

Correlates and consequences of injury in a large, predatory stream salamander (*Dicamptodon tenebrosus*)

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Abstract. Conspecific aggression is an important factor structuring population dynamics through intra- and interspecific interactions, but is rarely studied in un-manipulated populations. In this study, we evaluated rates of injury as a proxy for conspecific aggression using a depletion survey of predatory coastal giant salamanders (*Dicamptodon tenebrosus*) in a tributary of the South Fork Eel River, California. We tested a range of hypotheses including a suite of environmental and biotic factors for the rate of injury in a population by using an AIC model-selection approach that examined the weight of evidence for individual models. We examined both the probability of a given individual being injured, and the proportion of individuals within a given study pool being injured. We found strong support for models including salamander size, density of young-of-the-year steelhead, and density of the largest size-class of salamander as factors positively influencing the rate of injury at both the individual and habitat levels. We also found that density of older steelhead (1+ steelhead) had a strong, but highly variable positive impact on frequency of injury. This study shows that both conspecific and heterospecific factors influence intraspecific aggression for the dominant salamander throughout coastal Pacific Northwest streams. Our methodology demonstrates a non-manipulative approach to identifying correlates of natural injury in a cryptic species of amphibian. More work is needed to determine how these factors directly and indirectly influence the spatial distribution, individual fitness, and dynamics of salamander populations within streams.

Keywords: *Dicamptodon tenebrosus*, aggression, resource competition, territorialism, population structure.

Introduction

Intraspecific aggression in animal populations is a complex process that is often influenced by environmental and demographic factors, and has the potential to influence individual behaviour, movement, population dynamics, and food web interactions. Competition between conspecifics for habitat and forage resources can drive the frequency and severity of conspecific aggression (Slaney and Northcote, 1974; da Silva Nunes and Jaeger, 1989; Wildy et al., 2001), as can population size-class structure and ontogeny (Brunkow and Collins, 1998; Mott and Sparling, 2009). In addition to intraspecific influences, interspecific interactions, such as predation or competition for common resources, can also play a role in the pattern of aggressive behaviour among conspecifics (Reseraris Jr., 1991; Beachy, 1994; Brodman, 1996, 2004).

Individual fitness has been shown to be both directly and indirectly influenced by aggressive behaviours between conspecifics. The direct effects of aggression include loss of young during brooding (Tornick, 2010) and increased predation risk (Semlitsch, 1990), while indirect effects can include loss of energy reserves as stores are put towards somatic repair (Sepulveda et al., 2008). Aggression can also indirectly affect smaller individuals through interference competition over prime resource areas (Hahn and Peter, 2003). As a result of these varying interactions between individual conspecifics, aggression can play a fundamental role in mediating the spatial distribution of organisms and dynamics at the population level. Determining the biotic and environmental factors influencing conspecific aggression is therefore crucial to developing an understanding of population dynamics, but it can be difficult to identify these factors, and time consuming to test each one individually as they can be very complex and species-specific (Rudolf, 2008).

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In species that are difficult to observe directly, levels of aggression must often be inferred by the rate of observed injury in a given population (Schoener and Schoener, 1980; Crockett and Pope, 1988). Many amphibian species exhibit conspecific aggression, but studies have generally been performed in artificial settings (laboratory or manipulated environment) due to the difficulty of observing aggressive behaviour in situ (Semlitsch and Reichling, 1989; Wildy et al., 2001; Tornick, 2010). Direct observation becomes especially difficult in dynamic environments such as stream ecosystems. For example, aggression in terrestrial plethodontid salamanders is a well-documented phenomenon (e.g. Jaeger, 1981, 1984; Marvin, 1998), but stream species are difficult to find or observe without direct manipulation, and so data on these species remains sparse. The paedomorphic form of the coastal giant salamander (*Dicamptodon tenebrosus*; Good, 1989) is the largest stream salamander in the US Pacific Northwest and is highly predatory, though little is known regarding its population dynamics. *Dicamptodon tenebrosus* is found in high densities in streams from southern British Columbia to central California (Nussbaum, Brodie and Storm, 1983). It occurs from steep headwater streams to mainstem rivers, often in sympatry with predatory juvenile steelhead or resident rainbow trout (*Oncorhynchus mykiss*), hereafter steelhead trout. As a result of overlapping habitat and foraging niches, these two predators may compete for common resources, such as drifting invertebrate prey and refugia habitats (Antonelli, Nussbaum and Smith, 1972; Parker, 1994).

