

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

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

19 predictions of optimality models that territory size decreases with increasing predation

20 risk.

21

22 **Keywords:** Damage-released chemical alarm cue, Space use, Population regulation,

23 Threat-sensitive trade-off, Temporal scale, Territory size, Home range, Optimality,

24 Young-of-the-year, *Salmo salar*

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

43 Territorial aggression may increase the conspicuousness of the defender to local  
44 predators, resulting in an increased cost associated with holding a territory (Lima & Dill  
45 1990). For example, common mergansers (*Mergus merganser*) are more likely to attack  
46 moving rather than stationary coho salmon (*Oncorhynchus kisutch*; Martel & Dill 1995),  
47 whereas cutthroat trout (*Salmo clarki*) attack territorial threespine stickleback models  
48 (*Gasterosteus aculeatus*) rather than non-territorial ones (Moodie 1972). Likewise,  
49 animals engaged in aggressive interactions may be less vigilant and allow potential  
50 predators to approach closer than non-aggressive conspecifics (Jakobsson et al. 1995;  
51 Brick 1998; Díaz-Uriarte 1999; Dukas 2002). Thus, animals under increased predation  
52 risk are predicted to decrease their rate of aggression (Martel & Dill 1993) and territory  
53 size to compensate for the increased cost (Schoener 1983; Dubois & Giraldeau 2005).  
54 Similarly, animals engaged in foraging may also increase their conspicuousness and

55 decrease their vigilance, leading to increased predation risk (Godin & Smith 1988;  
56 Brown & Kotler 2004). Animals defending a feeding territory are therefore also  
57 predicted to decrease their foraging rate in response to an elevated risk of predation  
58 (Helfman 1989; Lima & Dill 1990). Because of the difficulty of manipulating predation  
59 risk, there have been few direct tests of this hypothesis under natural conditions.

60 Stream-dwelling salmonids have been a popular model system for  
61 investigating territoriality because they defend feeding territories both in the lab  
62 (Slaney & Northcote 1974; Keeley 2000) and the field (Elliott 1990; Steingrímsson &  
63 Grant 2008). The territory size of salmonids is inversely related to habitat visibility  
64 (Imre et al. 2002; Venter et al. 2008), food abundance (Slaney & Northcote 1974),  
65 density of fish (Keeley 2000), and dominance rank (Harwood et al. 2003; Höjesjö et al.  
66 2007) and is directly related to body size (Elliott 1990). Young-of-the-year (YOY)  
67 Atlantic salmon (*Salmo salar*) typically defend multiple, central-place territories that  
68 are much larger than the territories of similar sized stream-dwelling salmonids  
69 (Steingrímsson & Grant 2008). Central-place territories contain a single foraging  
70 station from which the individual initiates all foraging and aggressive behaviour (Getty  
71 1981; Ford 1983), whereas in multiple central-place territories fish move between  
72 many foraging stations within a larger territory to initiate foraging and aggressive

73 behaviour (Covich 1976; Chapman et al. 1989; Steingrímsson and Grant 2008).  
74 Because they move frequently between many foraging stations, multiple, central-place,  
75 foraging salmon may be more conspicuous and exposed to greater predation risk than  
76 salmon with a single central-place territory. When exposed to an acute increase in  
77 predation risk under laboratory conditions, juvenile Atlantic salmon reduce their  
78 foraging rate or spend more time in refuges (Metcalfé et al. 1987; Blanchet et al. 2007).  
79 Under natural conditions, juvenile salmonids exhibit antipredator behaviour in  
80 response to chemical cues indicating the presence or activity of predators (Leduc et al.  
81 2006; Blanchet et al. 2007; Kim et al. 2009). However, relatively little is known about  
82 how short- and long-term increases in predation pressure influence the territorial  
83 behaviour of juvenile Atlantic salmon under natural conditions.

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

90

91 **METHODS**

92 *Study Site*

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

98 *Collection of Alarm Cue*

99 We obtained hatchery-reared Atlantic salmon parr (1+) from the Rocky Brook  
100 population of the Miramichi watershed (fork length,  $X \pm SD$ , 2006,  $8.57 \pm 0.74$  cm,  $N$   
101  $= 199$ ; 2007,  $10.64 \pm 0.72$  cm,  $N = 163$ ; 2008,  $9.55 \pm 0.89$  cm,  $N = 141$ ) from the  
102 Miramichi Salmon Conservation Centre, South Esk, New Brunswick for use as skin  
103 donors. Fork length is the distance from the snout (upper lip) of the focal fish to the tip  
104 of medial caudal fin ray ('fork' of caudal fin). To collect alarm cue, we killed skin  
105 donors with a single blow to the head in accordance with Concordia University Animal  
106 Care Committee Protocol AC-2005-BROW. We removed skin fillets from both sides  
107 and immediately placed them into an ice-chilled container filled with stream water. We  
108 homogenized the skin fillets and diluted them with stream water. The resulting

109 concentration ( $0.09 \text{ cm}^2 \cdot \text{ml}^{-1}$ ) of cue elicits a consistent anti-predator response in  
110 juvenile Atlantic salmon in Catamaran Brook under natural conditions (Leduc et al.  
111 2007; Kim et al. 2009). We froze the alarm cue at  $-20^\circ\text{C}$  until needed in 20 and 50 ml  
112 aliquots for experiment 1 and 2, respectively, whereas stream water was obtained at the  
113 site. We thawed the frozen solutions 60 min prior to use. For this study, we used 30 20-  
114 ml aliquots of alarm cue for experiment 1, and 609 and 420 50-ml aliquots of alarm  
115 cue in 2007 and 2008 respectively, for experiment 2, sufficient for 29 and 20 days of  
116 the experiment; the remainder of the alarm cue was used in other ongoing studies.

