Acute and chronic increases in predation risk affect the territorial behaviour of juvenile Atlantic salmon in the wild

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Optimality models predict that territory size will decrease as the costs of defence increase. One poorly understood cost is predation risk, especially the relative influence of short- vs. long-term increases in predation risk. Under natural conditions, we quantified the territorial behaviour of juvenile Atlantic salmon (*Salmo salar*) exposed to either acute or chronic increases in perceived predation risk. The effects of an acute increase in predation risk were assessed by exposing 18 young-of-the-year (YOY) Atlantic salmon to a control of stream water and to an alarm cue (i.e. conspecific skin extract) while monitoring their territorial behaviour. We investigated the effects of a chronic increase in perceived predation risk by quantifying the territorial behaviour of YOY salmon in control vs. risky sections of seven sites, where we manipulated the perceived predation risk over a four week period by releasing stream water in control sections and alarm cue in risky sections. We found that salmon exposed to the alarm cue decreased the number of switches between foraging stations, but they did not change their territory size or foraging rate. As predicted, YOY salmon in risky sections had smaller territories than in control sections. However, their foraging rates and number of switches between foraging stations did not differ between treatments. Our study suggests that juvenile Atlantic salmon are sensitive to both acute and chronic increases in perceived predation risk under natural conditions, and support the predictions of optimality models that territory size decreases with increasing predation risk.

Keywords: Damage-released chemical alarm cue, Space use, Population regulation, Threat-sensitive trade-off, Temporal scale, Territory size, Home range, Optimality, Young-of-the-year, *Salmo salar*

Optimality models predict that territory size will decrease when the benefits or costs of defence increase (Hixon 1980; Schoener 1983). Numerous field and laboratory studies have verified these predictions, typically by manipulating food abundance or intruder pressure (for a review, see Grant 1997; Adams 2001). However, other factors affecting the benefits or costs of territorial defence, such as predation hazard, may alter this trade-off and influence the optimal size of a territory.

Territorial aggression may increase the conspicuousness of the defender to local predators, resulting in an increased cost associated with holding a territory (Lima & Dill 1990). For example, common mergansers (*Mergus merganser*) are more likely to attack moving rather than stationary coho salmon (*Oncorhynchus kisutch*; Martel & Dill 1995), whereas cutthroat trout (*Salmo clarki*) attack territorial threespine stickleback models (*Gasterosteus aculeatus*) rather than non-territorial ones (Moodie 1972). Likewise, animals engaged in aggressive interactions may be less vigilant and allow potential predators to approach closer than non-aggressive conspecifics (Jakobsson et al. 1995; Brick 1998; Díaz-Uriarte 1999; Dukas 2002). Thus, animals under increased predation risk are predicted to decrease their rate of aggression (Martel & Dill 1993) and territory size to compensate for the increased cost (Schoener 1983; Dubois & Giraldeau 2005). Similarly, animals engaged in foraging may also increase their conspicuousness and decrease their vigilance, leading to increased predation risk (Godin & Smith 1988; Brown & Kotler 2004). Animals defending a feeding territory are therefore also predicted to decrease their foraging rate in response to an elevated risk of predation (Helfman 1989; Lima & Dill 1990). Because of the difficulty of manipulating predation risk, there have been few direct tests of this hypothesis under natural conditions.

Stream-dwelling salmonids have been a popular model system for investigating territoriality because they defend feeding territories both in the lab (Slaney & Northcote 1974; Keeley 2000) and the field (Elliott 1990; Steingrímsson & Grant 2008). The territory size of salmonids is inversely related to habitat visibility (Imre et al. 2002; Venter et al. 2008), food abundance (Slaney & Northcote 1974), density of fish (Keeley 2000), and dominance rank (Harwood et al. 2003; Höjesjö et al. 2007) and is directly related to body size (Elliott 1990). Young-of-the-year (YOY) Atlantic salmon (*Salmo salar*) typically defend multiple, central-place territories that are much larger than the territories of similar sized stream-dwelling salmonids (Steingrímsson & Grant 2008). Central-place territories contain a single foraging station from which the individual initiates all foraging and aggressive behaviour (Getty 1981; Ford 1983), whereas in multiple central-place territories fish move between many foraging stations within a larger territory to initiate foraging and aggressive behaviour (Covich 1976; Chapman et al. 1989; Steingrímsson and Grant 2008). Because they move frequently between many foraging stations, multiple, central-place, foraging salmon may be more conspicuous and exposed to greater predation risk than salmon with a single central-place territory. When exposed to an acute increase in predation risk under laboratory conditions, juvenile Atlantic salmon reduce their foraging rate or spend more time in refuges (Metcalfe et al. 1987; Blanchet et al. 2007). Under natural conditions, juvenile salmonids exhibit antipredator behaviour in response to chemical cues indicating the presence or activity of predators (Leduc et al. 2006; Blanchet et al. 2007; Kim et al. 2009). However, relatively little is known about how short- and long-term increases in predation pressure influence the territorial behaviour of juvenile Atlantic salmon under natural conditions.

