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

Jae-Woo Kim*, Jacquelyn L.A. Wood [1], James W.A. Grant [1], Grant E. Brown [1]

Department of Biology, Concordia University

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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- versus 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 versus risky sections of seven sites, where we manipulated the perceived predation risk over a 4-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.

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 (reviewed in: 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, *Gasterosteus aculeatus*, models rather than nonterritorial ones (Moodie 1972). Likewise, animals engaged in aggressive interactions may be less vigilant and allow potential predators to approach closer than nonaggressive 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 laboratory (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

* Correspondence and present address: J.-W. Kim, Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada.
E-mail address: jaew.kim@utoronto.ca (J.-W. Kim).
[1] J. L. A. Wood, J. W. A. Grant and G. E. Brown are at the Department of Biology, Concordia University, 7141 Sherbrooke W., Montreal, Quebec H4B 1R6, Canada.

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& 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 & 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 juvenile salmon decrease their (1) territory size, (2) foraging rate and (3) number of switches between foraging stations in response to both an acute and chronic increase in perceived predation risk.

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 (experiment 1) and from 21 June to 25 July 2007 and 23 June to 16 July 2008 (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 (mean ± SD fork length: 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/ml) of cue elicits a consistent antipredator 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 experiments 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 snorkeller 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/s) (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 × 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 metre 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 were observed from 14 to 18 August 2006. The observer (J.L.A.W) conducted each observation via snorkelling between 1200 and 1900 hours 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 snorkeller (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