

How does predation risk affect aggression in the Lake Tanganyika cichlid, *Julidochromis ornatus*?

Thesis

By

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2015

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Biodiversity worldwide is being threatened by human-induced rapid environmental change (HIREC; Sih et al., 2011), including climate change, overexploitation, invasive species, and nutrient pollution (Charmantier et al., 2008). One such threatened ecosystem is Lake Tanganyika (East Africa), which has been experiencing rising water temperature due to climate warming. Surface water temperatures have increased by 1.3°C during the past 40 years, with deeper waters (1000 m depth contour) increasing by 0.2°C over the last 30 years (O'Reilly et al., 2003). Owing to these changes, the density gradient between the epilimnion (surface layer) and hypolimnion (bottom layer) has strengthened, which has caused reduced vertical mixing within the water column (Dettman et al., 2005; O'Reilly et al., 2003). As a result, nutrient availability to the epilimnion, and hence associated primary productivity, has decreased (Verburg and Hecky 2009). Such reductions are alarming because these changes may result in reduced food available to higher consumers such as fish, as well as potentially sub-optimally high water temperatures (O'Reilly et al. 2003).

These changes in temperature and food availability, in turn, would be expected to alter the behavior of aquatic ectotherms such as fish by increasing their need to secure food resources to support an expected increase in their basal metabolic rate (Stamps 2007; Biro & Stamps 2008). For example, a 3°C increase in temperature led up to a six-fold increase in activity, boldness, and aggression in the coral reef fish *Pomacentrus moluccensis* (Biro et al. 2010). Likewise, movement behavior in *Oncorhynchus gorbuscha* increased with increasing time since being last fed (Magnhagen 1988). The increases in these behaviors were attributed to an increase in foraging activity. Similar examples of increasing aggressiveness with increasing temperature have been demonstrated with other ectotherms (Nowicki et al. 2012; Biro et al. 2007; Brodie & Russell 1999; Angilletta et al. 2009).

Such changes in behavior (i.e., increased activity, boldness, aggressiveness) to satisfy metabolic needs, however, may also increase predation risk, if individuals are forced to leave their refuge to secure food (Biro et al. 2006; Stamps 2007). Thus, individuals might be expected

to reduce these behaviors in response to increased predation risk, whether real or perceived (Lima and Dill 1989; Staudinger et al. 2013). For example, while pink salmon (*Oncorhynchus gorbuscha*) fry reduced their use of open-water feeding areas in the presence of a potential predator (Mangnhagen 1988), Atlantic salmon (*Salmo salar*) individuals attacked passing food items less frequently after being exposed to predation risk relative to beforehand (Metcalf et al. 1987). Similarly, Nonacs and Dill (1990) showed that, when given the choice between a high and low sugar foods, the ant *Lasius pallitarsis* chose the more nutritious high-sugar option. However, when predation risk accompanied the high-sugar option, the ants chose the low-sugar option in exchange for less risk.

The response of individuals to predation risk can vary within species, and have consequences for the demographics of a population (Lawrence and Smith 1989; Lima and Dill 1989). For example, while reduced foraging activity has been shown lead to reduced growth rates in many species (Biro et al. 2006), the net effect of predation risk on foraging and growth rates could be size-dependent. Reindhart (1999), for instance showed that, upon the introduction of a perceived predator risk, large *Oncorhynchus kisutch* individuals reduced their activity, which allowed smaller individuals to profit from the lack of intraspecific aggression (Reindhart 1999).

Many fish species have evolved mechanisms to use chemical cues in the water to assess predation risk (Chivers et al. 2013). For example, certain predators can release chemical cues within their feces that can alert prey to the diets of these predators (Chivers and Smith 1998). If the diet consists of prey of the same species, individuals may respond with antipredator behaviors (Chivers and Mirza 2001, Dalesman and Inchley 2008).