In this study, we examined the potential effects of both acute and chronic increases in perceived predation risk on the territorial behaviour of juvenile Atlantic salmon in the wild. Specifically, we tested the predictions that in response to both an acute and chronic increase in perceived predation risk juvenile salmon will decrease their (1) territory size, (2) foraging rate, and (3) number of switches between foraging stations.

METHODS

Study Site

We conducted observations in the lower reach of Catamaran Brook, New Brunswick, Canada (46°52’42”N, 66°06’00”W) from 12 to 20 July and 14 to 18 August, 2006, for experiment 1 and 21 June to 25 July, 2007, and 23 June to 16 July, 2008, for experiment 2. Catamaran Brook is a nursery stream for a naturally reproducing population of anadromous Atlantic salmon (Cunjak et al. 1990).

Collection of Alarm Cue

We obtained hatchery-reared Atlantic salmon parr (1+) from the Rocky Brook population of the Miramichi watershed (fork length, X ± SD, 2006, 8.57 ± 0.74 cm, *N* = 199; 2007, 10.64 ± 0.72 cm, *N* = 163; 2008, 9.55 ± 0.89 cm, *N* = 141) from the Miramichi Salmon Conservation Centre, South Esk, New Brunswick for use as skin donors. Fork length is the distance from the snout (upper lip) of the focal fish to the tip of medial caudal fin ray (‘fork’ of caudal fin). To collect alarm cue, we killed skin donors with a single blow to the head in accordance with Concordia University Animal Care Committee Protocol AC-2005-BROW. We removed skin fillets from both sides and immediately placed them into an ice-chilled container filled with stream water. We homogenized the skin fillets and diluted them with stream water. The resulting concentration (0.09 $cm^2 \cdot ml^{-1}$) of cue elicits a consistent anti-predator response in juvenile Atlantic salmon in Catamaran Brook under natural conditions (Leduc et al. 2007; Kim et al. 2009). We froze the alarm cue at -20°C until needed in 20 and 50 ml aliquots for experiment 1 and 2, respectively, whereas stream water was obtained at the site. We thawed the frozen solutions 60 min prior to use. For this study, we used 30 20-ml aliquots of alarm cue for experiment 1, and 609 and 420 50-ml aliquots of alarm cue in 2007 and 2008 respectively, for experiment 2, sufficient for 29 and 20 days of the experiment; the remainder of the alarm cue was used in other ongoing studies.

Behavioural Observations

To conduct an observation, a snorkeler approached from downstream, randomly selected a YOY Atlantic salmon (hereafter, a focal fish), typically found in sites of relatively shallow depth (< 50 cm) and slow current (range: 0.2 – 0.5 $m \cdot s^{-1}$) (Girard et al. 2004), and waited 5 min before recording behaviour to ensure that the focal fish was foraging normally (Leduc et al. 2006; Steingrímsson & Grant 2008). The observer was approximately 1.5 m downstream of the focal fish, to ensure a clear view and to minimize interference with drifting items and the stream current. Prior to the onset of observation, we sketched a map of the local streambed on a water resistant Mylar sheet. During the observation, we mapped each foraging station (defined as any location where the fish maintained position for at least 5 s), recorded all switches between foraging stations and the direction (1-12 o'clock, with 12 o'clock as directly upstream) and distance (in body lengths) of all foraging attempts and aggressive acts as well as the station from which they were initiated (Steingrímsson & Grant 2008). A foraging attempt is defined as a movement of at least half a body length towards a drifting particle or a particle on the substratum (Leduc et al. 2007; Kim et al. 2009). YOY Atlantic salmon in Catamaran Brook feed opportunistically on all major types of invertebrates in the drift (e.g. chironomid larvae, dipteran pupae and adults, ephemeropteran larvae, and trichopteran larvae) (Keeley & Grant 1997). We estimated the population density by counting all the visible fish in a 3 m X 3 m quadrat surrounding the focal fish.

After each observation, we placed a numbered steel washer at the location of each foraging station and measured the x and y coordinates (± 5 mm) of each foraging station of a focal fish in relation to a reference point selected at random in each site using a meter stick and measuring tape. We used these data to create a digital map using ArcView GIS 3.2 with the Animal Movement extension (Hooge & Eichenlaub 2000). To estimate territory size, we calculated the minimum convex polygon (Schoener 1981) that included 100% of all events (foraging stations, foraging attempts, and aggressive acts).

