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Competition for food in 2 populations of a wild-caught fish

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Abstract

Aggressive behavior when competing for resources is expected to increase as the ratio of competitors-to-resource ratio (CRR) units increases. Females are expected to be more aggressive than males when competing for food when body size is more strongly related to reproductive success in females than in males, whereas aggression is predicted to decrease under high ambient predation risk by natural selection. Under the risk allocation model, however, individuals under high ambient predation risk are expected to be more aggressive, and forage more in the absence of imminent risk than their low risk counterparts. An interaction between adult sex ratio (i.e., adult males/females), ambient predation risk (high vs. low), and sex on intrasexual competition for mates in Trinidadian guppies *Poecilia reticulata* has been shown. The interaction suggested an increase in aggression rates as CRR increased, except for males from the high predation population. To compare the patterns of competition for food versus mates, we replicated this study by using food patches. We allowed 4 male or 4 female guppies from high and low predation populations to compete for 5, 3, or 1 food patches. The foraging rate was higher in a high rather than low ambient predation risk population. Surprisingly, CRR, sex, and population of origin had no effect on aggression rates. Despite other environmental differences between the 2 populations, the effect of ambient predation risk may be a likely explanation for differences in foraging rates. These results highlight the importance for individuals to secure food despite the cost of competition and predation.

Key words: aggression, competitor-to-resource ratio, foraging, *Poecilia reticulata*, population differences, predation risk, sex

Interference competition, when individuals use aggression or other means to prevent others from consuming a resource (Keddy 2001), for food is common when resources are clumped and predictable in space and time, and at intermediate levels of abundance (e.g., Grand and Grant 1994; Schmidt et al. 1998; Weir and Grant 2004; Hodge et al. 2009; Tanner et al. 2011; Morandini and Ferrer 2015). Among prey populations, competitive aggression (*sensu* Archer 1988) tends to be balanced against antipredator behavior to increase survival (Huntingford 1982). In addition to resource availability and predation risk, individuals within prey populations are expected to show different competitive patterns based on their sex. Females have a greater pre-natal investment in reproduction because they produce larger gametes than males (Trivers 1972; Kokko and Jennions 2008), and tend to be the more competitive sex in a

foraging context (e.g., Nummelin 1988; Uccheddu et al. 2015), while males tend to compete for females. The effects of resource availability, predation risk, and sex on intraspecific competitive patterns have been studied intensively, but in most cases in isolation from one another, thus ignoring any potential interactions.

The term competitor-to-resource ratio (CRR; Grant et al. 2000) was introduced as a measure to allow the comparison of patterns of competition for access to different resources (i.e., food, mates, and territories) based on the predictions of operational sex ratio (OSR) theory regarding mating competition (Emlen and Oring 1977). Just as operational sex ratio predicts the rates of aggression (Weir et al. 2011), CRR, the ratio of individual competitors over the number of resource units available (e.g., patches of food, mates; Grant et al. 2000), predicts the rate of aggression (Noel et al. 2005). The rate of

competitive aggression peaks at intermediate values of CRR, approximately 2 (e.g., Kvarnemo et al. 1995; Grant et al. 2000). Game theory models also predict that hawk will be an ESS at a CRR of 2, if the gain from the resource is greater than the cost related to aggression (Parker 1984). CRR also predicts a decrease in aggression rates as resource units (i.e., amount of resource) become relatively abundant or scarce (Grant et al. 2000; Noel et al. 2005). When the resource is abundant, aggression is not necessary as all individuals can forage to satiation. Conversely, if the resource is too scarce, the cost of aggression exceeds the potential gain in foraging opportunities (Brown 1964), resulting in a decrease in aggression rates (Grant et al. 2002; Toobaie and Grant 2013). However, these patterns might be altered by predation risk as both the availability of resources and the risk of predation are known to affect aggression rates.

