

RESEARCH ARTICLE

Fight, fatigue and flight: narrowing of attention to a threat compensates for decreased anti-predator vigilance

Kazutaka Ota*

ABSTRACT

Fighting carries a predation risk because animals have limited attention, constraining their ability to simultaneously engage in aggression and anti-predator vigilance. However, the influence of interspecific aggression and fatigue on the predation cost of fighting is seldom examined, although both are unignorable aspects of fighting. Here, I incorporated both factors in a series of field experiments on the cichlid *Lamprologus ocellatus*. If territorial males respond more strongly to conspecific territorial intruders than to heterospecific intruders, then they should delay escape more frequently during intraspecific fighting than during interspecific fighting. Consequently, although I predicted that vigilance would be decreased as fighting progresses in both cases, intraspecific aggression should decrease vigilance more than interspecific aggression. Males were also exposed to a predator approaching at different (slow or fast) speeds during these fighting bouts. Delays in predator detection and flight initiation were quantified and these predictions were tested. As predicted, males responded more strongly to intraspecific intruders, resulting in slower predator detection and fleeing times than when encountering interspecific intruders. Furthermore, flight latency decreased with increasing fight duration, suggesting that fatigue negatively influenced escape responses. However, contrary to the prediction, the vigilance decrement rate was faster in response to slow predators than in response to rapid predators, and was not influenced by intruder identity. This suggests that fighting males reserve their attention for information critical to their survival and are less vigilant toward a less-threatening (slowly approaching) predator. This cognitive allocation may be an adaptive compensation for fatigue-related low vigilance during fighting.

KEY WORDS: Cognitive trade-off, Decision making, Interspecific competition, Intraspecific competition, Limited attention, Predation

INTRODUCTION

Predator avoidance can take the form of active flight or hiding. Because early detection of approaching predators would greatly reduce the risk of capture, prey animals spend a considerable amount of time and energy on anti-predator vigilance (i.e. scanning the surroundings) (Beauchamp, 2015). However, such behaviours can be impaired if prey are engaged in another cognitive activity. For example, foraging prey are less vigilant than non-foraging prey, thus allowing predators to approach closer (Kaby and Lind, 2003; Krause and Godin, 1996) and elevating mortality risk (Godin and Smith,

1988; Krause and Godin, 1996). Impaired vigilance and delayed flight could be due to cognitive limitations, such as reduced attentional and information-processing capacity (Clark and Dukas, 2003; Dukas, 2004). Under a scenario of limited attention, the cognitive load required to engage in a difficult task decreases attention that would otherwise be directed towards anti-predator vigilance. For example, blue tits, *Parus caeruleus*, are restricted in their anti-predator vigilance ability when foraging whole, live mealworms that demand much attention and difficult handling skills but not when foraging chipped mealworms that are relatively easy to handle (Kaby and Lind, 2003).

Aggressive behaviours also require cognitive processing (Elwood and Arnott, 2012; but see Fawcett and Mowles, 2013) and induce an attentional trade-off with anti-predator activities (Dunn et al., 2004; Hess et al., 2016). For instance, when alerted to the presence of a predator, fighting individuals suppress aggression and increase vigilance (Brick and Jakobsson, 2002; see also Wisenden and Sargent, 1997), despite an elevated risk of losing resources (LaManna and Eason, 2007). Furthermore, fighting individuals are slower than solitary individuals to detect and escape from experimentally presented predators (Brick, 1998; Cooper, 1999; Díaz-Uriarte, 1999; Hess et al., 2016; Jakobsson et al., 1995).

To date, the effects of fighting on escape responses have only been investigated in limited situations, where predators slowly approach males engaged in agonistic encounters with conspecifics. Thus, some important aspects of this topic remain unexplored. For example, existing studies examining the predation costs of aggression have focused only on intraspecific interactions, yet interspecific fighting also occurs frequently, suggesting the potential for attentional costs. In support of this, a recent study in the West African cichlid *Pelvicachromis taeniatus* revealed that predator cues caused territorial males to suppress interspecific aggression (Meuthen et al., 2016). However, the attentional cost of interspecific fighting may be lower than that of intraspecific conflicts. The niche overlap hypothesis predicts that animals respond more aggressively to conspecific intruders than to heterospecifics (Peiman and Robinson, 2010), and this is partly supported in several African cichlid fishes (Dijkstra et al., 2005; Pauers et al., 2008). A stronger aggressive response could translate into expending more energy towards conspecifics and less towards heterospecifics, leaving more attention for anti-predator vigilance in the latter case. Given evidence that escalated conflicts cause greater delays in anti-predator responses than low-intensity aggression (e.g. displays) (Dunn et al., 2004; Jakobsson et al., 1995), animals may notice predators faster during interspecific encounters than during intraspecific encounters.