#### 117 *Behavioural Observations*

118 To conduct an observation, a snorkeler approached from downstream,  
119 randomly selected a YOY Atlantic salmon (hereafter, a focal fish), typically found in  
120 sites of relatively shallow depth ( $< 50 \text{ cm}$ ) and slow current (range:  $0.2 - 0.5 \text{ m} \cdot \text{s}^{-1}$ )  
121 (Girard et al. 2004), and waited 5 min before recording behaviour to ensure that the  
122 focal fish was foraging normally (Leduc et al. 2006; Steingrímsson & Grant 2008). The  
123 observer was approximately 1.5 m downstream of the focal fish, to ensure a clear view  
124 and to minimize interference with drifting items and the stream current. Prior to the  
125 onset of observation, we sketched a map of the local streambed on a water resistant  
126 Mylar sheet. During the observation, we mapped each foraging station (defined as any



127 location where the fish maintained position for at least 5 s), recorded all switches  
128 between foraging stations and the direction (1-12 o'clock, with 12 o'clock as directly  
129 upstream) and distance (in body lengths) of all foraging attempts and aggressive acts as  
130 well as the station from which they were initiated (Steingrímsson & Grant 2008). A  
131 foraging attempt is defined as a movement of at least half a body length towards a  
132 drifting particle or a particle on the substratum (Leduc et al. 2007; Kim et al. 2009).  
133 YOY Atlantic salmon in Catamaran Brook feed opportunistically on all major types of  
134 invertebrates in the drift (e.g. chironomid larvae, dipteran pupae and adults,  
135 ephemeropteran larvae, and trichopteran larvae) (Keeley & Grant 1997). We estimated  
136 the population density by counting all the visible fish in a 3 m X 3 m quadrat  
137 surrounding the focal fish.

138         After each observation, we placed a numbered steel washer at the location of  
139 each foraging station and measured the x and y coordinates ( $\pm 5$  mm) of each foraging  
140 station of a focal fish in relation to a reference point selected at random in each site  
141 using a meter stick and measuring tape. We used these data to create a digital map  
142 using ArcView GIS 3.2 with the Animal Movement extension (Hooge & Eichenlaub  
143 2000). To estimate territory size, we calculated the minimum convex polygon  
144 (Schoener 1981) that included 100% of all events (foraging stations, foraging attempts,

145 and aggressive acts).

146

### 147 **Experiment 1: Acute Increase in Predation Risk**

148 To examine the effects of an acute increase in perceived predation risk, we  
149 quantified the territorial behaviour (territory size, foraging rate, and the number of  
150 switches between foraging stations) of 18 YOY Atlantic salmon that were exposed first  
151 to stream water and then to a chemical alarm cue; 10 were observed from 12 to 20 July  
152 and eight from 14 to 18 August, 2006. The observer (J.L.A.W) conducted each  
153 observation via snorkelling between 1200 and 1900h for 45 min, consisting of three  
154 15-min observation periods (baseline, post stream water, and post alarm cue) using the  
155 protocol described above. During 15-min observation periods, a focal fish typically  
156 revisited each of its foraging stations more than once. After the 15 min-baseline  
157 observation, a second snorkeler (J.-W.K) moved in slowly from upstream to release 20  
158 ml of stream water from a syringe in the middle of the water column approximately 1  
159 m upstream of the focal fish. After the release of the stream water, the post-stream-  
160 water observation continued for 15 min. At the end of post-stream-water observation,  
161 20 ml of alarm cue was released as described above, followed by the post-alarm-cue  
162 observation for another 15 min. We acknowledge that exposing the fish first to stream

163 water and then to the alarm cue, rather than the alarm cue first and then the stream  
164 water, opens the possibility that the treatment effects could result from consecutive  
165 disturbances of the fish. We opted to present the stream water first and then the alarm  
166 cue to ensure we could measure accurately territorial behaviour without any lingering  
167 effects of alarm cue in either the water or on the behaviour of the fish. Though not  
168 optimal, this experimental design, which was part of a larger study of the territorial  
169 behaviour of unmanipulated fish, should have been powerful enough to detect any  
170 strong effects of alarm cue on fish behaviour (e.g. Chivers et al. 1995; Brown et al.  
171 2006).

172

### 173 *Statistical Analyses*

174 We used repeated measures ANOVAs to detect changes in three dependent  
175 variables: territory size, foraging rate, and the number of switches between foraging  
176 stations over the three observation periods: baseline, post-stream-water, and post-alarm  
177 cue. Because the data were not completely spherical, we used the Hyunh-Feldt  
178 correction for the number of switches between foraging stations (Quinn & Keough  
179 2002), and the adjusted degrees of freedom when calculating and reporting p-values, as  
180 recommended by SPSS. However, unadjusted df are reported in the text, to avoid

181 confusing the reader.

182

### 183 **Experiment 2: Chronic Increase in Predation Risk**

184 We selected seven 75 m<sup>2</sup> sites of relatively shallow depth (< 50 cm) and slow  
185 current (range: 0.2 – 0.5 m · s<sup>-1</sup>), which are the preferred habitats for YOY Atlantic  
186 salmon in Catamaran Brook (Girard et al. 2004). To examine the effects of a chronic  
187 increase in perceived predation risk, we manipulated the risk in each 25 m<sup>2</sup> section of a  
188 site by releasing either the alarm cue or stream water twice a day for 29 and 20 days in  
189 2007 and 2008, respectively (Fig. 1). To ensure that chemical alarm cues from the risky  
190 section had no effect on the control section, we always assigned the control to the  
191 upstream quadrat of the site (Fig. 1). Furthermore, we added a buffer section between  
192 the control and risky sections so that fish emigrating from the risky section in an  
193 upstream direction could settle in habitat other than the control section during  
194 settlement (Fig. 1). Because there were no barriers or enclosures, each site was also  
195 exposed to the ambient risk of predation from potential predators, such as common  
196 merganser, belted kingfisher (*Megaceryle alcyon*), brook charr (*Salvelinus fontinalis*),  
197 and Atlantic salmon parr (Scott & Crossman 1973; Dolinsek et al. 2007). To minimize  
198 the potential cumulative effects of chemical alarm cues dispersing from upstream to

199 downstream (Dionne & Dodson 2002; Kim et al. 2009), sites were at least 30 m  
200 (range: 30 - 93 m) apart.