The non-consumptive effects of predation strongly affect the behavior of potential prey organisms (Preisser et al. 2005). The risky competition hypothesis (Chuard et al. 2016) predicts a decrease in intraspecific aggression rates under high ambient predation risk (i.e., in populations adapted to high predation regime), in the absence of an imminent predation threat (e.g., Qvarnstrom et al. 2012); there is presumably a trade-off between conspicuously competing for limited resources and predator detection and avoidance (Huntingford 1982). In the absence of an imminent threat, individuals may perceive the risk of a predation event as constant or variable. If the former, then, an elevated ambient predation risk should lead to a decrease in the rates of foraging (e.g., Romero et al. 2011) and intraspecific aggression (e.g., Magurran and Seghers 1991; Herczeg and Valimaki 2011; Heinen et al. 2013), in favor of antipredator behavior, even in the absence of an imminent risk of predation. Under high ambient predation risk, individuals need to trade-off acquiring resources (e.g., competing for resources, foraging) with survival. In the latter, the risk-allocation model (Lima and Bednekoff 1999; Ferrari et al. 2009) suggests higher rates of resource acquisition (e.g., aggression to secure resources, foraging, mating) in populations experiencing high versus low ambient predation risk in the absence of an imminent predation risk. Based on this model, individuals perceive predation risk as variable and take advantage of opportunities when predation risk is perceived as low (i.e., no imminent risk of predation). For instance, in the absence of an imminent risk, female sand tilefish *Malacanthus plumieri* from high-predation risk sites have higher foraging rates than their low-predation risk counterparts (Baird and Baird 2006; see also Magurran and Seghers 1994).

Another determinant of competitive patterns is the sex of individuals. When competing for mates, males are typically more aggressive than females (Clutton-Brock and Parker 1992) likely due to the indirect effect of higher reproductive rates of males compared with females. This difference in rates of reproduction leads to stronger sexual selection on males by females, which in turn makes

reproductive success quite variable in males (Magurran and Garcia 2000), potentially leading to more male–male aggression. Conversely, female–female competition may be more prevalent in a foraging context (e.g., Nummelin 1988; Uccheddu et al. 2015) because body size is usually more strongly related to reproductive success in females than in males (Charnov 1993).

Recent findings suggest an interaction between CRR, ambient predation risk, and sex on mating competition in Trinidadian guppies (Chuard et al. 2016). Both males and females typically increased their aggression rates toward same-sex individuals as the relative number of mates decreased, except for males from the high ambient predation population: hence, the significant interaction. Chuard et al. (2016) argue that this exception might be due to the use of less risky alternative mating tactics by males instead of aggression to secure mates under high-ambient predation risk. We are not aware of any study on the simultaneous effects of CRR and ambient predation risk on foraging competition that directly compares males to females. Here, we explored whether similar patterns of competition were observed in a foraging context, and determine the effects of any potential interaction.

We compared intrasexual aggression and foraging rates of wild-caught male and female Trinidadian guppies, from a high versus low ambient predation risk population (i.e., the same 2 populations used by Chuard et al. 2016), and under different food CRRs, to test the following predictions (Table 1). (1) Individuals will increase their aggression rates as CRR initially increases up to a CRR of 2, above which aggression rates should decrease due to the cost of competition (Grant et al. 2000; Noel et al. 2005). Female Trinidadian guppies show indeterminate growth and forage for longer periods than males, whereas male guppies stop growing after sexual maturity (Magurran 2005) and quickly switch from foraging to courting after ingesting some food (Abrahams 1993). For these reasons, (2) females will be more aggressive than males when competing for food. Based on the risky-competition hypothesis, in the absence of an imminent risk of predation, individuals from the high versus low ambient predation risk population will be (3) less aggressive, and (4) forage less. Alternatively, following the risk-allocation model (Lima and Bednekoff 1999), we expect the opposite of predictions 3 and 4, if the absence of an imminent predation risk indicates a "safe period."