Another factor that is infrequently examined is the role of aggression-induced fatigue. High levels of vigilance and attention cannot be maintained indefinitely, leading to gradual impairment over time, even in the absence of other cognitive activities (vigilance decrement). This time effect is more pronounced for cognitively intensive and thus fatiguing tasks (Lambourne and Tomporowski,

Department of Biology and Geosciences, Osaka City University, Sumiyoshi, Osaka 558-8585, Japan.

*Author for correspondence (otkztk@gmail.com)

 K.O., 0000-0002-7097-7330

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2010; Mizunoya et al., 2004). Because antagonistic interactions can escalate from ritualized displays to physical aggression as an encounter continues (Enquist et al., 1990), prolonged instances of fighting should cause fatigue and impair attention. Moreover, as intraspecific conflict is more likely to escalate and last longer (Dijkstra et al., 2005; Pauers et al., 2008), it should increase the rate of vigilance decrement relative to interspecific conflict.

Lamprologus ocellatus (Steindachner 1909) is a cichlid endemic to Lake Tanganyika and ideal for examining how antagonistic encounters influence anti-predator responses. This fish exclusively inhabits sandy–muddy substrate, embedded with empty gastropod *Neothauma tanganyicense* shells that they use for breeding and shelter (Sato and Gashagaza, 1997). The species exhibits a harem mating system, with a territorial male holding a small breeding territory containing several shells. Males defend one to two shelter shells against conspecific same-sex rivals and other shell-breeding cichlids (Bills, 1997). One to three females typically reside within a male territory and use a separate shell for breeding and shelter (Bills, 1997; Sato and Gashagaza, 1997). Territorial males often remain motionless in front of shells to guard them, but rapidly escape into the shells upon detecting predators, and this behaviour appears to be their primary form of defence (Bills, 1997). Therefore, escape responses can be easily quantified under standardized conditions of male posture and distance from the refuge.

In this study, field experiments were designed to examine the male *L. ocellatus* response to a simulated predator approach during antagonistic encounters with conspecifics or heterospecifics. The effects of fighting-induced fatigue were also investigated. Territorial males were exposed to simulated territory intrusions from conspecifics or heterospecifics, coupled with low- or high-threat predator approaches.

Based on the niche overlap hypothesis, I made the following predictions regarding the experimental outcome. First, anti-predator vigilance will be more impaired during intraspecific fighting than during interspecific fighting, resulting in closer flight initiation distance (FID, distance from the predator when the prey begins to flee) and alert distance (AD, distance where the prey detects predator approach). A similar but smaller effect is expected when the territorial male's attention is simply drawn to intruders (without aggression). Second, males will respond earlier to a higher threat level from the predator, as escape is threat sensitive (Helfman, 1989; Ydenberg and Dill, 1986): faster-approaching predators pose a greater threat of predation, and thus prey animals escape earlier in response to faster approaches than to slower approaches (Bateman and Fleming, 2011; Cooper, 2006; Cooper and Sherbrooke, 2013; Cooper and Whiting, 2007; Hemmi and Pfeil, 2010; Stewart et al., 2014). Third, fatigue will further exacerbate the negative effect of aggression on anti-predator response, indicated by even shorter FID and AD as fighting progresses. Fourth, intraspecific competition will increase the rate of vigilance decrement more than interspecific competition.

MATERIALS AND METHODS

Study sites and species

Field experiments were performed using SCUBA from late August to September 2016 at Wonzye Point (8°45.5'S, 31°06.1'E), near Mpulungu on the southern end of Lake Tanganyika, Zambia. The habitat is sandy–muddy with a flat bottom (6–11 m deep), embedded with empty shells but without rocks or vegetation. I checked water transparency every morning using a small white acrylic plate (100×200 mm), and experiments were not conducted on days when the plate could not be seen by the human eye at a distance of >2 m.

The habitat's primary predator (Brandtmann et al., 1999) is the fast-striking piscivorous cichlid *Lepidiolamprologus elongatus*.