Experiment 1: Acute Increase in Predation Risk

To examine the effects of an acute increase in perceived predation risk, we quantified the territorial behaviour (territory size, foraging rate, and the number of switches between foraging stations) of 18 YOY Atlantic salmon that were exposed first to stream water and then to a chemical alarm cue; 10 were observed from 12 to 20 July and eight from 14 to 18 August, 2006. The observer (J.L.A.W) conducted each observation via snorkelling between 1200 and 1900h for 45 min, consisting of three 15-min observation periods (baseline, post stream water, and post alarm cue) using the protocol described above. During 15-min observation periods, a focal fish typically revisited each of its foraging stations more than once. After the 15 min-baseline observation, a second snorkeler (J.-W.K) moved in slowly from upstream to release 20 ml of stream water from a syringe in the middle of the water column approximately 1 m upstream of the focal fish. After the release of the stream water, the post-stream-water observation continued for 15 min. At the end of post-stream-water observation, 20 ml of alarm cue was released as described above, followed by the post-alarm-cue observation for another 15 min. We acknowledge that exposing the fish first to stream water and then to the alarm cue, rather than the alarm cue first and then the stream water, opens the possibility that the treatment effects could result from consecutive disturbances of the fish. We opted to present the stream water first and then the alarm cue to ensure we could measure accurately territorial behaviour without any lingering effects of alarm cue in either the water or on the behaviour of the fish. Though not optimal, this experimental design, which was part of a larger study of the territorial behaviour of unmanipulated fish, should have been powerful enough to detect any strong effects of alarm cue on fish behaviour (e.g. Chivers et al. 1995; Brown et al. 2006).

Statistical Analyses

We used repeated measures ANOVAs to detect changes in three dependent variables: territory size, foraging rate, and the number of switches between foraging stations over the three observation periods: baseline, post-stream-water, and post-alarm cue. Because the data were not completely spherical, we used the Hyunh-Feldt correction for the number of switches between foraging stations (Quinn & Keough 2002), and the adjusted degrees of freedom when calculating and reporting p-values, as recommended by SPSS. However, unadjusted df are reported in the text, to avoid confusing the reader.

Experiment 2: Chronic Increase in Predation Risk

We selected seven 75 m^2 sites of relatively shallow depth (< 50 cm) and slow current (range: 0.2 – 0.5 $m \cdot s^{-1}$), which are the preferred habitats for YOY Atlantic salmon in Catamaran Brook (Girard et al. 2004). To examine the effects of a chronic increase in perceived predation risk, we manipulated the risk in each 25 m^2 section of a site by releasing either the alarm cue or stream water twice a day for 29 and 20 days in 2007 and 2008, respectively (Fig. 1). To ensure that chemical alarm cues from the risky section had no effect on the control section, we always assigned the control to the upstream quadrat of the site (Fig. 1). Furthermore, we added a buffer section between the control and risky sections so that fish emigrating from the risky section in an upstream direction could settle in habitat other than the control section during settlement (Fig. 1). Because there were no barriers or enclosures, each site was also exposed to the ambient risk of predation from potential predators, such as common merganser, belted kingfisher (*Megaceryle alcyon*), brook charr (*Salvelinus fontinalis*), and Atlantic salmon parr (Scott & Crossman 1973; Dolinsek et al. 2007). To minimize the potential cumulative effects of chemical alarm cues dispersing from upstream to downstream (Dionne & Dodson 2002; Kim et al. 2009), sites were at least 30 m (range: 30 - 93 m) apart.

To coincide with the peak activity of YOY Atlantic salmon (Breau et al. 2007), we released the chemical stimuli (alarm cue or stream water) at 1100 h (1030-1130) and 1700 h (1630-1730) for a total volume of 150 ml per section per day. Studies simulating a single predation event typically use about 20 ml from 1.8 cm^2 of skin (Leduc et al. 2006; Kim et al. 2009), roughly equivalent to the size of a wound left by a predator (Smith & Lemly 1986). Hence, the release of 150 ml per section per day would be equivalent to about eight predation events, or the skin of one parr, being released in the 25 m^2 section per day. We used a 60-ml syringe to release the chemical stimuli continuously within 20 cm of the substrate, while slowly walking across the site. To minimize the potential disturbance when releasing the stimulus (alarm cue or stream water), we walked across the stream upstream of the control section to release stream water and across the buffer section to release the alarm cue in risky sections. Furthermore, YOY Atlantic salmon do not seem to react to overhead movements, including a person walking slowly in the stream (J.-W. Kim, personal observation).

To ensure that sections within a site were similar in habitat characteristics, we measured the depth and current velocity at 40% of the water column depth, using a

Marsh-McBirney meter (Model 201D, Fredericton, MD, U.S.A.) five times along a transect across each section. The depth (X ± SD = 41.35 ± 13.36 cm) and current velocity (0.25 ± 0.10 m · s^{-1}), the two key variables used in habitat selection (Girard et al. 2004), did not differ significantly among treatments or years (*P*-values all > 0.11).

We quantified the territorial behaviour (territory size, foraging rate, and the number of switches between foraging stations) of 32 YOY from 12 to 25 July, 2007 and eight YOY from 15 to 16 July, 2008. To ensure that fish in the alarm cue sections experienced the increased perceived risk of predation for as long as possible, we began the observations after 16 and 19 days of treatment in 2007 and 2008, respectively. We observed 16 focal fish in each of the risky (alarm cue) and control (stream water) sections in 2007. Because of extremely low densities in 2008, we observed only four fish in the risky treatment and one in the control treatment. However, we also observed three fish in the buffer section (no alarm cue) and used them as “control fish” under these extraordinary circumstances.