At present our knowledge of how Lake Tanganyika's biodiverse and endemic cichlid (fish) assemblage might respond to climate warming remains limited. Thus, while Brodnik (2015) and Kua (2016) respectively documented increased metabolic rates and aggression at the projected future water temperature for Lake Tanganyika in 2100 (29°C; O'Reilly et al. 2003)

relative to current water temperature (25°C), as expected (sensu Nowicki et al. 2012; Biro et al. 2007), how the presence of predation risk might affect aggressive behavior remains only speculative. This knowledge gap is important because cichlid fishes in Lake Tanganyika serve as prey for piscivores like *Lepidolamprologus elongatus* (Heg et al. 2007). Towards this end, I conducted a controlled laboratory experiment to quantify how aggressive behavior in a common Lake Tanganyika cichlid, *Julidochromis ornatus*, varies in the presence and absence of perceived predation risk at both high and low water temperatures. I hypothesized that predation risk would cause aggression to decrease, regardless of temperature, but that the low-temperature treatment would experience a greater reduction in aggression because the need to secure food is lower relative to the high-temperature treatment.

Methods

Study species

J. ornatus is a small substrate-brooding cichlid endemic to Lake Tanganyika. It resides in the shallow, rocky parts of the lake, where it participates in bi-parental care of its broods (Awata 2004). The individuals used in this study were from the same age cohort (two generations removed from Lake Tanganyika). They were originally purchased as juveniles during September 2012 and subsequently reared at The Ohio State University's Aquatic Ecology Laboratory (OSU-AEL).

Previous work on these individuals has shown that the mass-specific routine metabolic rate of individuals held at 29°C is significantly higher than those held at 25°C (Brodnik 2015). At the same time, individuals held at 29°C experienced reduced somatic growth and an ~80% reduction in reproductive output, as compared to individuals in the 25°C treatment (Brodnik 2015). Additionally, despite much variation in aggressiveness among individuals within

treatments, the individuals held at 29°C were shown to be more aggressive than those held at 25°C (Kua 2016).

Experimental Design

J. ornatus individuals were kept together in groups of 5-10. Breeding pairs emerged within these groups; pairs were then removed from the group tanks and allocated to individual tanks (one pair per tank). All pairs were exposed to identical conditions in the laboratory until 11 August 2014, after which time each breeding pair was randomly assigned to one of two temperature conditions (25°C and 29°C). None of these individuals had prior exposure to a predator.

All fish used in the experiment were housed in 57 L aquaria under flow-through conditions, with the individual tanks being equally divided in number between two independent recirculating systems that varied in temperature (~25°C or ~29°C). All aquaria contained crushed coral substrate and a breeding shelter made of two pieces of slate (3in x 3in) in an inverted V-shape. All aquaria were maintained at a pH of ~8, with dissolved oxygen saturation being maintained at >90% throughout the lifetime of these individuals. Light levels consisted of 12 hours of simulated daylight and 12 hours of darkness, with individuals being fed daily (two medium-sized Hikari Cichlid Staple food pellets). Temperature, dissolved oxygen, and pH were monitored daily, dissolved nutrients (ammonia, nitrite, nitrate) were monitored weekly, and 10% water changes occurred weekly to biweekly (depending on nutrient levels).

I measured aggression on 26 individuals (see “Aggression trials”; Table 1). These individuals consisted of a mix of males and females. Owing to natural mortality that has occurred since the inception of breeding pairs (nearly two years ago), some of these individuals were still part of their original breeding pair, whereas others no longer had a mate (Table 1). Individuals were evenly split across treatments to minimize confounding effects associated with sex and pair status (Table 1).

Aggression trials

General overview. All aggression trials occurred in a 76 L aquarium that contained 3 cm of black sand substrate and LED strip lights (located along the bottom and top edges of the tank) to help video quality for later analysis. The aggression trials were confined to a small section of the tank (1/6 of the total tank area), with the remainder of the tank being used to test boldness and exploration (results not reported herein). Water temperatures, dissolved oxygen concentrations, and nutrients were maintained at the conditions of each individual's home tank using an *in situ* heater, aerator, and charcoal filter. During testing, the filter, heater, and aerator were removed.

Observations of aggression were conducted during two discrete time periods. The first set of aggression trials, which were conducted in the absence of predation risk, occurred during summer 2015 as part of another Ohio State University thesis project (Kua 2016). These trials provided a baseline measurement of aggression to which the second set of trials, which occurred during fall 2015, could be compared. In this second set of trials, I exposed all 26 individuals to perceived predation risk.