Materials and Methods

Collection and holding of individuals

To test the effect of ambient predation risk, we used wild-caught adult individuals from 2 populations: high versus low levels of background predation risk. The Upper Aripo River, a low-risk population, experiences predation from 2 species which prey upon newborns, juveniles, and small male guppies: Hart's rivulus

Table 1. Predictions and results based on the effects of CRR[a], sex, and ambient predation risk population differences on foraging competition

Explanatory variables	Predictions	Results
As CRR increases	(1) Intrasexual aggression rate increases initially to then decrease above a CRR of 2	No effect
Sex	(2) Intrasexual aggression rate is greater in females than in males	No effect
High versus low ambient	(3) Intrasexual aggression rate is lower or higher[b]	No effect
Predation risk population	(4) Foraging rate is lower or higher[b]	Significant effect – higher

[a]CRR is defined here as the ratio of individual competitors over the number of food patches available.

[b]Activities expected to decrease if the cost of ambient predation risk is high (e.g., foraging is conspicuous to predators) OR increase in the absence of a perceived imminent predation risk as it would indicate a "safe" period, as predicted by the risk allocation model (Lima and Bednekoff 1999).

Anablepsoides hartii (Magurran 2005), and a freshwater prawn *Macrobrachium crenulatum* (personal observations). Further downstream, the Lower Aripo River population has a high-background predation risk (Croft et al. 2006) with species preying upon both adult and juvenile guppies. These predators include, but are not limited to: pike cichlids *Crenicichla* sp.; blue acara cichlids *Andinoacara pulcher*; and brown coscorub cichlids *Cichlasoma bimaculatum* (Croft et al. 2006; Botham et al. 2008). While high ambient predation risk sites tend to correlate with low guppy densities, high stream productivity (Grether et al. 2001), and higher-quality diets for guppies (Zandonà et al. 2011), we will refer to the Lower Aripo and Upper Aripo populations as "high predation" and "low predation" sites for now (see Discussion, "Population differences").

We collected guppies using seine nets between 29 April and 7 June 2013 throughout the duration of the experimental trials. We transported fish to the laboratory, a 45-min drive, in 30-L buckets filled with 30–40 guppies and approximately 10 L of water from the individuals' original river. Once in the laboratory, individuals were held in mixed-sex groups by population of origin. The standard lengths (±SD) of individuals by sex and population were 18.2 ± 1.2 mm for males and 19.1 ± 4.8 mm for females in the low predation site and 14.6 ± 1.1 mm for males and 15.3 ± 3.1 mm for females in the high predation site. As expected, stronger predation pressures on high predation individuals seem to have selected against larger size and later age of sexual maturation compared with the low predation population (Magurran 2005). We ensured high water quality in the holding tanks by continuously aerating the water using air stones, and by continuously filtering the water with filters filled with floss and activated charcoal. We removed the excess food and wastes twice a day to avoid bacterial outbreaks. Regarding testing tanks, we changed the water after each trial to maintain high levels of oxygen and water quality. All fish were fed commercial flakes (TetraMin™ provided by Tetra, Blacksburg, VA, USA) and brine shrimp twice daily, except the day before a trial for individuals to be tested the next day (see below). We released guppies back to their original rivers using hand nets after a maximum of 41 days (min: 1 day; mean: 20.5 days) in the laboratory.

Experimental procedure

To enhance foraging competition, we did not feed individuals in the 24 h preceding observations. The day before testing, we made defendable patches of food by dipping standard microscope slides (75 × 25 mm) into unflavored gelatine (Indulge™, General Foods Corporation, White Plains, NY, USA) using about 20 g gelatine/100 mL water. Once the slides were covered with a thin layer of gelatine, we applied flake food (Tetramin™), fragmented into smaller pieces, to a square area (25 × 25 mm) at the center of one side of the slide and allowed the gelatine to set. All slides had approximately the same amount of food as only one thin layer of flakes would stick to the gelatine. Enough food was applied for the patches to last for the entire length of a trial (10 min of acclimation and 10 min of observation). We observed males and females separately from each population to avoid any confounding effects of mating competition (Nordell 1998). To manipulate CRR, we used 4 fish exposed to 5, 3, or 1 food patches (i.e., CRRs = 0.8, 1.3, or 4). Thus, we used a 3-way factorial design (i.e., 2 populations × 2 sexes × 3 CRRs) with 30 replicates of each. Each individual was used only once, for a total of 1,440 individuals. We tested unused individuals after a median of 3 days (range = 1–7 days) in captivity. We randomly assigned groups of 4 individuals to the different treatments.