The sympatric cichlid *Lepidiolamprologus* sp. 'meeli-boulengeri' (see Schelly et al., 2006) was chosen as a primary heterospecific competitor of *L. ocellatus* in this habitat (Brandtmann et al., 1999). Bills (1997) briefly described that both *L. ocellatus* and *Lepidiolamprologus* sp. 'meeli-boulengeri' (hereafter *Lepidiolamprologus* sp.) prey on benthic invertebrates, but *L. ocellatus* remains in its own territory to feed, whereas *Lepidiolamprologus* sp. forage for food beyond their breeding territories and do not hold feeding territory. Therefore, competition should be higher within *L. ocellatus* than between the two species, and *Lepidiolamprologus* sp. are likely to wander into the territory of a male *L. ocellatus*, lending ecological validity to the experimental design. Furthermore, the two species also compete for shells, which are used for shelter and as breeding sites (Bills, 1997; Brandtmann et al., 1999; Sato and Gashagaza, 1997; Sunobe and Munehara, 2003). In particular, female *Lepidiolamprologus* sp. are an appropriate competitor of territorial male *L. ocellatus* over shells. This is because they are close in size (45–60 mm) and use shells matching their body size (Bills, 1997; Walter and Trillmich, 1994). Male *Lepidiolamprologus* sp. are also territorial, but grow to a larger size than territorial male *L. ocellatus* (up to 80 mm total length, TL). In Lake Tanganyika cichlids, males are generally more aggressive than females (O'Connor et al., 2015; Reddon et al., 2011; Wood et al., 2014), but aggressiveness is also associated with relative body size, independently of sex (Barlow and Lee, 2005; Wood et al., 2014). Given the fact that the shell is a critical resource of both sexes in both *L. ocellatus* and *Lepidiolamprologus* sp., the motivation for fighting should be at least as high between sexes as between males.

Fish collection

To simulate natural conditions, actual (dead) fish were used as predators and intruders. Local fishermen provided fresh *L. elongatus* specimens (210–230 mm TL, $n=17$). Territorial male *L. ocellatus* (45–55 mm TL, $n=6$) and female *Lepidiolamprologus* sp. (48–51 mm TL, $n=6$) were caught for use as conspecific and heterospecific intruders, respectively. Fish were killed by holding them in a 50 ml syringe to which at least 1% eugenol (FA100, Tanabe Seiyaku Co. Ltd, Saitama, Japan) was added using a 10 ml syringe. The exact eugenol concentration could not be obtained during handling underwater. Fish were exposed to eugenol for 10 min. Each specimen was used for one full day and then exchanged for a fresh fish. Intruder specimens were captured several dozen metres away from the experimental sites to avoid a familiarity effect (Griffiths et al., 2004).

Territorial *L. ocellatus* males were visually identified based on size (≥ 45 mm TL), as they are larger than females (Bills, 1997). Their behaviours were then briefly observed to confirm harem possession and the presence of receptive (ready-to-spawn) females based on patrolling activity near shells and expression of courtship behaviour, respectively. Males that expressed courtship behaviour during the brief observation were excluded from this study to minimize differences of breeding resources between the focal male and the intruder (Cooper, 1999).

Experimental procedure

A predator approach was simulated by manual presentation of a rockfish specimen tied to the end of a transparent acrylic rod (90 cm long, 1 cm diameter) to the experimental *L. ocellatus* male. After preparation of this predator stimulus underwater, the experimenter

(K.O.) remained stationary 1 m behind the focal fish, while holding the rod for 2 min before beginning the experiment, to allow acclimation. The predator stimulus was hidden under a soft, green polypropylene plate, 1 m behind the experimental fish, until presentation. Here, predator threat was manipulated through varying the approach speed, as faster movement is considered to be more threatening (Bateman and Fleming, 2011; Cooper, 2006; Cooper and Sherbrooke, 2013; Cooper and Whiting, 2007; Hemmi and Pfeil, 2010; Stewart et al., 2014). Because the strike speed of *L. elongatus* has not been reported, I approximated imminent strike attempts (high threat) based on the approach speed of a piscivorous pike cichlid, *Crenicichla alta*, when successfully hunting guppies, *Poecilia reticulata* ($>1.5 \text{ m s}^{-1}$; Walker et al., 2005). A low-threat approach was set at 0.2 m s^{-1} , an approximate cruising speed of reef fishes (Fulton, 2007). In total, 221 trials were conducted (fast: $n=109$, slow: $n=112$). I practised these approach exercises before the experiments to achieve constant speeds among trials.