General testing procedure. Both sets of aggression trials were conducted on individuals (one at a time) following the methods of Schurch and Heg (2010) , with the only difference between protocols being the presence of perceived predation risk during the second set of trials (see below for predator cue descriptions). Prior to each aggression trial, each individual was allowed to acclimate in the testing tank for 10 min before behavioral observations were recorded. At the outset of the test, a mirror was slid into the test chamber, to simulate the presence of another individual. The behavior of the fish during the next 10 min was recorded using a high-definition video camera that was located above the testing tank. Once the 10 min aggression trial was completed, the individual was returned to its home tank. After each trial, a

50% (non-predation risk trials) or 100% (predation-risk trials) water change occurred to remove any leftover chemicals that the previous fish may have emitted.

Fish were tested from each temperature treatment in a stratified random design (e.g., 2-4 low temperature fish were randomly selected for testing, then 2-4 high temperature fish were randomly selected for testing) to avoid confounding effects of testing order. A complete random design was not practical, owing to the temperature differences between treatments.

Predation cue generation and testing procedure. To invoke a strong signal of perceived predation risk, both a chemical cue and a visual cue were used, as the use of two cues has been recommended if predation risk is not going to be real (Wisenden et al. 2004a). Both cues were generated using *Lepidolamprologus elongatus*, which is a known predator of *Neolamprologus pulcher*, another native Lake Tanganyika cichlid (Heg et al. 2007). While previous observations of *L. elongatus* preying on *J. ornatus* do not exist in the literature, I assumed that *L. elongatus* would be perceived as a predator by *J. ornatus* because it and *N. pulcher* are of similar in size and distribute themselves in the same areas along the shoreline in Lake Tanganyika (Nagoshi 1983). In addition, a previous study successfully used chemical cues from *L. elongatus* to invoke a predation-risk response in *N. pulcher* in the laboratory (Heg et al. 2004).

To generate the predator chemical cue, three *L. elongatus* individuals were placed in a 38 L tank that was maintained at similar conditions as the low temperature (baseline) treatment (i.e., 25°C, pH of ~8, >90% dissolved oxygen saturation). These individuals were fed frozen bloodworms and brine shrimp *ad libitum* daily for a 36-hour acclimation period. Afterwards, the predators were held without food for 24 hours to ensure that any previous food in its system passed and then the tank's filter and heater were removed to minimize refugia for *J. ornatus* prey and also minimize absorption of any chemical cue by the by the filter. Live *J. ornatus* fry (n=23) that were produced by our study specimens were placed into the predator tank for a 24-hour period, during which time 19 individuals were consumed. After the 24-hour cohabitation

period, the remaining fry were removed and the predators were allowed to remain in their test tank for another 24 hours, with the goal that a predator kairomone (Schreckstoff & Pfeiffer 1963) would be excreted/egested that could complement any stress pheromone produced by the live prey. After this 24-hour period, I pipetted the test water into 30 mL glass vials and froze them at -80°C until use in the second set of aggression trials (Ferrari et al. 2005).

To generate the visual predator cue, a 15 min high-definition video of one of our predators was recorded. *J. ornatus* fry were placed in the tank during the video recording as well, to further simulate the effect of a real predator on video recording. Several recordings were made, with the one chosen having the most predator activity. This video was edited to enlarge the predator so that the predator might appear more threatening to the *J. ornatus* individuals (D'Eath 1998).

For the second set of aggression trials (i.e., those with increased perceived predation risk), the chemical and visual cues were used simultaneously. Thawed water with the predator cue (300 mL) was added to the behavioral testing tank prior to the introduction of the test subject. The tank's water was then manually mixed to distribute the cue throughout the tank prior to the start of the experiment, and also to minimize any disturbance caused by adding water after the test subject was in the tank. To elicit the visual cue, two LCD computer monitors were placed flush with the behavioral testing tank (along the backside, long edge), which played the predator video for the 10 min testing period. The two screens were connected to the same computer such that the predator could swim seamlessly from one screen into the other, and hence navigate the entire tank's longest dimension. During the acclimation period, I placed an opaque card outside of the acclimation chamber, in-between the tank and the monitor displaying the visual predator cue, to ensure that the fish saw the same image during their period of acclimation. At the completion of an aggression test, *J. ornatus* individuals were placed back into their home tanks.