We placed 4 individuals from the same holding tank in a test tank (45 × 30 × 30 cm) and allowed them 1 h to acclimate. We chose individuals who were noticeably different in size so that individuals could be readily recognized. The percentage standard length (±SD) of the 2nd, 3rd, and 4th female ranked by size compared with the 1st were, respectively, 83% (±11), 72% (±11), and 64% (±11); and the percentage standard length (±SD) of the 2nd, 3rd, and 4th male ranked by size compared with the 1st were, respectively, 96% (±3), 92% (±4), and 88% (±5). The slides were introduced 10 min before the beginning of observations so individuals could acclimate to and begin feeding from the food patches, which avoided hunger-biased behavior (i.e., increased foraging attempts in males, Griffiths 1996). We removed loose flakes by blowing on slides before introducing them into test tanks. In the one-patch treatment, the single slide was placed on the substrate, in the center of the tank. For the 3- and 5-patches treatments, slides were placed evenly across the tank, but at least 25 mm from the side of the tank, to make it difficult for a single fish to defend more than one patch (i.e., >30 mm from one another, Magurran and Seghers 1991). All 4 individuals could potentially forage on the same patch without direct physical interaction. The observer recorded behavior from the front of the tank; we covered the outside of the remaining sides with white plastic sheets to prevent disturbance. A single observer (P.J.C. Chuard) recorded behavior for 10 min, divided into two 5-min periods. Guppies were individually identified by a combination of color patterns, size, and shape. Within each period of 5 min, we observed the 4 fish in a randomized sequence for 75 s each, without observing a fish twice consecutively (i.e., the last focal individual of the first period was not used as the first focal individual of the second period). We summed all focal observations from the 2 periods.

We recorded the frequency of agonistic behavior, performed and received separately, including chasing, biting (Gorlick 1976), pushing (Magurran and Seghers 1991), and tail beating (Liley 1966). We did not record encounter rate to measure aggression propensity (i.e., aggression rate corrected by the number of encounters; *sensu* de Jong et al. 2012) as individuals could see one another (i.e., no visual barrier). In addition, the frequency of foraging was quantified, defined as when an individual pecked directly on a food patch, or pecked within one body length of a patch as food might be found here quickly after the beginning of a trial (i.e., flakes detached from the patch due to foraging). As food rarely detached and fell more than one body-length away from a patch, the difference in body size between individuals is not likely to have biased the foraging rate recorded per focal individual (i.e., more foraging for longer individuals as the area where foraging is recorded depends on the body length).

Statistical analysis

We performed all analyses using generalized linear mixed models (GLMM) in the R software (3.1.2; R Development Core Team 2015) with the *glmmadmb()* function of the *glmmADMB* package. Due to a right-skewed distribution of our count data (i.e., many zeros), we first attempted to fit our data to a Poisson distribution. As the models were significantly over-dispersed, we ran each model fitted to the negative binomial distribution. As expected, when validated, the negative binomial distribution effectively dealt with the over-dispersion issue ($P > 0.99$; Lindén and Mäntyniemi 2011). We used population, sex, and CRR (quadratic contrasts to test for a dome-shaped relationship, and linear contrasts to detect a linear increase in aggression; see Chuard et al. 2016) as fixed factors in all analyses. We also added the coefficient of variation of individual