We observed each focal fish for 30 min via snorkelling between 1200 and 1900h using the experimental protocol described above. We conducted all observations at least one hour before or after the release of the chemical stimuli at 1100 and 1700, respectively. We also observed at least two fish per section, always starting from downstream to upstream to minimize the potential disturbance to the subsequent focal fish. To avoid observing the same fish twice, we completed all observations within a given section without leaving the site. To minimize the variation in environmental variables, we completed observations for each site within one or two consecutive days. At the end of each observation, we captured the focal fish using dipnets and measured their fork length (± 1 mm). Because YOY salmon typically defend a territory of about 1 m^2 (Steingrímsson & Grant 2008) and move less than 5 m during their growing season (Steingrímsson & Grant 2003), it is likely that the focal fish we observed experienced the experimental treatments for most, if not all of the experimental period.

Statistical Analyses

We used the behaviour of individual fish as a datum in the analyses (i.e. N = 16 control and 16 alarm cue in 2007, and 4 control and 4 alarm cue in 2008). We examined the main effects of treatment (control and buffer versus alarm cue) and years (2007 and 2008) using two-way ANOVAs on four dependent variables: territory size, foraging rate, the number of switches between foraging stations, and fork length. We reported only significant interactions between the effects of treatments and years. Because territory size was heteroscedastic, particularly between years, to meet the assumptions of parametric tests, we $\log_{10}$ (x+1) transformed territory size. For visual purposes, territory size data are presented in box plots.

RESULTS

Acute Increase in Predation Risk

While territory size (ANOVAR: $F_{2, 34} = 1.53$, $P = 0.23$; Fig. 2a) and foraging rate (ANOVAR: $F_{2, 34} = 0.04$, $P = 0.96$; Fig. 2b) did not differ significantly among the three observation periods, the number of switches between foraging stations differed significantly among the three observation periods (ANOVAR: $F_{2, 34} = 5.37$, $P = 0.018$; Fig. 2c). Switch rate increased from the baseline to the post-stream water period and then decreased during the post-alarm cue period, as indicated by a significant quadratic contrast across the three observation periods (quadratic contrast: $F_{1, 17} = 9.78$, $P = 0.006$). On average, each fish spent 132, 145, and 155 sec at each foraging station during the baseline, post-stream water, and post-alarm cue periods, respectively. To examine changes in switch rate at a finer temporal scale, we analyzed the data for each of nine 5-min intervals in the 45 min observation periods. We also compared changes in response between baseline and the addition of stream water and post stream water and the addition of alarm cue using paired t-tests. Switch rate differed significantly among the nine observation periods (ANOVAR: $F_{8, 120} = 2.66$, $P = 0.025$), but did not change after the addition of stream water (paired *t* test: $t_{15} = 0.29$, $P = 0.78$; Fig. 3). However, switch rate increased over the first six 5-min intervals (linear contrast: $F_{1, 15} = 5.38$, $P = 0.035$), and then decreased significantly after the addition of alarm cue for 15 min (paired *t* test: $t_{17} = 2.86$, $P = 0.011$; Fig. 3).

Chronic Increase in Predation Risk

As predicted, territories of YOY salmon in risky habitats were significantly smaller than those in control habitats (two-way ANOVA: $F_{1, 36} = 6.07$, $P = 0.019$; Fig. 4). In addition, territories were larger in 2008 than in 2007 (two-way ANOVA: $F_{1, 36} = 5.16$, $P = 0.029$; Fig. 4), probably because the local density was lower in 2008 (0.19 fish · m^{-2}) than in 2007 (0.53 fish · m^{-2}) (two-way ANOVA: $F_{1, 36} = 14.21$, $P = 0.001$).

Contrary to the prediction, however, foraging rate (X ± SE, control, 2.94 ± 0.24; risky, 3.48 ± 0.23 · min^{-1}; two-way ANOVA: $F_{1, 36} = 0.39$, $P = 0.54$) and the number of switches between foraging stations (control, 45.80 ± 6.79; risky, 36.25 ± 5.46; two-way ANOVA: $F_{1, 36} = 0.92$, $P = 0.35$) did not differ significantly between treatments. In addition, the body length of focal fish did not differ significantly between treatments (control, 3.94 ± 0.07; risky, 3.97 ± 0.08 cm; two-way ANOVA: $F_{1,}$

$_{36}$ = 1.26, P = 0.27).

DISCUSSION

Acute Increase in Predation Risk

Our results suggest that juvenile Atlantic salmon responded to the detection of a single dose of alarm cue by decreasing their switch rate between foraging stations. Salmon may switch foraging stations to increase their encounter rate with benthic prey or as a means of defending their large, multiple-central place territories (Steingrímsson & Grant 2008). Hence, decreasing switching between foraging stations, even for 15 minutes may represent a trade-off between predator avoidance and efficiency of foraging or defence (Lima & Dill 1990; Brown 2003).

Interestingly, juvenile salmon did not decrease their territory size or foraging rate after detecting a single dose of alarm cue. Our data suggest that a single stimulus from somewhere upstream is not sufficiently threatening to cause territory owners to alter their foraging rate or territory size in the short term. After the exhaustion of the yolk sac, a feeding territory is important for the growth and survival of juvenile salmon during this early critical period in which salmonid populations are subject to density-dependent mortality and self-thinning (Martel 1996; Steingrímsson & Grant 1999;

Armstrong & Nislow 2006). Thus, juvenile salmon may choose to maintain their territory size even under a modest increase in predation risk (Blanchet et al. 2007).