Aggression measurements. Both direct and indirect measures of aggression were quantified in a randomized order using J-watcher software (Convolution, LLC, Version 1.0). Direct aggression measures included biting, caudal fin slapping, ramming, and charging, whereas indirect measures included side displaying, dorsal fin raising, and approaching the mirror. Total aggression was the combined scores of both direct and indirect aggression. All aggression was measured between the fish and the conspecific mirror.

Statistical Analyses

Standardization of observer scores. Because different researchers quantified aggression during the first set (Kua 2016) and second set (me) of trials, I needed to ensure that we scored aggression (both individually and cumulatively) similarly. Towards this end, I randomly selected 10 videos from the first set of trials and blindly scored aggression in them. Afterwards, I compared my scores to the initial set of scores.

To test for differences between observers, I conducted linear regression analyses (n=10 trials) and tested whether the slope and intercept for each individual aggressive behavior and combined behaviors (direct, indirect, and total) deviated from one and zero, respectively. If the upper and lower 95% confidence intervals for the slope and intercept overlapped one and zero, respectively, then I concluded no difference existed.

Consistency in aggression. To ensure that the first set of aggression trials could serve as a suitable baseline for the second set of measures, I conducted an additional set of aggression trials using eight random fish in the absence of predation cues from both the high (n=4) and low (n=4) temperature treatments. I tested whether there were differences between first and second trials in individual and summed aggression (total indirect, total direct, total) using paired t-tests.

Predation risk effects. To determine if individual and cumulative (indirect, direct, and total) aggression scores differed in the presence and absence of predation risk at both temperatures, I used a General Linear Mixed Model. The model included both temperature

(Low, High), predation risk (Absent, Present), and their interaction as fixed effects. It also included sex (fixed effect) and tank (random effect).

Statistical assumptions. Prior to analyses, I found all data to be normally distributed (Kolmogorov-Smirnov normality test: all $P > 0.20$) and with their variances being homogenous (Levene's test: $P \geq 0.39$). Normality and homogeneity tests were conducted using STATISTICA 64 (ver. 12, Dell, Inc. Tulsa, OK), and the General Linear Mixed Models were run in the R software environment (version 3.2.3) using the lme4 and car packages. For all analyses, I used a critical α -value of 0.05.

Results

Standardization of observer scores

Linear regression analyses showed that aggression scoring was similar between observers as the regression line did not differ from a 1:1 line through the origin (i.e., a slope of one and origin on zero was found between respective 95% confidence intervals; Table 2) for any individual behavior. Similarly, I compared cumulative scores for indirect (Figure 1a), direct (Figure 1b), and total (Figure 1c) aggressive behaviors, finding that a one-to-one line through the origin also fit the data (Table 2).

Consistency in aggression

Cumulative scores for total direct, total indirect, and total aggression did not differ between the summer and fall testing periods (paired t-tests: all $p \geq 0.09$; Table 3). Thus, I felt confident in the use of aggression scores from the first trials (without risk) as a baseline for the second set of trials (with risk).

Predation risk effects

Differences in aggressive behavior were observed in individuals between the trials with and without a perceived predation risk (Table 4; Figure 2). Counter to my expectation, total

aggression was higher in the presence of a perceived predation risk than without it (Figure 2a). Similarly, total indirect aggressive behavior was greater with predation risk than without it (Figure 2b). No significant differences were found between temperature treatments nor were any significant temperature x predation risk interactions found (Table 4).

Discussion

I originally predicted that, in the face of predation risk, aggression would decrease at both temperatures, with the decrease being greater at the lower temperature (25°C) than at the higher one (29°C). Counter to my expectations, aggression generally increased with predation risk, with no significant effect of temperature or a temperature x predation risk interaction on aggressive behavior. The increase in total and indirect aggression was driven by an increase in several individual behaviors (i.e., side displays, pelvic fin raises). In addition, I found that one direct behavior (i.e., tail slaps) did increase in the presence of predation risk, even though total direct aggression did not differ between predation-risk treatments.