The experimental male experienced only the predator stimulus in 45 out of the 221 trials (i.e. control treatment). In the remaining 176 trials, an intruder stimulus was presented to the experimental male before presentation of the predator approach. Territory intrusions were simulated by manual presentation of a fish specimen tied to the end of a transparent acrylic rod (90 cm length, 1 cm diameter) to the experimental male. Intruder rods were moved towards the male slowly ($<0.2 \text{ m s}^{-1}$) to a distance of 150 mm from the refuge, and positioned at a 90 deg angle, left of the experimental male's body axis (Fig. 1). In these intruder treatments, two antagonistic situations were simulated through the presentation of the predator at different times: first, when the experimental male had noticed the intruder but had not yet approached (pre-competition stage); second, when the experimental male approached and began to fight the intruder (fighting stage). The timing of predator approach was determined, with particular attention to the posture and body orientation of the experimental males, for both pre-competition and fighting stages of intruder encounters. In fish, head-down positions constrain the visual field and delay response (Krause and Godin, 1996); this position occurs in competitive contexts among *L. ocellatus* (Walter and Trillmich, 1994). In addition, detection ability is highly dependent on approach direction because the retinal cell density is highest in the temporal region, and posterior vision is blocked by the fish's own body (Lisney and Hawryshyn, 2010; van der Meer et al., 1995). Therefore, to maximize detectability across trials, predator presentation began only when experimental males were not in a head-down posture and when their body axis was $<45 \text{ deg}$ from an invisible line connecting the refuge entrance to the initial predator position (Fig. 1). Furthermore, for presentation during the fighting stage, predator movement was initiated at various time points from the initiation of an aggressive encounter (marked by approach towards the intruder), simulating different degrees of fatigue. This is because in *L. ocellatus*, aggression

escalates over time from displays to mouth-fighting during intraspecific competition (Walter and Trillmich, 1994) and during interspecific competition (K.O., personal observation), possibly indicating a relationship between fatigue and fight duration (Briffa and Elwood, 2005).

Consequently, the experiment consisted of 221 trials with 10 treatments. The first six occurred during the pre-competition stage (slow approach+conspecific intrusion, $n=23$; slow approach+heterospecific intrusion, $n=23$; slow approach+no intrusion, $n=23$; fast approach+conspecific intrusion, $n=21$; fast approach+heterospecific intrusion, $n=22$; fast approach+no intrusion, $n=22$). Four of these occurred at the fighting stage (slow approach+conspecific intrusion, $n=22$; slow approach+heterospecific intrusion, $n=21$; fast approach+conspecific intrusion, $n=23$; fast approach+heterospecific intrusion, $n=21$). By definition, predator-only treatment could not be conducted during the fighting stage. Intruder stimulus (conspecific, heterospecific or no intruder), approach speed (fast or slow) and stage of predator presentation (pre-competition or fighting) were randomly assigned to experimental males. The location was changed every experimental day and males used for experiments were identified on each day such that each male was used only once.

Data collection

A tripod-mounted video camera was set approximately 0.7 m above the lake bottom to record a top-view of the experimental male's escape responses in each trial. Video recordings began once cameras were in position, and stopped after males initiated flight. To calibrate distance, a 1 m ruler was placed between the approach start point and shell, and recorded in each trial. Recordings were scored on a computer to obtain two responses of the experimental males to the intruder, and three responses of the experimental males to the predator stimuli. The responses to the intruder were: (1) the time (s) taken for the experimental male to orient towards the intruder (henceforth 'approach latency'); and (2) the duration of the fight, which was calculated as the time from when the male first approached the intruder to when it escaped the predator. Approach latency was used as an index of aggressiveness toward intruders, with a shorter latency indicating more aggression (Oliveira et al., 1998). The responses to the predator were quantified by AD, FID and refuge use. AD is the distance between the experimental male and the predator when the male first detected the approaching predator. FID is the distance between the experimental male and the predator when the male began to flee. Refuge use was determined by whether the experimental male entered the shell refuge after detecting the predator or not. Here, the fish were considered to have detected the predator if freezing, turning and interruption of activity occurred (Hess et al., 2016; Krause and Godin, 1996; Wisenden et al., 1995). However, these behavioural cues were identifiable only in the slow predator approach condition. Therefore, AD was