In contrast to previous studies (Leduc et al. 2007; Kim et al. 2009), we detected no decrease in foraging rate following the exposure to an alarm cue. Juvenile salmon may forage at a greater rate when they resume feeding to offset any deficit incurred while responding to the predation threat (Talbot et al. 1984; Metcalfe et al. 1987). Switch rate tended to increase over time, perhaps because focal fish were habituating to the presence of the observer or responding to an increase in drift items dislodged by as a result of the observer (Kim et al. 2009).

Chronic Increase in Predation Risk

Unlike the effects of a single dose of alarm cue, our results demonstrate that juvenile salmon respond to a chronic increase in perceived predation risk by decreasing their territory size. This result is consistent with the predictions of optimal territory size models (Hixon 1980; Schoener 1983), if we assume that predation risk is a cost of defence. To our knowledge, this is the first demonstration of animals decreasing their territory size in response to an increase in predation risk under natural conditions.

Similar to the effects of an acute increase in predation risk, juvenile salmon did not change their foraging rate when exposed to a chronic increase in predation risk. Again, fitness-enhancing behaviour such as foraging may be less affected by an increase in perceived predation risk where the benefits from foraging may be at least as important as that of directly avoiding predators, at least for small fish (Martel 1996; Lind & Cresswell 2005; Blanchet et al. 2007). Even though YOY salmon responded to a chronic increase in predation risk by reducing the size of the defended area, they did not change their activity on the territory. Because foraging data were recorded when the risk was relatively low (i.e. during ‘safe’ periods between the daily releases of alarm cue), an alternative explanation may be that juvenile salmon in risky habitats increased their foraging efforts during safe periods to compensate for the lower foraging rate during times of elevated risk. Such an explanation is consistent with the risk allocation hypothesis where an animal is expected to allocate more antipredator effort during high-risk situations and more feeding effort during low-risk situations (Lima & Bednekoff 1999; Bell et al. 2009; Ferrari et al. 2009). Furthermore, there was no difference in size of the fish between treatments, suggesting that juvenile salmon in risky habitats compensated for the reduced size of their territories, perhaps by foraging at greater intensity during safe periods.

Interestingly, juvenile salmon also had larger territories in 2007 than in 2008.

While the sample size for 2008 was small compared to 2007, the differences in territory size between years may be because the local population density was 2.6 times higher in 2007 than in 2008. This finding is also consistent with other studies showing that territories of juvenile salmonid are density-dependent (Keeley 2000; Imre et al. 2004; Venter et al. 2008).

Acute vs. Chronic Increases in Predation Risk

How prey perceive and integrate predation risk over multiple time scales is amongst the more important unanswered questions in the field of predator-prey dynamics (Lima & Steury 2005). In our study, juvenile Atlantic salmon responded to both acute and chronic increases in perceived predation risk under natural conditions, but the type and the degree of the antipredator responses differed between the two time scales. While we acknowledge that a direct comparison between acute and chronic effects of predation risk would be ideal, the results of our study suggest that both immediate and long-term events can influence individual behavioural decisions (Brown et al. 2009) and that prey continually adjust their behavioural responses according to immediate or longer-term patterns of predation risk (Biro et al. 2007; Brown et al. 2009; Valeix et al. 2009). While the reduction in territory size may influence population density and self-thinning of salmon populations (Grant et al. 1998; Armstrong & Nislow 2006), how these short- and long-term behavioural patterns translate into future fitness such as growth rate (Martel 1996) or survival (Mirza & Chivers 2003; Lind & Cresswell 2005) remain to be tested. Moreover, how these behavioural decisions influence population and/or community dynamics (Werner & Peacor 2003; Blanchet et al. 2008; Valeix et al. 2009) should be addressed in future studies.

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Figure legends

Figure 1. Experimental design in one of seven stream sites during the settlement of young-of-the-year (YOY) Atlantic salmon where a risky section received conspecific alarm cues, a control section received stream water, and, a buffer received nothing.

Figure 2. Mean ± SE (*N* = 18) (a) territory size, (b) foraging rate, and (c) number of switches between foraging stations of YOY Atlantic salmon during three observation periods: baseline, post-stream water, and post-alarm cue.

Figure 3. Mean ± SE (*N* = 18) number of switches between foraging stations of YOY Atlantic salmon during nine 5-min observation periods.

Figure 4. Box plot showing variation in territory size of YOY Atlantic salmon after 16 and 19 days of treatments in 2007 (*N* = 16 each in control and risky) and 2008 (*N* = 4 each in control and risky), respectively. Medians (horizontal line within the box), quartiles (top and bottom of box), and the 0.05 and 0.95 quantiles (lines extending from the top and bottom of each box) are shown.