I am uncertain as to the cause of these counter-intuitive results. However, it may be related to how we tested for aggression. All of the aggression displayed by the test subjects was aimed at a conspecific (i.e., the mirror image of themselves). This could imply that, in the presence of assumed predation risk, intraspecific aggression increases among *J. ornatus*. Although other species, such as the *O. kisutch*, were shown to demonstrate reduced intraspecific aggression when exposed to predation risk, it is possible that *J. ornatus* feels threatened for any number of reasons by fish other than the predator (Reinhardt 1999). As with the *O. gorbuscha*, food could be scarce and encourage competition over the resources closest and considered less risky to obtain (Maghagen 1988). Previous literature, supports that with increasing temperatures, aggression levels in fish are going to increase (Nowicki et al. 2012; Biro et al. 2007; Brodie & Russell 1999; Angilletta et al. 2009). However, when faced with predation, fish in elevated and baseline temperatures experience similarly elevated trends in aggressive behaviors. As to why indirect behaviors were more significant, I am not certain. This

could mean that in a real world setting, *J. ornatus* in projected temperatures, while still more aggressive than in present, baseline temperatures, will still be able to respond to predators in such a way that their fitness will benefit.

With more indirect behaviors being displayed, evidence points towards *J. ornatus* being more cautious of risks in the presence of a perceived predator. It is possible that indirect aggression, when compared with direct aggression, has a greater pay off in the presence of predators within territorial fish such as *J. ornatus*. The risk of confronting a predator directly may be too great in regards to a payoff (Heg & Taborsky 2010). In the case of this experiment, aggression was displayed towards a conspecific. This potential risk avoidance behavior could be due to *J. ornatus* being able to acutely perceive varying levels of predator risk in the way that other researched fish have been shown to do (Staudinger et al. 2013).

While my research has improved our ability to understand how increased temperature might influence cichlid behavior in the face of predation risk, several information gaps still exist. For example, further exploration of what causes the differential response between direct and indirect aggression towards a conspecific and what determines the distinct switch between the two when confronted with an assumed predation risk. Future studies could also look at whether or not different types and/or intensities of predator cues could change the levels of aggression in individuals

Although my findings provide the possibility for a brighter outlook on rising temperatures, with fish being able to respond to predation risk in a similar manner to baseline temperatures, it is important to continue studies in these behavioral areas to fully understand the effects of HIREC on ecosystems. Such understanding allow for appropriate conservation measures to be implemented as climate change continues.

Acknowledgements

I would like to thank numerous people who contributed to my research. Stuart Ludsin, my thesis advisor, was an incredible source of encouragement and motivation. I would like to thank S. Conor Keitzer for help with statistical analyses. I would like to thank Alex Kua and Liz Hoskins for teaching me how to conduct the behavioral trials, and for running trials for me. I also would like to thank Alex for scoring aggression in the absence of predation risk during summer 2015. Kelli Ames, Erin Banaag, James Berry, Colin O'Connor, Joe Dillon, Steve Hadick, Elizabeth Hoskins, and Alex Kua helped care for fish during my time in the lab. Tyler Arnold, Reed Brodrik, and Jake Gilliland were instrumental in setting up and maintaining the experiment. I want to thank Ian Hamilton, Elizabeth Hoskins, and Stuart Ludsin for their comments and guidance, as they helped improve this thesis immensely. Stuart Ludsin and Ian Hamilton also provided the monetary necessary support for this project.

Table 1. Attributes of *J. ornatus* individuals used to quantify aggression in the absence and presence of predation risk at a low (25°C) and high (29°C) temperature. Sex, tank social status (paired, single), total length (TL; nearest 1 mm), and wet mass (nearest 0.1 g) are reported, as are sample sizes for each group.

Treatment	Low temperature		High temperature	
Attribute	No risk	With risk	No risk	With risk
Male	6	6	5	5
Female	7	7	8	8
Pair status				
Paired	6	6	7	7
Single	7	7	6	6
Mean TL \pm 1 SD	63 \pm 1 SD	63 \pm 1 SD	60 \pm 1 SD	60 \pm 1 SD
Mean mass \pm 1 SD	3.6 \pm 0.1x SD	3.6 \pm 0.1x SD	3.5 \pm 0.1x SD	3.5 \pm 0.1x SD

Table 2. Linear regression statistics for direct, indirect, and (summed) total aggression behaviors measured during summer 2015 and fall 2015 in *J. ornatus* individuals at 25°C, with and without perceived predation risk. Aggression scores were quantified on 10 randomly selected trials, with the second set of trials being scored blindly. Upper and lower 95% confidence intervals (CIs) around the slope and intercept of each least-squares regression line are provided.