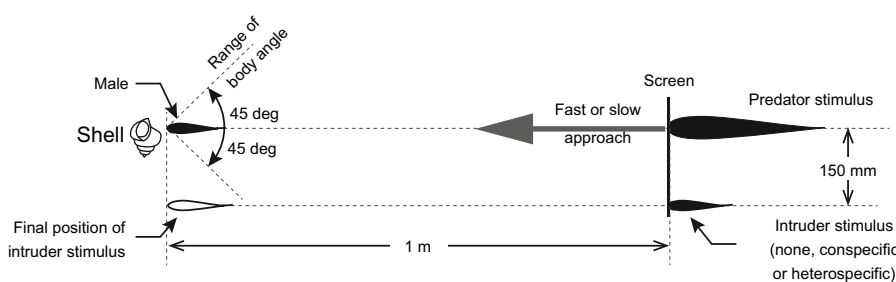


Fig. 1. Schematic representation of the predator approach experiment. See Materials and methods for details.

quantified only for the slow-approach treatment. AD and FID were measured in ImageJ 1.8 (<https://imagej.nih.gov/ij/>).

Sixty of 221 trials were omitted from the final analyses because of video failure ($n=14$), imperfect approach simulation ($n=19$) or improper body posture or direction ($n=27$), resulting in a total of 161 trials from 10 treatments.

To confirm that the predator approach speed actually differed between the slow and fast treatments, the period from the point at which the predator appeared on the monitor to the point at which the experimental male escaped was measured for each trial. Some variability was inevitable for each approach speed, but approach speeds actually differed between these treatments, with no overlap (fast: mean \pm s.d. 1.92 ± 0.38 m s $^{-1}$, range 1.20–2.60 m s $^{-1}$, $n=80$; slow: 0.20 ± 0.05 m s $^{-1}$, 0.11–0.31 m s $^{-1}$, $n=81$; Mann–Whitney U -test, $W=6480$, $P<0.001$).

Statistical analysis

Approach latency toward conspecific and heterospecific intruders was compared using the Mann–Whitney U -test. Refuge use, FID and AD were treated as anti-predator responses. Analyses were performed separately for pre-competition and fighting stages to avoid the confounding effect of consistently higher values during the fighting stage. This effect occurs because refuge use and FID generally increase with distance from refuges, independent of aggression, as a result of an associated elevation in predation risk (Dill, 1990; McLean and Godin, 1989).

The effects of predator approach speed (fast, slow) and intruder species (conspecific, heterospecific, none) on refuge use frequency was examined using generalized linear models (GLMs) with binomial distributions. These models were refined by a backward elimination of insignificant variables ($P>0.05$) with a χ^2 test statistic. The effects of the same two factors on FID were examined using GLMs with a Gaussian distribution. Because AD could only be measured in the slow predator condition, a one-factor GLM with a Gaussian distribution was used to examine the effect of intruder species. Next, the effects of fighting-related fatigue on FID were evaluated using a GLM; approach speed and intruder species were fixed effects and fighting duration was a covariate. Reduced models were obtained using backward elimination of insignificant variables ($P>0.05$).

The FID and fighting duration were log-transformed to obtain a normal distribution and homogeneity of variance. All analyses were performed in R version 3.3.1.

RESULTS

In all fighting treatments, male *L. ocellatus* eventually left their refuges to approach intruder stimuli. The response typically did not occur immediately after stimulus presentation. Approach latency to conspecifics was shorter (median 10 s, range 0–92 s, $n=24$) than that to heterospecifics (median 19 s, range 0–156 s, $n=28$; Mann–Whitney U -test, $W=226$, $P=0.043$).

Effect of intruder species and predator approach speed on anti-predator response

Males took flight from approaching predators in all trials but did not necessarily enter refuges, even if they were close by. FID and AD differed between conditions. In pre-competition stages, FID was positively affected by approach speed ($F_{1,95}=3.41$, $P<0.001$) but not by intruder species ($F_{2,95}=1.73$, $P=0.18$) or their interaction ($F_{2,95}=0.08$, $P=0.92$) (Fig. 2A). In contrast, during fighting stages, FID was positively affected by both speed ($F_{1,56}=63.56$, $P<0.001$) and intruder species ($F_{1,56}=7.12$, $P<0.01$), but not by any