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Figure 1

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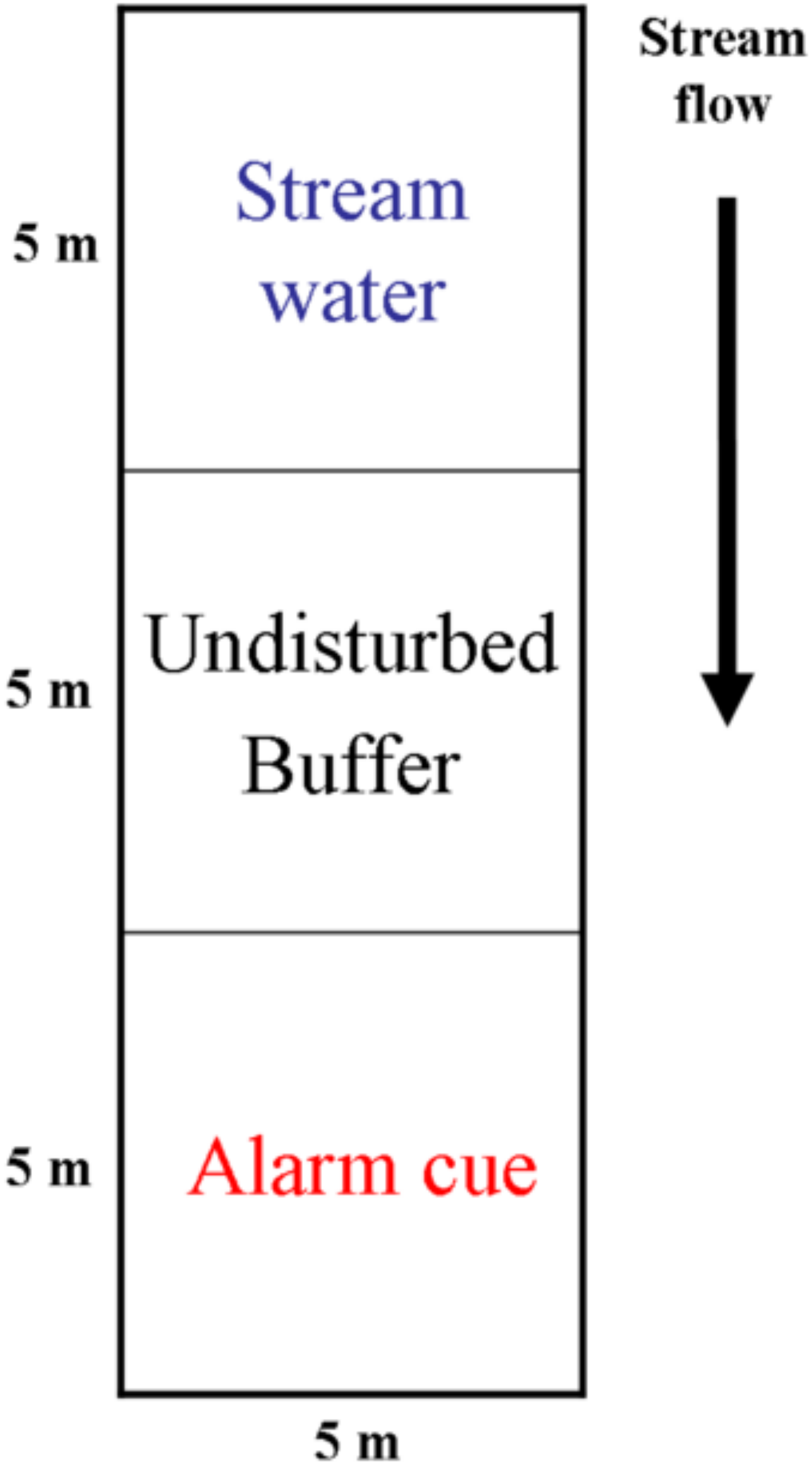
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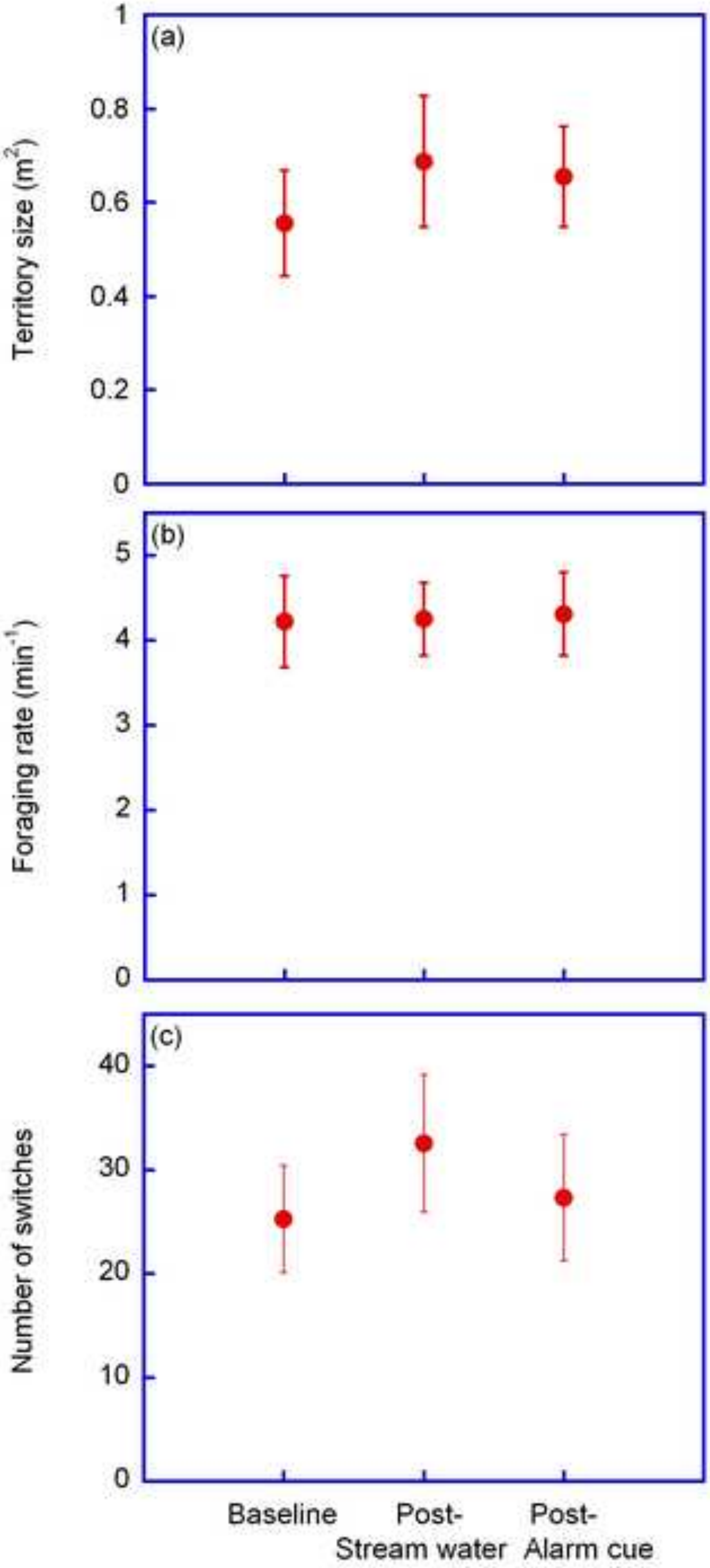