Table 2. Results of the GLMM testing for CRR[a] (quadratic and/or linear contrasts), population of origin (lower: high risk versus upper Aripo: low risk), sex, and CV of individual size (i.e., only for aggression rates) on intrasexual aggression and foraging rates in Trinidadian guppies

Variable	Main effect	Regression coefficient	95% confidence interval	z	P
Intrasexual aggression rates	CRR (quadratic contrasts)	−0.10	−0.39, 0.18	−0.71	0.48
	CRR (linear contrasts)	0.12	−0.17, 0.41	0.82	0.41
	Population	−0.070	−0.31, 0.16	−0.61	0.54
	Sex	0.27	−0.024, 0.56	1.80	0.072
	CV of individual size	−0.94	−1.54, −0.34	−3.06	0.0022
Foraging rates	CRR (linear contrasts)	−0.072	−0.48, 0.33	−0.35	0.73
	Population	−0.40	−0.74, −0.069	−2.36	0.018
	Sex	0.29	−0.038, 0.62	1.74	0.083

[a]CRR is defined here as the ratio of individual competitors over the number of food patches available.
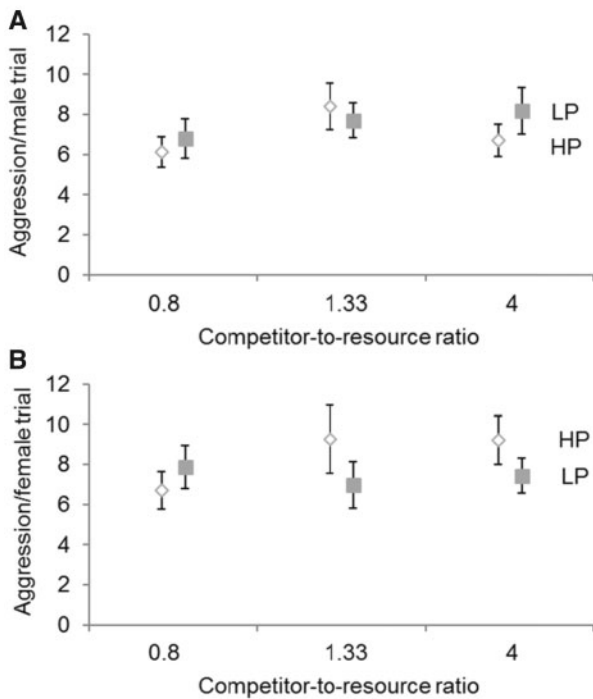

Figure 1. Mean (±SE, $N = 30$) aggression rate, sum of given and received, per trial in relation to 3 CRR (4 individuals competing for 5, 3, and 1 food patches, respectively 0.8, 1.33, 4) and 2 populations of origin: high predation (*HP*; *open diamonds*) and low predation (*LP*; *shaded squares*; low predation) in (**A**) males and (**B**) females.

Figure 2. Mean (±SE, $N = 30$) foraging rate per trial in relation to 3 CRRs (4 individuals competing for 5, 3, and 1 food patches, respectively 0.8, 1.33, 4) and 2 populations of origin: high predation (*HP*; *open diamonds*) and low predation (*LP*; *shaded squares*) in (**A**) males and (**B**) females.

size within a trial (CV; standard deviation/mean for each trial) as a covariate to take into account size differences within groups. We used the principal component of standard length and weight of individuals as a proxy for size. As expected, standard length and weight were highly correlated (98%). We used trial number as a random factor in all GLMM analyses.