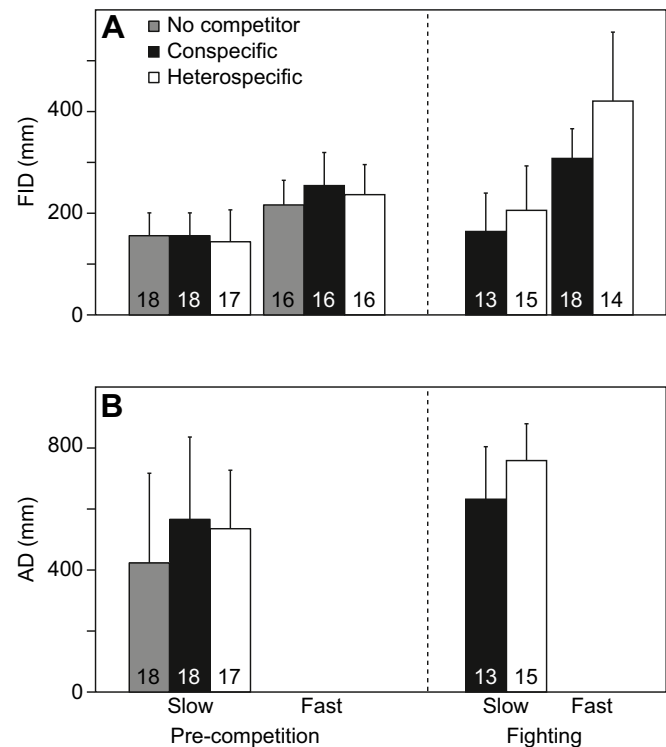


Fig. 2. Difference in flight initiation distance (FID) and alert distance (AD) between a male *Lampprologus ocellatus* and a simulated approaching predator. Experimental males were presented with an approaching predator during the pre-competition and fighting stages, and FID (A) and AD (B) were measured. Bar colours indicate differences in stimuli presented to the experimental male. Data are means \pm s.d., with sample sizes in the bars.

interaction effect ($F_{1,56}=0.25$, $P=0.62$) (Fig. 2A). Similarly, AD during the pre-competition stage did not differ across varying intruder stimuli ($F_{2,50}=2.38$, $P=0.103$), but was longer when males were fighting with heterospecifics than with conspecifics ($F_{1,26}=4.97$, $P=0.035$) (Fig. 2B).

Refuge use was more frequent in response to fast predators than to slow predators, regardless of intruder species. This outcome was true for pre-competition (binomial GLM, speed \times intruder: $\chi^2_2=0.30$, $P=0.86$; intruder: $\chi^2_2=0.83$, $P=0.66$; speed: $\chi^2_1=6.16$, $P=0.01$) and fighting stages (speed \times intruder: $\chi^2_1=0.19$, $P=0.66$; intruder: $\chi^2_1=0.14$, $P=0.71$; speed: $\chi^2_1=4.28$, $P=0.04$) (Fig. 3).

Effect of fatigue on anti-predator response

Overall, FID decreased with more time spent fighting (Fig. 4). Intruder species, as well as the interaction between fight duration and approach speed, had significant effects, which was at odds with the initial prediction (Table 1 and Fig. 4). The interactive effect shows that FID decreased markedly in males responding to slow predator approaches.

DISCUSSION

Approach latency was shorter for conspecific intruders than for heterospecifics, suggesting that experimental males were more aggressive towards conspecifics. Because the immediate opportunity of mating was removed in this experiment by removing males with ready-to-spawn females, mating competition should not be responsible for this difference. Consequently, refuge and food were probably the resources under competition. Because these resources are critical for the survival of both sexes (Bills, 1997), sex

Table 1. Summary of model selection for flight initiation distance based on fight duration

	Full model ($F_{7,48}=16.26$, $R^2=0.66$, $P<0.001$)				Best-fit model ($F_{4,51}=28.54$, $R^2=0.67$, $P<0.001$)			
	Estimate	s.e.	t	P	Estimate	s.e.	t	P
Intercept	5.83	0.31	18.61	<0.001	6.13	0.21	28.68	<0.001
Speed	0.39	0.54	0.72	0.48	0.07	0.33	0.21	0.84
Intruder species	0.70	0.42	1.67	0.11	0.18	0.08	2.36	0.02
Fight duration	-0.04	0.07	-0.50	0.62	-0.10	0.05	-2.01	0.05
Speed×duration	-0.26	0.13	-2.00	0.05	-0.20	0.08	-2.46	0.02
Speed×intruder	-0.52	0.70	-0.75	0.25				
Intruder×duration	-0.11	0.10	-1.11	0.46				
Speed×intruder×duration	0.09	0.17	0.55	0.58				

also should not be responsible for this difference, although the heterospecific intruders were female *Lepidolamprologus* sp. Observed differences in approach latency between conspecific and heterospecific treatments would therefore be associated with differences in the nature of intraspecific competition and heterospecific competition.