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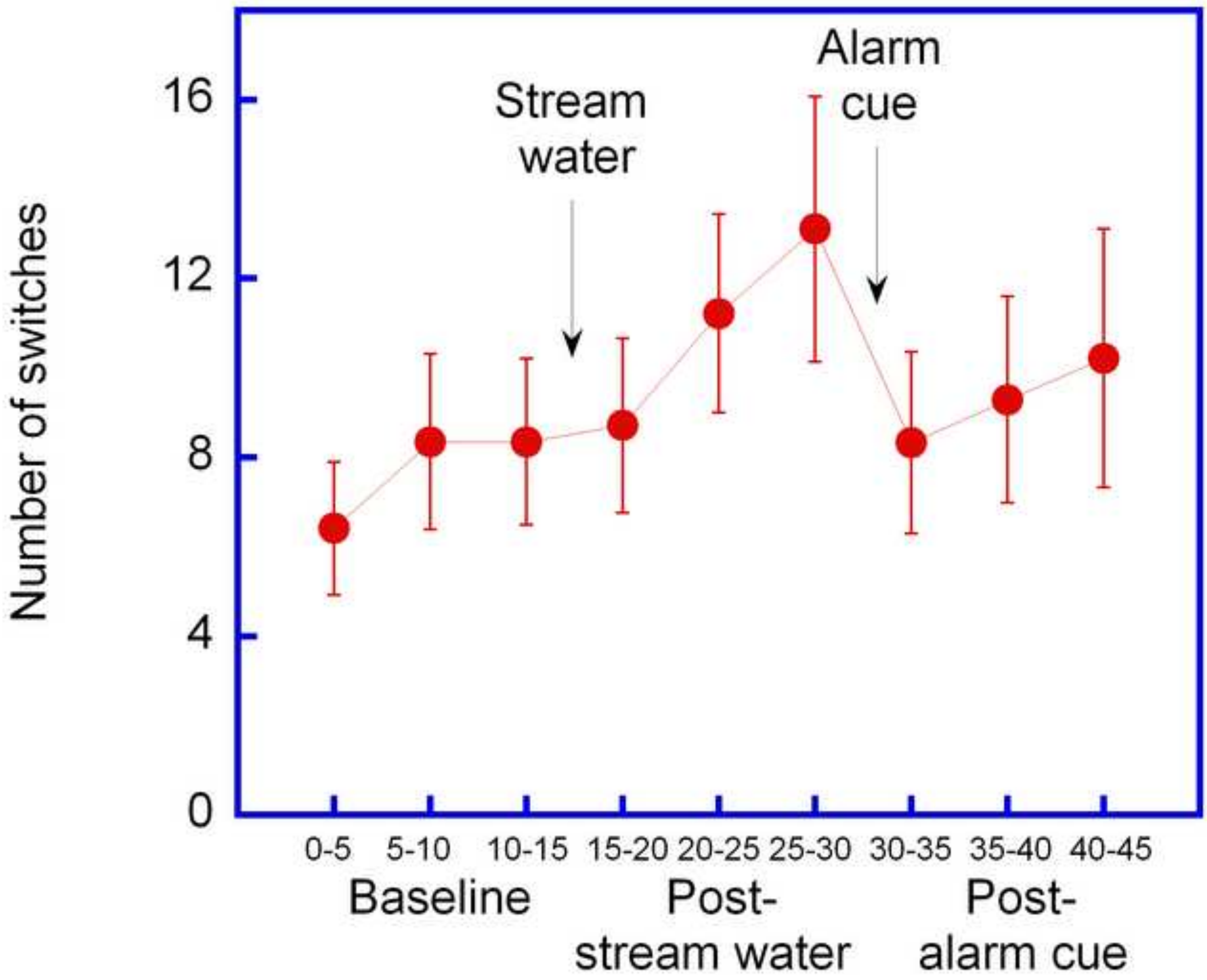