First, using GLMM, we tested total aggression rate per trial (given and received aggression summed up per trial) fitted to a negative binomial distribution. Using focal individual observations allowed us to estimate the total per capita rates of aggression, which were summed for the 4 fish to estimate total aggression in the trial. This total aggression for 5 min will underestimate the total aggression by 50% on average compared with simultaneously watching all 4 fish for 5 min. Out of the 6 possible pairs of competing individuals, we only recorded aggression given and received for the focal individual during a 5-min period, which accounts for 3 of the 6
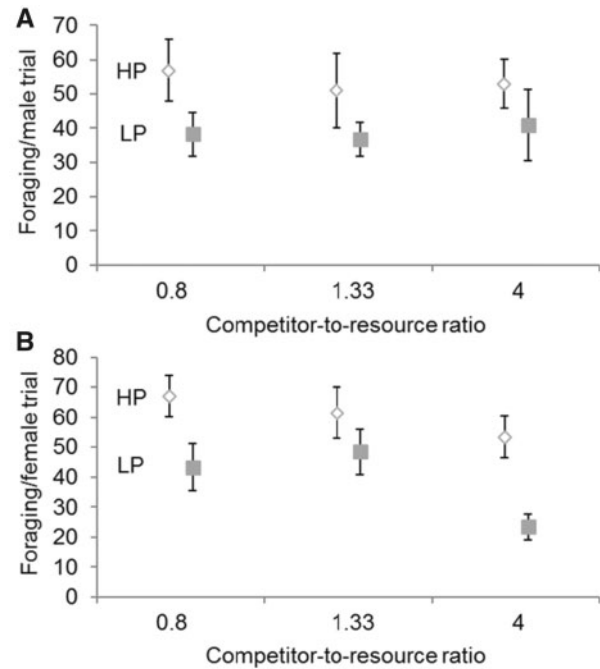
possible competing pairs. However, our main goal was to compare the relative aggression across treatments rather than estimating the total aggression within a given trial. Second, we analyzed total foraging rates fitted to a negative binomial distribution. Since we based our tests on a priori predictions, we did not apply any statistical correction to our tests.

Results

Contrary to our 3 first predictions, overall aggression rates (Table 2 and Figure 1) were not significantly affected by CRR, population of origin, sex, nor their interactions (Appendix 1). However, aggression rates increased as CV of individual size decreased within a trial (Table 2). Consistent with our fourth prediction, following the risk-allocation model (Lima and Bednekoff 1999), foraging rates were higher in the high than in the low predation population (Table 2 and Figure 2). However, CRR, sex, and the interactions of the 3

above-mentioned factors (Appendix 2) had no significant effects on foraging rate (Table 2 and Figure 2).

Discussion

Overall, our results support 1 of our 4 original predictions (Table 1). Surprisingly, CRR, sex, and population of origin did not influence aggression rates among guppies competing for access to foraging patches. Rather, foraging rates followed the risk-allocation model (Lima and Bednekoff 1999) with higher foraging rates in the high versus the low predation population. These results suggest that decreasing food availability at a constant competitor density does not affect aggression rates in guppies. However, the effect of elevated ambient predation risk seems to favor individuals able to forage more when an imminent risk is absent. As expected (Parker 1974), aggression rates increased as size differences between competing individuals decreased. These conclusions should be tested in future studies using more populations as our experimental design only included 2 of them. The composition of the predatory community of these 2 rivers, among other environmental factors, might be specific to them. For instance, the freshwater prawn, M. crenulatum, was not found in the Upper Aripo River in previous studies (Magurran 2005) but is now found. This recent invasion might have had an effect on how this specific population responds to ambient predation.

These results contrast with those of Chuard et al. (2016) where both CRR and ambient predation risk had an effect on aggression rates in a mating competition context (see Figure 1 in Chuard et al. 2016). Indeed, aggression rates increased as CRR increased, and low-predation guppies were more aggressive than their high-predation counterparts as expected under the risky-competition hypothesis (Chuard et al. 2016). However, similar to our findings in a foraging context, males and females did not differ significantly in their aggression rates (Chuard et al. 2016). The most notable difference between the 2 experiments was the observed rates of aggression, which were more than 3 times greater in the food- rather than the mating-competition experiment once we corrected for methodological differences (i.e., scanning vs. focal observations, trial length). Perhaps fixed food patches are easier to monopolize and defend than mobile mates, resulting in a greater pay-off for individuals who invest energy in aggressive behavior when competing for food.