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

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

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

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

231 We observed each focal fish for 30 min via snorkelling between 1200 and  
232 1900h using the experimental protocol described above. We conducted all observations  
233 at least one hour before or after the release of the chemical stimuli at 1100 and 1700,  
234 respectively. We also observed at least two fish per section, always starting from

235 downstream to upstream to minimize the potential disturbance to the subsequent focal  
236 fish. To avoid observing the same fish twice, we completed all observations within a  
237 given section without leaving the site. To minimize the variation in environmental  
238 variables, we completed observations for each site within one or two consecutive days.  
239 At the end of each observation, we captured the focal fish using dipnets and measured  
240 their fork length ( $\pm 1$  mm). Because YOY salmon typically defend a territory of about  
241  $1 \text{ m}^2$  (Steingrímsson & Grant 2008) and move less than 5 m during their growing  
242 season (Steingrímsson & Grant 2003), it is likely that the focal fish we observed  
243 experienced the experimental treatments for most, if not all of the experimental period.

244

#### 245 *Statistical Analyses*

246 We used the behaviour of individual fish as a datum in the analyses (i.e.  $N =$   
247 16 control and 16 alarm cue in 2007, and 4 control and 4 alarm cue in 2008). We  
248 examined the main effects of treatment (control and buffer versus alarm cue) and years  
249 (2007 and 2008) using two-way ANOVAs on four dependent variables: territory size,  
250 foraging rate, the number of switches between foraging stations, and fork length. We  
251 reported only significant interactions between the effects of treatments and years.  
252 Because territory size was heteroscedastic, particularly between years, to meet the

253 assumptions of parametric tests, we  $\log_{10}(x+1)$  transformed territory size. For visual  
254 purposes, territory size data are presented in box plots.

255

## 256 **RESULTS**

### 257 **Acute Increase in Predation Risk**

258 While territory size (ANOVAR:  $F_{2,34} = 1.53$ ,  $P = 0.23$ ; Fig. 2a) and foraging rate  
259 (ANOVAR:  $F_{2,34} = 0.04$ ,  $P = 0.96$ ; Fig. 2b) did not differ significantly among the  
260 three observation periods, the number of switches between foraging stations differed  
261 significantly among the three observation periods (ANOVAR:  $F_{2,34} = 5.37$ ,  $P = 0.018$ ;  
262 Fig. 2c). Switch rate increased from the baseline to the post-stream water period and  
263 then decreased during the post-alarm cue period, as indicated by a significant quadratic  
264 contrast across the three observation periods (quadratic contrast:  $F_{1,17} = 9.78$ ,  $P =$   
265  $0.006$ ). On average, each fish spent 132, 145, and 155 sec at each foraging station  
266 during the baseline, post-stream water, and post-alarm cue periods, respectively. To  
267 examine changes in switch rate at a finer temporal scale, we analyzed the data for each  
268 of nine 5-min intervals in the 45 min observation periods. We also compared changes  
269 in response between baseline and the addition of stream water and post stream water  
270 and the addition of alarm cue using paired t-tests. Switch rate differed significantly



271 among the nine observation periods (ANOVAR:  $F_{8,120} = 2.66$ ,  $P = 0.025$ ), but did not  
272 change after the addition of stream water (paired  $t$  test:  $t_{15} = 0.29$ ,  $P = 0.78$ ; Fig. 3).  
273 However, switch rate increased over the first six 5-min intervals (linear contrast:  $F_{1,15}$   
274  $= 5.38$ ,  $P = 0.035$ ), and then decreased significantly after the addition of alarm cue for  
275 15 min (paired  $t$  test:  $t_{17} = 2.86$ ,  $P = 0.011$ ; Fig. 3).

276

### 277 **Chronic Increase in Predation Risk**

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

283 Contrary to the prediction, however, foraging rate ( $X \pm \text{SE}$ , control,  $2.94 \pm$   
284  $0.24$ ; risky,  $3.48 \pm 0.23 \cdot \text{min}^{-1}$ ; two-way ANOVA:  $F_{1,36} = 0.39$ ,  $P = 0.54$ ) and the  
285 number of switches between foraging stations (control,  $45.80 \pm 6.79$ ; risky,  $36.25 \pm$   
286  $5.46$ ; two-way ANOVA:  $F_{1,36} = 0.92$ ,  $P = 0.35$ ) did not differ significantly between  
287 treatments. In addition, the body length of focal fish did not differ significantly  
288 between treatments (control,  $3.94 \pm 0.07$ ; risky,  $3.97 \pm 0.08 \text{ cm}$ ; two-way ANOVA:  $F_{1,$

289  $s_{36} = 1.26, P = 0.27$ ).

290

## 291 **DISCUSSION**

### 292 **Acute Increase in Predation Risk**

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

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

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

309 In contrast to previous studies (Leduc et al. 2007; Kim et al. 2009), we  
310 detected no decrease in foraging rate following the exposure to an alarm cue. Juvenile  
311 salmon may forage at a greater rate when they resume feeding to offset any deficit  
312 incurred while responding to the predation threat (Talbot et al. 1984; Metcalfe et al.  
313 1987). Switch rate tended to increase over time, perhaps because focal fish were  
314 habituating to the presence of the observer or responding to an increase in drift items  
315 dislodged by as a result of the observer (Kim et al. 2009).