Conspecific stimuli elicited shorter FID (males escaped from predators later) and AD (males detected predators later) than heterospecific stimuli in the fighting stage but not in the pre-competition stage, partially supporting my prediction that conspecific fighting impairs vigilance more than heterospecific fighting. Two possible explanations exist for why FID did not differ across intruder stimuli (conspecific, heterospecific and none) during the pre-competition stage. First, the mere presence of an intruder may not influence the timing of escape from predators. However, this explanation is unlikely because attending to the intruder, even without approach or aggression, demands cognitive resources (Hess et al., 2016). Second, experimental males may not have paid sufficient attention to intruder presence, instead opting to scan for potential predators. In general, distance from a refuge increases predation risk (Dill and Fraser, 1997; Martín and López, 2001), meaning that fish should scan their surroundings before deciding to leave the refuge. In pre-competition periods, the fish should therefore meet the two conflicting demands of risk assessment for territory intrusion and predation, which would induce them to make decisions for whether and where to leave the refuge. In these

decision-making processes, predation risk should arguably be assessed following intruder assessment. The lack of FID variation across intruder stimuli in the pre-competition period implies that presentation of the predator stimulus coincided with when males chose to assess predation risk. Future studies could clarify whether and to what extent anti-predator vigilance is impaired when males simply observe intruders without direct aggression.

Economic escape is a potential alternative explanation for the shorter FID during conspecific fighting than during heterospecific fighting. Economic escape theory predicts that prey will assess potential risk from a predator and continue to engage in a beneficial activity until the benefit of fleeing exceeds the cost (Ydenberg and Dill, 1986). Although quantification of AD could not be achieved in the fast-approach treatment, in the slow predator approach treatment, males had a shorter AD when fighting with conspecifics than with heterospecifics, suggesting that they detected predators later under intraspecific competition. This result indicates that in the slow predator approach treatment, later escape results from later detection of predators when males are fighting with conspecifics, but not from increased impairment of anti-predator vigilance. Indeed, there was a ~1 s gap between detection and flight, showing that males did not flee immediately after predator detection. In this period, males could assess the risk of slowly approaching predators, which lends support to economic escape as an explanation. However, the very short time from rapid predator approach to flight initiation, compared with the slow approach, implies limited risk assessment (Chittka et al., 2009). Subjects were therefore likely to flee immediately despite incomplete

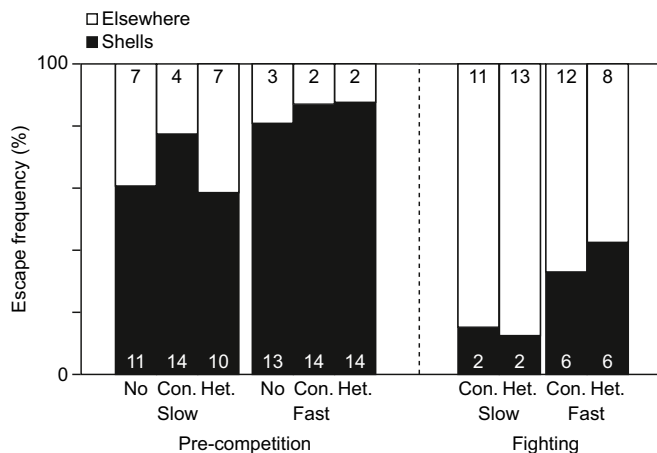


Fig. 3. Pre-competition versus fighting stage differences in refuge use frequency by male *L. ocellatus* in response to slow- and fast-approaching predators. Before predator approach, experimental males were first exposed to a conspecific (Con.), heterospecific (Het.) or no intruder and escape responses to a shell or elsewhere were recorded. Sample sizes are given in the bars.

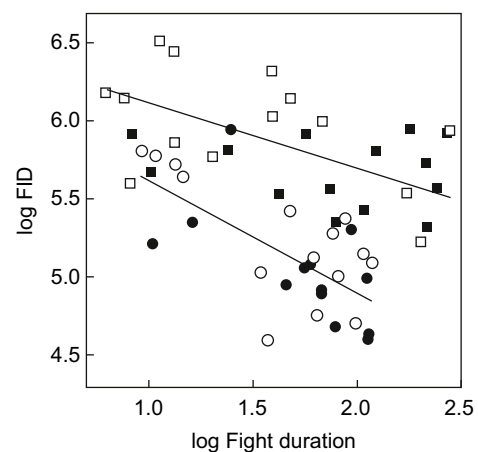


Fig. 4. Relationship between FID and fight duration. FID was measured in mm and fight duration in s. Circles, slow approach; squares, fast approach; black, conspecific intruder; white, heterospecific intruder. A regression line was drawn for each approach speed (dashed line: fast approach, solid line: slow approach).