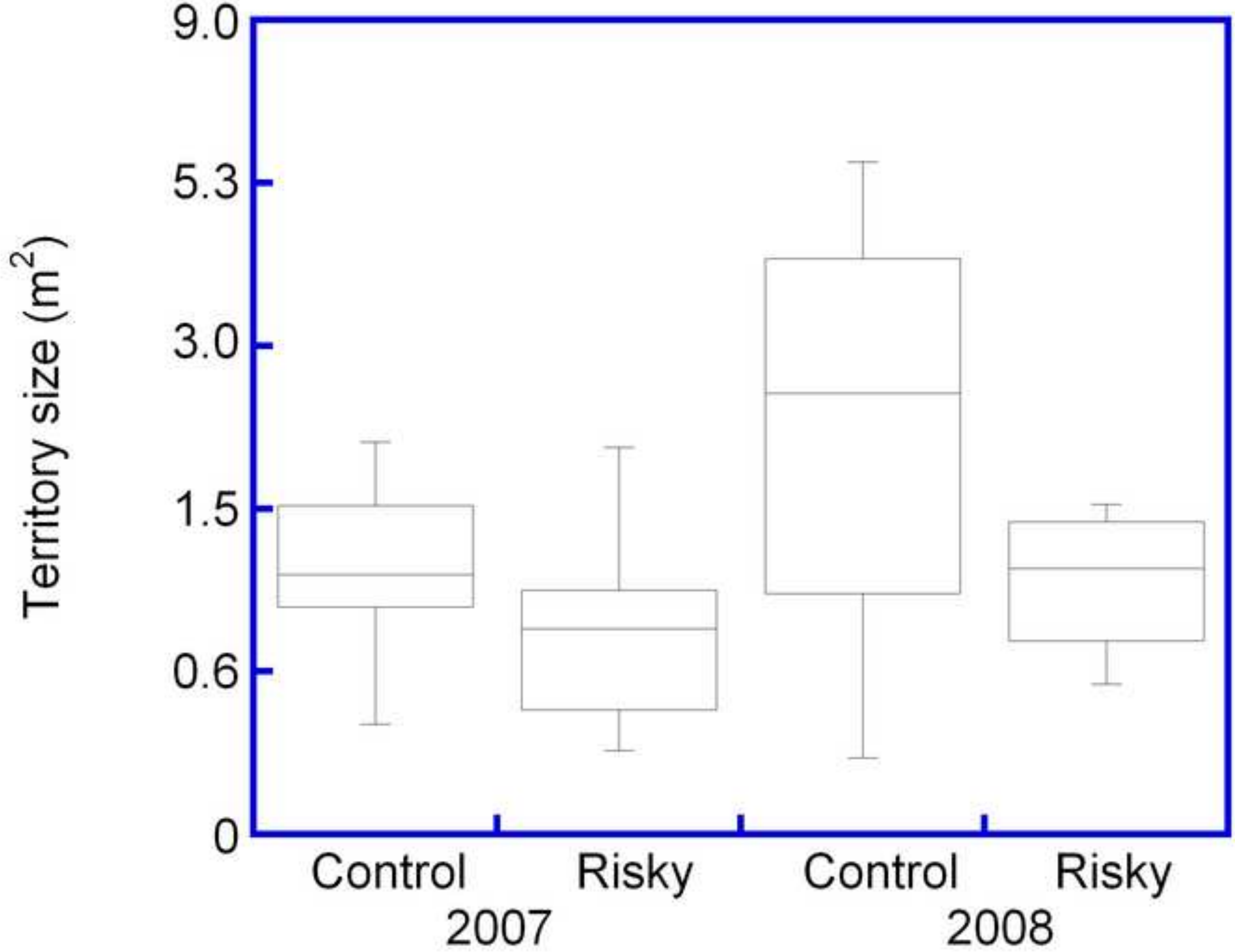


Figure 4

Click here to download high resolution image