316

### 317 **Chronic Increase in Predation Risk**

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

324 Similar to the effects of an acute increase in predation risk, juvenile salmon

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

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

343 While the sample size for 2008 was small compared to 2007, the differences in  
344 territory size between years may be because the local population density was 2.6 times  
345 higher in 2007 than in 2008. This finding is also consistent with other studies showing  
346 that territories of juvenile salmonid are density-dependent (Keeley 2000; Imre et al.  
347 2004; Venter et al. 2008).

348

#### 349 **Acute vs. Chronic Increases in Predation Risk**

350 How prey perceive and integrate predation risk over multiple time scales is  
351 amongst the more important unanswered questions in the field of predator-prey  
352 dynamics (Lima & Steury 2005). In our study, juvenile Atlantic salmon responded to  
353 both acute and chronic increases in perceived predation risk under natural conditions,  
354 but the type and the degree of the antipredator responses differed between the two time  
355 scales. While we acknowledge that a direct comparison between acute and chronic  
356 effects of predation risk would be ideal, the results of our study suggest that both  
357 immediate and long-term events can influence individual behavioural decisions  
358 (Brown et al. 2009) and that prey continually adjust their behavioural responses  
359 according to immediate or longer-term patterns of predation risk (Biro et al. 2007;  
360 Brown et al. 2009; Valeix et al. 2009). While the reduction in territory size may

361 influence population density and self-thinning of salmon populations (Grant et al.  
362 1998; Armstrong & Nislow 2006), how these short- and long-term behavioural patterns  
363 translate into future fitness such as growth rate (Martel 1996) or survival (Mirza &  
364 Chivers 2003; Lind & Cresswell 2005) remain to be tested. Moreover, how these  
365 behavioural decisions influence population and/or community dynamics (Werner &  
366 Peacor 2003; Blanchet et al. 2008; Valeix et al. 2009) should be addressed in future  
367 studies.

368

## 369 **References**

- 370 **Adams, E. S.** 2001. Approaches to the study of territory size and shape. Annual  
371 Review of Ecology and Systematics, **32**, 277-303.
- 372 **Armstrong, J. D. & Nislow, K. H.** 2006. Critical habitat during the transition from  
373 maternal provisioning in freshwater fish, with emphasis on Atlantic salmon  
374 (*Salmo salar*) and brown trout (*Salmo trutta*). Journal of Zoology, **269**, 403-  
375 413.
- 376 **Bell, M. B. V., Radford, A. N., Rose, R., Wade, H. M. & Ridley, A. R.** 2009. The  
377 value of constant surveillance in a risky environment. Proceedings of the  
378 Royal Society B: Biological Sciences, **276**, 2997-3005.

- 379 **Biro, P. A., Abrahams, M. V. & Post, J. R.** 2007. Direct manipulation of behaviour  
380 reveals a mechanism for variation in growth and mortality among prey  
381 populations. *Animal Behaviour*, **73**, 891-896.
- 382 **Blanchet, S., Bernatchez, L. & Dodson, J. J.** 2007. Behavioural and growth  
383 responses of a territorial fish (Atlantic salmon, *Salmo salar*, L.) to multiple  
384 predatory cues. *Ethology*, **113**, 1061-1072.
- 385 **Blanchet, S., Loot, G. & Dodson, J. J.** 2008. Competition, predation and flow rate as  
386 mediators of direct and indirect effects in a stream food chain. *Oecologia*, **157**,  
387 93-104.
- 388 **Breau, C., Weir, L. K. & Grant, J. W. A.** 2007. Individual variability in activity  
389 patterns of juvenile Atlantic salmon (*Salmo salar*) in Catamaran Brook, New  
390 Brunswick. *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 486-494.
- 391 **Brick, O.** 1998. Fighting behaviour, vigilance and predation risk in the cichlid fish  
392 *Nannacara anomala*. *Animal Behaviour*, **56**, 309-317.
- 393 **Brown, G. E.** 2003. Learning about danger: chemical alarm cues and local risk  
394 assessment in prey fishes. *Fish and Fisheries*, **4**, 227-234.
- 395 **Brown, G. E., Macnaughton, C. J., Elvidge, C. K., Ramnarine, I. & Godin, J.-G. J.**  
396 2009. Provenance and threat-sensitive predator avoidance patterns in wild-

397 caught Trinidadian guppies. Behavioral Ecology and Sociobiology, **63**, 699-  
398 706.

399 **Brown, G. E., Rive, A. C., Ferrari, M. C. O. & Chivers, D. P.** 2006. The dynamic  
400 nature of antipredator behavior: prey fish integrate threat-sensitive  
401 antipredator responses with background levels of predation risk. Behavioral  
402 Ecology and Sociobiology, **61**, 9-16.

403 **Brown, J. S. & Kotler, B. P.** 2004. Hazardous duty pay and the foraging cost of  
404 predation. Ecology Letters, **7**, 999-1014.

405 **Chapman, C. A., Chapman, L. J. & McLaughlin, R. L.** 1989. Multiple central place  
406 foraging by spider monkeys: travel consequences of using many sleeping  
407 sites. Oecologia, **79**, 506-511.

408 **Chivers, D. P., Brown, G. E. & Smith, R. J. F.** 1995. Acquired recognition of  
409 chemical stimuli from pike, *Esox-lucius*, by brook sticklebacks, *culaea*  
410 *inconstans* (Osteichthyes, Gasterosteidae). Ethology, **99**, 234-242.

411 **Covich, A. P.** 1976. Analysing shapes of foraging areas: some ecological and  
412 economic theories. Annual Review of Ecology and Systematics, **7**, 235-257.

413 **Cunjak, R. A., Caissie, D. & El-Jabi, N.** 1990. The Catamaran Brook habitat research  
414 project: description and general design of study. Canadian Technical Report



415 of Fisheries and Aquatic Sciences, **1751**, 14 p.