Aggression	Slope (95% CIs)	Intercept (95% CIs)	Model R², p
Total direct	0.96 (0.87, 1.04)	3.53 (-1.59, 8.64)	(0.99, <0.001)
Total indirect	0.92 (0.76, 1.08)	8.45 (-7.81, 24.71)	(0.96, <0.001)
Total aggression	0.93 (0.81, 1.06)	11.68 (-7.54, 30.89)	(0.97, <0.001)

Table 3. Paired t-test results conducted direct, indirect, and (summed) total aggression scores taken on eight *J. ornatus* individuals at 25°C without predation risk. Aggression was quantified by two different observers, once during summer 2015 and once during fall 2015.

Aggression	<i>t</i>	<i>p</i>
Total direct	-1.72	0.13
Total indirect	-1.43	0.20
Total aggression	-1.945	0.09

Table 4. Results from General Linear Mixed Models ($df = 1$) performed on *J. ornatus* aggression metrics in the presence and absence of perceived predation risk at a low (25°C) and high (29°C) temperature. Statistics for the main factors (Temp=temperature; Pred=predation) and their interaction are reported. Behaviors that differed ($p < 0.05$) between predation risk treatments are bolded.

Type of Behavior	Aggressive Behavior	Effects	Chisq	P
Summed	Total aggression	Temp	3.75	0.05
		Pred	18.90	<0.001
		Temp x Pred	1.23	0.27
	Total direct	Temp	1.98	0.16
		Pred	1.63	0.20
		Temp x Pred	0.74	0.39
	Total indirect	Temp	0.79	0.38
		Pred	29.24	<0.001
		Temp x Pred	0.49	0.49

Figure 1. Relationship between cumulative aggression scores measured during summer 2015 (Observer 1) and fall 2015 (Observer 2) on 10 *J. ornatus* individuals at 25°C and without predation risk. Regression lines for a) cumulative indirect aggression scores, b) cumulative direct aggression scores, and 3) combined (indirect plus direct) aggression scores are shown. The statistics for these lines can be found in Table 2. The dashed red lines are the 1:1 lines for each plot.