Competitor-to-resource ratio

Unlike Magurran and Seghers (1991), we found no effect of CRR on aggression rate. However, Magurran and Seghers (1991) manipulated CRR in one of their 4 experiments (i.e. "the effect of tank size and group size") by increasing the number of competitors foraging on a single food patch, whereas we decreased the number of resources (i.e., food patches) while holding the number of competitors constant. A possible explanation for this discrepancy is that aggression rates increased significantly above a CRR of 4 in Magurran and Seghers' (1991) experiment, while 4 was the highest CRR in our study. Future studies should also try to disentangle the effects of CRR, fish density, and food abundance, by using higher CRRs while keeping the number of individuals constant (i.e., more than 4 individuals per trial), as well as test aggression rates at equal CRRs but varying fish density (e.g., Clark and Grant 2010). In addition, the food patches might have been close enough together in our experiment such that the dominant fish could defend them against 3 other competitors. This explanation is supported by the high rates of aggression in our experiment compared with Chuard et al. (2016), and the absence of differences in dominance structure (i.e.,

coefficient of variation of net aggression) between CRRs (see Chuard 2017). Because an increase in density leads to an increase in aggression rates (Magurran and Seghers 1991) but a decrease in the number of food patches does not (our results), seasonal changes in guppy density might be more ecologically relevant to guppies than changes in food abundance. Indeed, there is no strong evidence that food availability varies across seasons in Trinidadian streams (Magurran 2005; but see Reznick 1989).

Sex

We found no difference in aggression and foraging rates between males and females. While male guppies forage just enough to satisfy their immediate hunger (Griffiths 1996), female guppies devote a greater portion of their time budget to foraging (Magurran and Seghers 1994), presumably to produce eggs, and to match the energetic requirements associated with indeterminate growth (Magurran 2005). Given that individuals fasted for 24 h before testing, it is possible that a 10-min observation period was not sufficient for males to start reducing their foraging rates, and associated aggression, compared with females. For example, after at least a 3-h fast, male guppies switched from primarily feeding to courting after about 10 min [see Figure 3 in Abrahams (1993)].

Population differences

We found that the low and high predation populations showed similar levels of aggression. These results do not support the risky competition hypothesis (Chuard et al. 2016; see also Magurran and Seghers 1991). However, those 2 same populations did differ in aggression rates related to mating competition (Chuard et al. 2016). As courtship displays have the potential to attract predators (Zuk and Kolluru 1998), aggression might be more likely traded-off for antipredator behavior in a mating rather than a foraging competition context. The absence of a difference in aggression rates between the 2 populations might also be due to the predator assemblage of each population. Indeed, guppy populations have been shown to be adapted to their local environments along a continuous environmental gradient, where the predatory community plays an important role (Torres-Dowdall et al. 2012). The 2 populations we used are not located at the extreme ends of the predation risk gradient encountered in nature (Torres-Dowdall et al. 2012), and thus predation risk might not be different enough to cause differences in aggression rates related to foraging.

Foraging rates between populations were consistent with the predictions of the risk allocation theory in the absence of an imminent risk of predation (Lima and Bednekoff 1999); high-predation individuals foraged more than low-predation conspecifics. In the absence of an imminent risk of predation, individuals from a high versus low ambient predation risk site seem to compensate for lost foraging opportunities during previous periods of high imminent predation risk. Future studies should replicate this experiment with the addition of imminent predation risk treatments to validate this hypothesis. However, due to the cost of predation, high ambient predation risk guppies seem to spend less time foraging than their low ambient predation risk counterparts (Magurran and Seghers 1994), suggesting selection for higher foraging rates under high ambient predation risk, and more time spent on antipredator behavior. Given the smaller size of individuals from high versus low predation risk sites (Magurran 2005), foraging more to sustain higher growth rates in low predation risk females is not likely. As males stop growing after sexual maturity (Magurran 2005), this explanation is even less likely for them.