416 **Díaz-Uriarte, R.** 1999. Anti-predator behaviour changes following an aggressive  
417 encounter in the lizard *Tropidurus hispidus*. Proceedings of the Royal Society  
418 B: Biological Sciences, **266**, 2457-2464.

419 **Dionne, M. & Dodson, J. J.** 2002. Impact of exposure to a simulated predator  
420 (*Mergus merganser*) on the activity of juvenile Atlantic salmon (*Salmo salar*)  
421 in a natural environment. Canadian Journal of Zoology, **80**, 2006-2013.

422 **Dolinsek, I. J., Grant, J. W. A. & Biron, P. M.** 2007. The effect of habitat  
423 heterogeneity on the population density of juvenile Atlantic salmon *Salmo*  
424 *salar* L. Journal of Fish Biology, **70**, 206-214.

425 **Dubois, F. D. & Giraldeau, L.-A.** 2005. Fighting for resources: The economics of  
426 defense and appropriation. Ecology, **86**, 3-11.

427 **Dukas, R.** 2002. Behavioural and ecological consequences of limited attention.  
428 Philosophical Transactions of the Royal Society B – Biological Sciences, **357**,  
429 1539-1547.

430 **Elliott, J. M.** 1990. Mechanisms responsible for population regulation in young  
431 migratory trout, *Salmo trutta*. III. The role of territorial behaviour. Journal of  
432 Animal Ecology, **59**, 803-818.

- 433 **Ferrari, M. C. O., Sih, A. & Chivers, D. P.** 2009. The paradox of risk allocation: a  
434 review and prospectus. *Animal Behaviour*, **78**, 579-585.
- 435 **Ford, R. G.** 1983. Home range in a patchy environment: optimal foraging predictions.  
436 *American Zoologist*, **23**, 315-326.
- 437 **Getty, T.** 1981. Analysis of central-place space-use patterns: the elastic disc revisited.  
438 *Ecology*, **62**, 907-914.
- 439 **Girard, I. L., Grant, J. W. A. & Steingrímsson, S. Ó.** 2004. Foraging, growth and  
440 loss rate of young-of-the-year Atlantic salmon (*Salmo salar*) in relation to  
441 habitat use in Catamaran Brook, New Brunswick. *Canadian Journal of*  
442 *Fisheries and Aquatic Sciences*, **61**, 2339-2349.
- 443 **Godin, J.-G. J. & Smith, S. A.** 1988. A fitness cost of foraging in the guppy. *Nature*,  
444 **333**, 69-71.
- 445 **Grant, J. W. A.** 1997. Territoriality. In: *Behavioural Ecology of Teleost Fishes* (Ed. By  
446 J.-G. J. Godin), pp. 81-103. New York: Oxford University press.
- 447 **Grant, J. W. A., Steingrímsson, S. Ó., Keeley, E. R. & Cunjak, R. A.** 1998.  
448 Implications of territory size for the measurement and prediction of  
449 salmonids abundance in stream. *Canadian Journal of Fisheries and Aquatic*  
450 *Sciences*, **55**, 181-190.

- 451 **Harwood, A. J., Griffiths, S. W., Metcalfe, N. B. & Armstrong, J.D.** 2003. The  
452 relative influence of prior residency and dominance on the early feeding  
453 behaviour of juvenile Atlantic salmon. *Animal Behaviour*, **65**, 1141-1149.
- 454 **Helfman, G. S. 1989.** Threat-sensitive predator avoidance in damselfish-trumpetfish  
455 interactions. *Behavioral Ecology and Sociobiology*, **24**, 47-58.
- 456 **Hixon, M. A.** 1980. Food production and competitor density as the determinants of  
457 feeding territory size. *American Naturalist*, **31**, 729-735.
- 458 **Höjesjö, J., Okland, F., Sundstrom L. F., Pettersson, J. & Johnsson J. I.** 2007.  
459 Movement and home range in relation to dominance; a telemetry study on  
460 brown trout *Salmo trutta*. *Journal of Fish Biology*, **70**, 257-268.
- 461 **Hooge, P. N. & Eichenlaub, B.** 2000. Animal movement extension to Arcview,  
462 version 2.0. Alaska. Science Center – Biological Science office, U.S.  
463 Geological Survey, Anchorage, AK, USA.
- 464 **Imre, I., Grant, J. W. A. & Keeley, E. R.** 2002. The effect of visual isolation on  
465 territory size and population density of juvenile rainbow trout (*Oncorhynchus*  
466 *mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 303-309.
- 467 **Imre, I., Grant J. W. A. & Keeley, E. R.** 2004. The effect of food abundance on  
468 territory size and population density of juvenile steelhead trout

469                   (*Oncorhynchus mykiss*). *Oecologia*, **138**, 371-378.

470   **Jakobsson, S., Brick, O. & Kullberg, C.** 1995. Escalated fighting behaviour incurs  
471                   increased predation risk. *Animal Behaviour*, **49**, 235-239.

472   **Keeley, E. R.** 2000. An experimental analysis of territory size in juvenile steelhead  
473                   trout. *Animal Behaviour*, **59**, 477-490.

474   **Keeley E. R. & Grant, J. W. A.** 1997. Allometry of diet selectivity in juvenile Atlantic  
475                   salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*,  
476                   **54**, 1894-1902.

477   **Kim, J.-W., Brown, G. E., Dolinsek, I. J., Brodeur, N. N., Leduc, A. O. H. C. &**  
478                   **Grant, J. W. A.** 2009. Combined effects of chemical and visual information  
479                   in eliciting antipredator behaviour in juvenile Atlantic salmon *Salmo salar*.  
480                   *Journal of Fish Biology*, **74**, 1280-1290.

481   **Leduc, A. O. H. C., Roh, E., Breau, C. & Brown, G. E.** 2007. Learned recognition of  
482                   a novel odour by wild juvenile Atlantic salmon, *Salmo salar*, under fully  
483                   natural conditions. *Animal Behaviour*, **73**, 471-477.