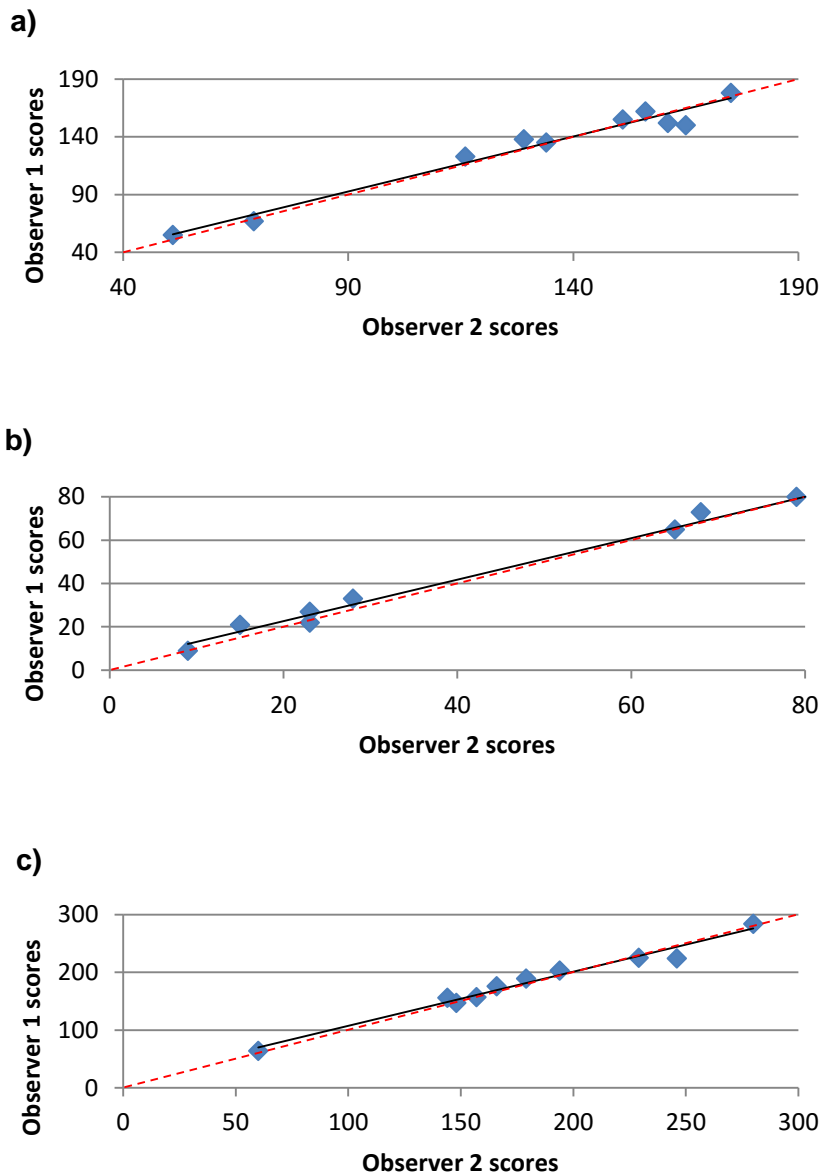
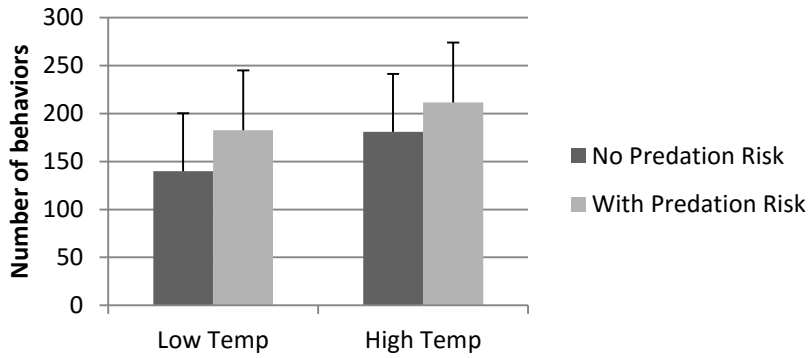
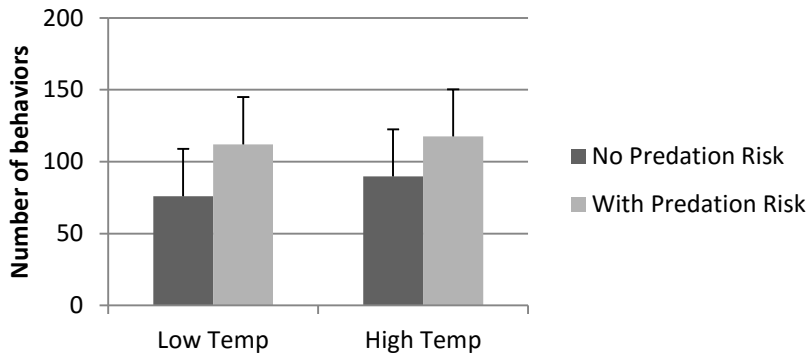


Figure 2. Mean (\pm 95% CI) a) total, b) indirect and c) direct aggressive behavior in *J. ornatus* individuals in the presence and absence of predation risk at a low (25°C) and high (29°C) temperature.

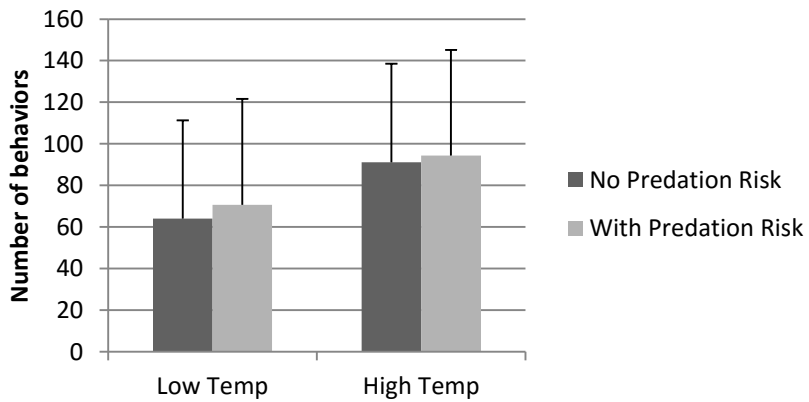
a)



b)



c)



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