risk assessment, because the risk of capture was extremely high (Díaz-Uriarte, 1999). This is also supported by the fact that, in contrast to the slow approach treatment, behavioural signs of predator detection were not observed in the fast-approach treatment. Together, these data suggest that *L. ocellatus* males use different decision rules depending on predator approach speed, with economic escape in the slow-approach treatment and immediate escape in the fast-approach treatment. Evidence for such flexible decision making is available in guppies; individuals that were slow to detect a predator fled immediately, whereas individuals that observed a predator early engaged in economic escape (Krause and Godin, 1996).

Faster predator approach speeds led to earlier flight and increased refuge use in both pre-competition and fighting stages, independently of intruder species. These responses support the threat-sensitivity hypothesis (Ydenberg and Dill, 1986; Helfman, 1989; Cooper, 2003; see Cooper and Whiting, 2007, for details) and suggest that males perceived the faster approach as more dangerous. Refuge use limits opportunities for other activities, such as foraging and mating (Amo et al., 2007; Reaney, 2007). In *L. ocellatus*, using the refuge to escape from predators can actually increase vulnerability to subsequent predation. Because *L. ocellatus* individuals enter shells head-first and cannot turn inside (Haussknecht and Kuenzer, 1991), they emerge in a highly risky tail-first posture that seems to severely restrict visibility (Takahashi and Ota, 2016). Given these high costs, the optimal response of male *L. ocellatus* should be to focus on perceived predation threats, irrespective of territorial intrusion. The present study supports this optimal response, as intruder stimulus did not exert a significant effect on refuge use. Taken together, the present findings indicate that fighting quantitatively diminishes the ability to detect approaching predators, but does not influence the ability to accurately perceive predation threats.

As predicted, I found that latency to flee tended to increase with fight duration, suggesting that fatigue diminishes anti-predator vigilance. Contrary to my prediction, however, the vigilance decrement over time was independent of intruder species. Instead, predator approach speed largely explained vigilance decrement, which was faster under slow approaches. This implies that the escape response was disproportionally maintained, even with prolonged fighting, in fast-approach treatments compared with slow-approach treatments. There are two non-mutually exclusive explanations for this unexpected decrease in vigilance. First, the greater vigilance decrement in the slow approach may reflect a male response to diminished attention as a result of fighting, where males selectively focus their diminished attention only on faster-approaching predators, while reducing attention to slowly approaching predators. Given that slow predators pose relatively little danger, fatigued individuals could reduce their mortality risk by allocating their attention to rapid, dangerous predators. This narrowing of attention, termed selective attention, has been reported, particularly in food search behaviour, in many animals (Kamil and Bond, 2006), such as in blue jays *Cyanocitta cristata* (Dukas and Kamil, 2001). However, this study suggests that selective attention should also apply to predator detection by prey, with anti-predator vigilance heightened against a specific, high-priority target when attention is limited. Second, the greater vigilance decrement in the slow approach may simply reflect a perceptual response. In the present study, detection of an approaching predator by the experimental males might be obtained through visual, motion and auditory perception, because a predator specimen was presented to them. In fish, faster-moving predators mechanistically increase the speed of water flow, which may facilitate detection of an imminent threat through the lateral line

system (Stewart et al., 2014). Increased sensitivity to fast motion may allow males to detect a fast-approaching predator more easily than a slow-approaching predator and cause instinctive responses in males to rapidly approaching predators, even when they are fatigued during prolonged fights. Given that faster-moving subjects may be perceived as a greater threat in fish (Bianco et al., 2011), such motion-sensitive perception would be beneficial for prey animals.

In conclusion, this is the first study to demonstrate the predation costs of heterospecific fighting. The present findings indicate that intraspecific competition has higher predation costs than interspecific competition because of the greater reduction in anti-predator vigilance. Furthermore, territorial fighting does not diminish the ability to perceive serious predation threats. Finally, fighting-related fatigue elevates predation cost through delayed flight, but *L. ocellatus* can compensate for increased vulnerability and limited information processing through a narrowing of attention on more dangerous threats. Fatigue is often ignored in animal behavioural studies, but the present study indicates that it may play an important role in animal behavioural decisions through cognitive processes.

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Competing interests

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