484   **Leduc, A. O. H. C., Roh, E., Harvey, M. C. & Brown, G. E.** 2006. Impaired  
485                   detection of chemical alarm cues by juvenile wild Atlantic salmon (*Salmo*  
486                   *salar*) in a weakly acidic environment. *Canadian Journal of Fisheries and*

487 Aquatic Sciences, **63**, 2356-2363.

488 **Lima, S. L. & Bednekoff, P. A.** 1999. Temporal variation in danger drives  
489 antipredator behavior: the predation risk allocation hypothesis. American  
490 Naturalist, **153**, 649–659.

491 **Lima, S. L. & Dill, L. M.** 1990. Behavioral decisions made under the risk of  
492 predation: a review and prospectus. Canadian Journal of Zoology, **68**, 619-  
493 640.

494 **Lima, S. L. & Steury, T. D.** 2005. Perception of predation risk: the foundation of  
495 nonlethal predator-prey interactions. In: *Ecology of Predator-Prey*  
496 *Interactions* (Ed. by P. Barbosa & I. Castellanos), pp. 166-188. Oxford  
497 University Press.

498 **Lind, J. & Cresswell, W.** 2005. Determining the fitness consequences of antipredation  
499 behavior. Behavioral Ecology, **16**, 945-956.

500 **Martel, G.** 1996. Growth rate and influence of predation risk on territoriality in  
501 juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries  
502 and Aquatic Sciences, **53**, 660-669.

503 **Martel, G. & Dill, L. M.** 1993. Feeding and aggressive behaviors in juvenile coho  
504 salmon (*Oncorhynchus-kisutch*) under chemically-mediated risk of predation.

505 Behavioral Ecology and Sociobiology, **32**, 365-370.

506 **Martel, G. & Dill, L. M.** 1995. Influence of movement by coho salmon  
507 (*Oncorhynchus kisutch*) parr on their detection by common mergansers  
508 (*Mergus merganser*). Ethology, **99**, 139-149.

509 **Metcalf, N. B., Huntingford, F. A. & Thorpe, J. E.** 1987. The influence of predation  
510 risk on the feeding motivation and foraging strategy of juvenile Atlantic  
511 salmon. Animal Behaviour, **35**, 901-911.

512 **Mirza, R. S. & Chivers, D. P.** 2003. Response of juvenile rainbow trout to varying  
513 concentrations of chemical alarm cue: response thresholds and survival  
514 during encounters with predators. Canadian Journal of Zoology, **81**, 88-95.

515 **Moodie, G. E. E.** 1972. Predation, natural selection and adaptation in an unusual  
516 threespine stickleback. Heredity, **28**, 155-167.

517 **Quinn, G. P. & Keough, M. J.** 2002. *Experimental design and data analysis for*  
518 *biologists*. Cambridge, UK: Cambridge University Press.

519 **Schoener, T. W.** 1981. An empirically based estimate of home range. Theoretical  
520 Population Biology, **20**, 281-325.

521 **Schoener, T. W.** 1983. Simple models of optimal territory size: a reconciliation.  
522 American Naturalist, **121**, 608-629.

- 523 **Scott, W. B. & Crossman, E. J.** 1973. Freshwater fishes of Canada. Fisheries  
524 Research Board of Canada Bulletin, **184**, 192-197.
- 525 **Slaney, P. A. & Northcote, T. G.** 1974. Effects of prey abundance on density and  
526 territorial behaviour of young rainbow trout (*Salmo gairdneri*) in a laboratory  
527 stream channel. Journal of the Fisheries Research Board of Canada, **31**, 1201-  
528 1209.
- 529 **Smith, R. J. F. & Lemly, A. D.** 1986. Survival of fathead minnows after injury by  
530 predators and its possible role in the evolution of alarm signals.  
531 Environmental Biology of Fishes, **15**, 147-149.
- 532 **Steingrímsson, S. Ó. & Grant, J. W. A.** 1999. Allometry of territory size and  
533 metabolic rate as predictors of self-thinning in young-of-the-year Atlantic  
534 salmon. Journal of Animal Ecology, **68**, 17-26.
- 535 **Steingrímsson, S. Ó. & Grant, J. W. A.** 2003. Patterns and correlates of movement  
536 and site fidelity in individually tagged young-of-the-year Atlantic salmon  
537 (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences, **60**, 193-  
538 202.
- 539 **Steingrímsson, S. Ó. & Grant, J. W. A.** 2008. Multiple central-place territories in wild  
540 young-of-the-year Atlantic salmon (*Salmo salar*). Journal of Animal Ecology,

541           77, 448-457.

542   **Talbot, C., Higgins, P. J. & Shanks, A. M.** 1984. Effects of pre- and post-prandial  
543           starvation on meal size and evacuation rate of juvenile Atlantic salmon, *Salmo*  
544           *salar* L. Journal of Fish Biology, **25**, 551-560.

545   **Valeix, M., Loveridge, A. J., Chamaille-Jammes, S., Davidson, Z., Murindagomo,**  
546           **F., Fritz, H. & Macdonald, D. W.** 2009. Behavioral adjustments of African  
547           herbivores to predation risk by lions: Spatiotemporal variations influence  
548           habitat use. Ecology, **90**, 23-30.

549   **Venter, O., Grant, J. W. A., Noel, M. V. & Kim, J.-W.** 2008. Mechanisms underlying  
550           the increase in young-of-the-year Atlantic salmon (*Salmo salar*) density with  
551           habitat complexity. Canadian Journal of Fisheries and Aquatic Sciences, **65**,  
552           1956-1964.

553   **Werner, E. E. & Peacor, S. D.** 2003. A review of trait-mediated indirect interactions in  
554           ecological communities. Ecology, **84**, 1083-1100.

