011. Eco-evolutionary trophic dynamics: loss of top predators drives trophic evolution and ecology of prey. – PLoS One 6:e18879.

Pärssinen, V. et al. 2021. Data from: Variation in predation regime drives sex-specific differences in mosquitofish foraging behaviour. Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.cc2fqz65n>.

Peacor, S. D. and Werner, E. E. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. – Proc. Natl Acad. Sci. USA 98: 3904–3908.

Perrin, N. and Mazalov, V. 2000. Local competition, inbreeding and the evolution of sex-biased dispersal. – Am. Nat. 155: 116–127.

Pichegru, L. et al. 2013. Sex-specific foraging behaviour and a field sexing technique for endangered African penguins. – Endangered Species Res. 19: 255–264.

Piyapong, C. et al. 2010. Sex matters: a social context to boldness in guppies Poecilia reticulata. – Behav. Ecol. 21: 3–8.

Plath, M. et al. 2011. Giant water bug (Belostoma sp.) predation on a cave fish Poecilia mexicana: effects of female body size and gestational state. – Evol. Ecol. Res. 13: 133–144.

Preisser, E. L. et al. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. – Ecology 86: 501–509.

Rehage, J. S. et al. 2005. Foraging behaviour and invasiveness: do invasive Gambusia exhibit higher feeding rates and broader diets than their noninvasive relatives? – Ecol. Freshwater Fish 14: 352–360.

Reznick, D. A. et al. 1990. Experimentally induced life-history evolution in a natural population. – Nature 346: 357–359.

Reznick, D. N. et al. 2019. Eco-evolutionary feedbacks predict the time course of rapid life-history evolution. – Am. Nat. 194: 671–692.

Riesch, R. et al. 2013. Predation’s role in life-history evolution of a livebearing fish and a test of the Trexler–Deangelis model of maternal provisioning. – Am. Nat. 181: 78–93.

Riesch, R. et al. 2020. Multiple traits and multifarious environments: integrated divergence of morphology and life history. – Oikos 129: 480–492.

Schneider, C. A. et al. 2012. NIH Image to ImageJ: 25 years of image analysis. – Nat. Methods 9: 671–675.

Schug, M. D. et al. 1998. Isolation and genetic diversity of Gambusia hubbi (mosquitofish) populations in blueholes on Andros island, Bahamas. – Heredity 80: 336–346.

Sha, Y. et al. 2020. Diverging responses to threats across generations in zooplankton. – Ecology 101: e03145.

Strong, D. R. and Frank, T. K. 2010. Human involvement in food webs. – Annu. Rev. Environ. Resour. 35: 1–23.

Svensson, J. E. 1997. Fish predation on Eudiaptomus gracilis in relation to clutch size, body size and sex: a field experiment. – Hydrobiologia 344: 155–161.

Swaddle, J. P and Lockwood, R. 1998. Morphological adaptations to predation risk in passerines. – J. Avian Biol. 29: 172–176.

Valeix, M. et al. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. – Ecology 90: 23–30.

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk tradeoffs in terrestrial systems. – Behav. Ecol. Sociobiol. 60: 457–464.

Yoshida, T. et al. 2003. Rapid evolution drives ecological dynamics in a predator–prey system. – Nature 424: 303–306.

Yoshida, T. et al. 2004. Evolutionary tradeoff between defence against grazing and competitive ability in a simple unicellular alga, Chlorella vulgaris. – Proc. R. Soc. B 271: 1947–1953.

Zanette, L. Y. et al. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. – Science 334: 1398–1401.

Zuk, M. and Kolluru, R. G. 1998. Exploitation of sexual signals by predators and parasitoids. – Q. Rev. Biol. 73: 415–438.