Our conclusions cannot be limited to the effect of ambient predation risk alone, as low ambient predation risk streams tend to have higher guppy densities (as a direct effect of predation) and lower productivity (Grether et al. 2001), resulting in higher competition for food. Differences in productivity could then act as a factor selecting for high versus low productivity-adapted behaviors (Walsh and Reznick 2010). These differences in the intensity of foraging competition between sites lead to differences in diets. As a response to intense competition, guppies from low-predation localities tend to feed on proportionally more low-quality food than their high-predation sites counterparts [Bassar et al. 2010; Zandonà et al. 2011; but see Zandonà et al. (2017) for a counterargument during the rainy season]. Because they feed on low-quality food, we would expect these individuals to forage more than conspecifics from high-predation sites in order to meet their metabolic requirements. These adaptations could lead to different energy allocation trade-offs between foraging competition and antipredator behavior, opposite to the effect of the risk allocation theory. Indeed, contrary to our results, individuals inhabiting low-productivity streams (low predation) should invest more energy in foraging and competing for foraging opportunities, and less energy into antipredator behavior compared with populations living in high-productivity streams (high predation; Magurran and Seghers 1991; but see Kolluru et al. 2007). While the 2 populations did not differ in rates of aggression (see above), guppies from the low-predation/low-productivity population had lower foraging rates than their high-predation/high productivity counterparts. These results suggest that differences in density, productivity, and diet between the 2 populations are not likely explanations for the observed competitive foraging patterns.

In conclusion, relative food density did not seem to affect intrasexual aggression rates in guppies. Ambient predation risk reflects, at least in part, the long-term exposure to imminent predation risk (Brown et al. 2006). Individuals experiencing high levels of ambient predation risk do not always face high imminent predation threats, as they can select habitats that lower this risk (e.g., Main et al. 1996). Conversely, individuals facing low ambient predation risk can still face high imminent predation risk, such as just prior to a predator attack. Consequently, it would be of great value to explore aggression rates in relation to food abundance under varying intensities of imminent predation risk to fully investigate the risk allocation hypothesis, in populations that also vary in ambient predation risk.

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Appendix

Table A1. Results of the interactions of the GLMM testing for the effects of CRR[a] (quadratic and linear contrasts), population of origin (lower: high risk versus upper Aripo: low risk), and sex on intrasexual aggression rates in Trinidadian guppies

Interaction	Regression coefficient	95% confidence interval	z	P
CRR (quadratic contrasts)×population	0.014	−0.39, 0.42	0.070	0.95
CRR (linear contrasts)×population	−0.038	−0.45, 0.37	−0.18	0.86
CRR (quadratic contrasts)×sex	0.31	−0.099, 0.72	1.49	0.14
CRR (linear contrasts)×sex	0.069	−0.34, 0.48	0.33	0.74
Population×sex	0.072	−0.26, 0.40	0.43	0.67
CRR (quadratic contrasts)×population×sex	0.047	−0.53, 0.62	0.16	0.87
CRR (linear contrasts)×population×sex	−0.15	−0.73, 0.42	−0.52	0.60

[a]CRR is defined here as the ratio of individual competitors over the number of food patches available.

Table A2. Results of the interactions of the GLMM testing for the effects of CRR[a] (linear contrasts), population of origin (lower: high risk versus upper Aripo: low risk), and sex on foraging rates in Trinidadian guppies

Interaction	Regression coefficient	95% confidence interval	z	P
CRR (linear contrasts)×population	−0.13	−0.71, 0.45	−0.45	0.65
CRR (linear contrasts)×sex	−0.23	−0.80, 0.34	−0.80	0.42
Population×sex	−0.29	−0.76, 0.18	−1.21	0.23
CRR (linear contrasts)×population×sex	0.021	−0.80, 0.84	0.050	0.96

[a]CRR is defined here as the ratio of individual competitors over the number of food patches available.