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559 **Figure legends**

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

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

566 Figure 3. Mean  $\pm$  SE ( $N = 18$ ) number of switches between foraging stations of YOY  
567 Atlantic salmon during nine 5-min observation periods.

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

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Figure 1  
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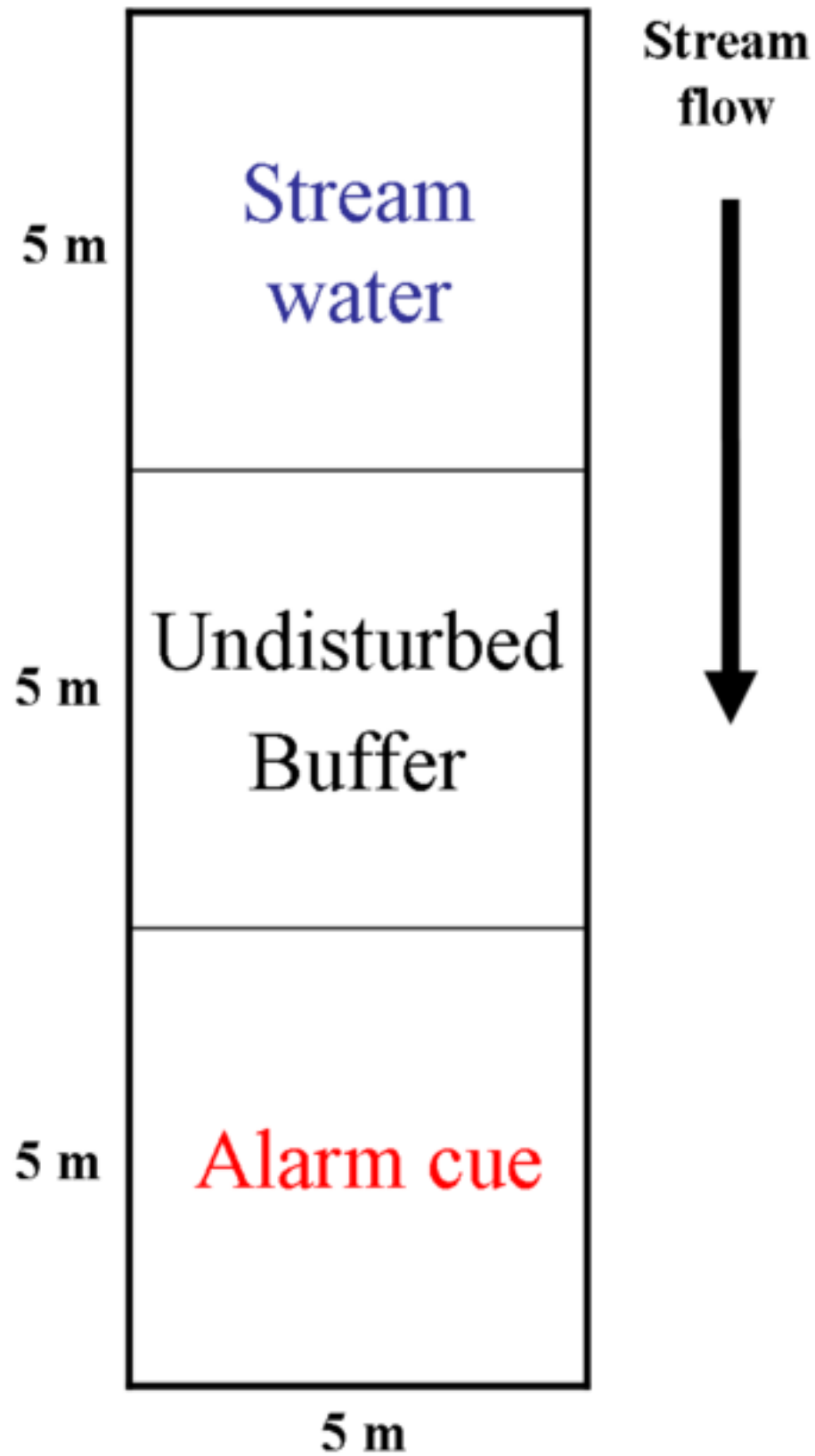


Figure 2

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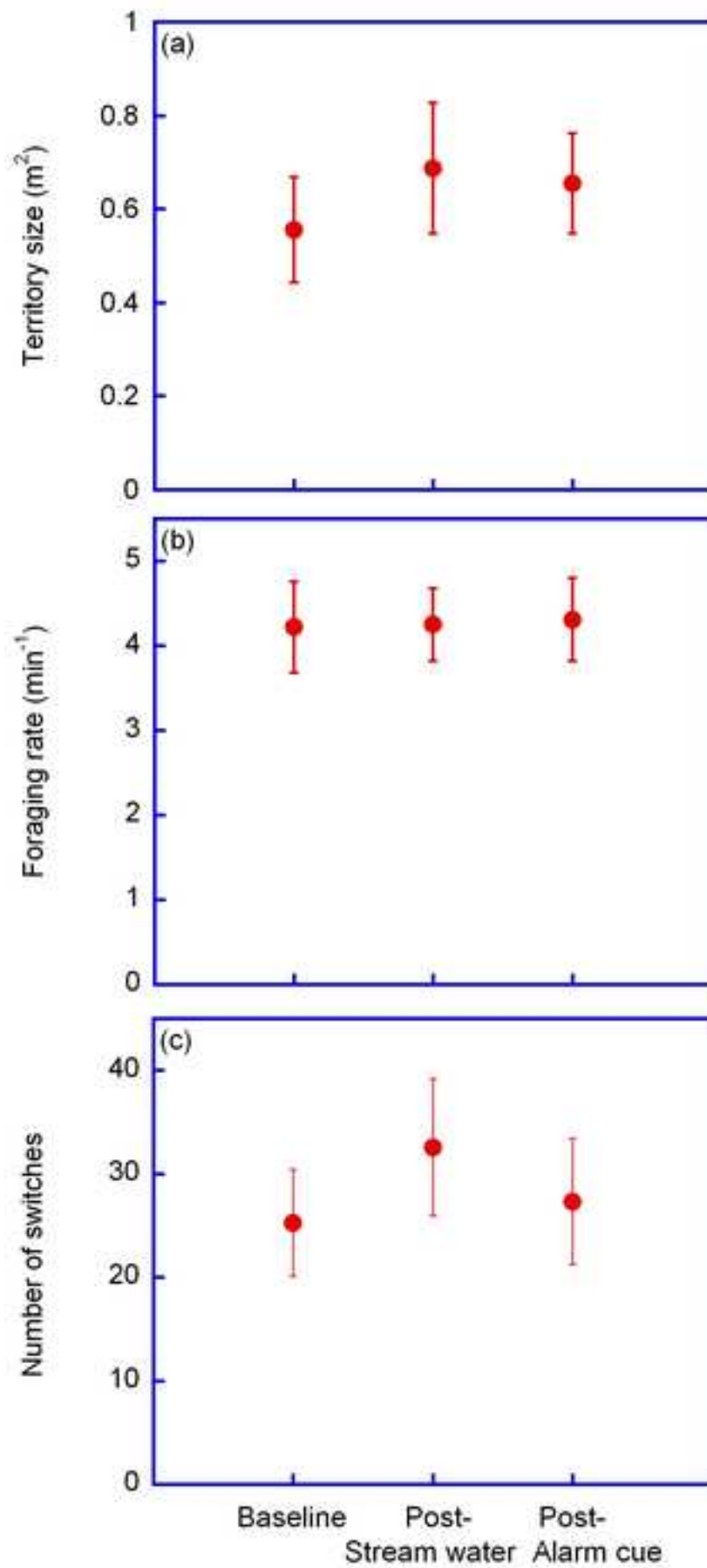


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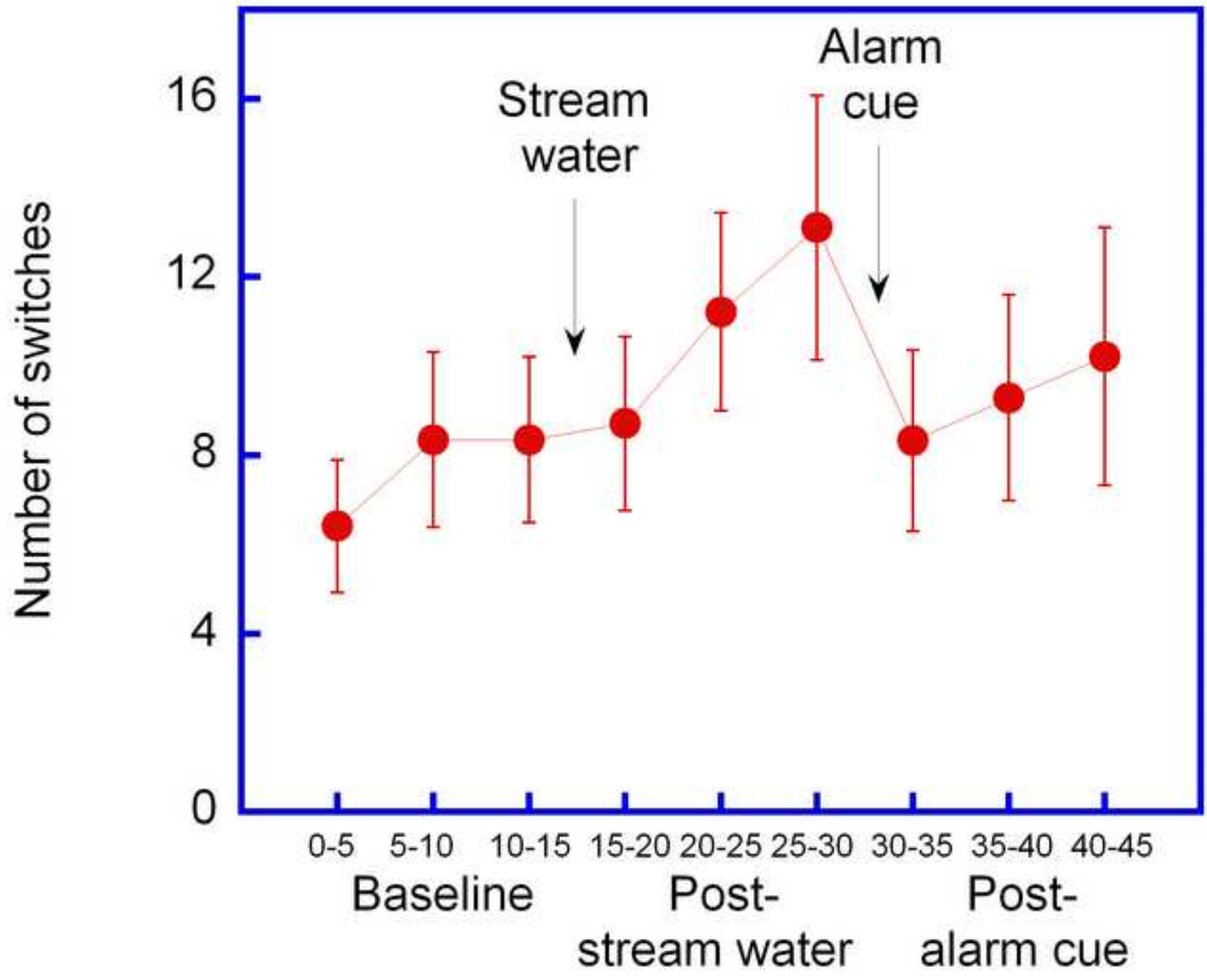


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