Here we evaluated the level of support for a range of biotic and environmental factors that are hypothesized to influence the frequency and pattern of intraspecific aggression. We used observed injuries in a population of *D. tenebrosus* as a proxy for intraspecific aggression, and evaluated the potential impact of aggression on individual fitness. We tested whether natural variation in the density and size structure of coastal giant salamanders, presence of steelhead

competitors, individual body size, and location within a watershed influence the occurrence of aggression in a population of stream dwelling *D. tenebrosus*. We hypothesized that higher densities of co-occurring salamanders and steelhead would be correlated with a higher rate of injury as a result of increased competition for habitat and resources. We also sought to understand the potential for intraspecific aggression to influence individual fitness in coastal giant salamanders. We chose individual mass as a proxy for reproductive fitness as much of salamander mass is attributable to lipid stores in the tail, which is essential for reproductive investment (Fitzpatrick, 1976) and post-metamorphic survival (Scott et al., 2007). We predicted that salamanders with injuries would have reduced body mass at a given length compared to uninjured individuals of the same size.

Methods

To examine the factors affecting injury rates among stream salamanders, we surveyed *D. tenebrosus* in a small tributary stream (Fox Creek, South Fork Eel river watershed, UTM: 10S 445880E, 4399070N, 2.6 km² drainage area) in the Northern California coast range. We collected data on *D. tenebrosus* abundance, frequency and type of injury (e.g. tail bitten, limb missing), the size and mass of salamanders within each habitat unit (a single stream reach including an upstream riffle and a downstream pool) as well as the local density of steelhead trout. Fox Cr. is a perennial stream that experiences high winter discharge and very low summer base-flow (Parker, 1994) resulting in a step-pool channel form during low flow. The stream is located entirely within the University of California Angelo Coast Range Reserve, where it runs through a mature forest of Douglas fir (*Pseudotsuga menziesii*), Coast redwood (*Sequoia sempervirens*), and mixed conifer-deciduous vegetation. The stream alluvium is comprised of a large proportion of boulders and cobbles embedded in a matrix of sand and pebbles. Fox Cr. is inhabited by two species of vertebrate predators: steelhead trout (*O. mykiss*) and coastal giant salamander (*D. tenebrosus*), both of which are present year-round. Steelhead are numerically dominated by juvenile age classes, young of the year (YOY) and 1-2 year old (1+ steelhead), with a few adults that have adopted a resident life history (remaining in natal streams) instead of anadromy (migration to sea; Nehlsen, 1997; Shapovalov and Taft, 1954). *Dicamptodon tenebrosus* also exhibit divergent life-histories at reproductive maturity (~2-3 yrs. of age; Nussbaum and Clouthier, 1973); salamanders will either metamorphose into terrestrial adults or remain aquatic as paedomorphic adults.

To determine the factors contributing to injuries among salamanders, we performed a depletion survey of all individuals of both species across a subset of habitat units in Fox Cr. We surveyed 32 units in a 1.3 km section of Fox Cr. where both species co-occur. Each reach was isolated using block-nets at the top of the upstream riffle and the bottom of each pool, then serially depleted using a combination of snorkel surveys, hand capture, and electrofishing. Captured individuals were anaesthetised (MS-222; Stuart et al., 2007), weighed (g), measured for snout-vent length (SVL; mm) for salamanders and standard length (SL; mm) for steelhead, examined for injuries, and then released at their location of capture. Fish were classified as either 1+ steelhead (≥ 60 mm SL) or as YOY (< 60 mm SL). The wetted area of each habitat unit was measured in order to calculate density estimates for both predators.

To examine how injuries affect individual salamanders, we regressed log-transformed mass on SVL for uninjured individuals and used the relationship to predict the mass of injured individuals. For each size-class (size-class 1: SVL < 45 mm, size class 2: $45 \leq$ SVL < 75 mm, size class 3: SVL ≥ 75 mm; Parker, 1994), we constructed a mass-length regression for uninjured individuals, then used the relationship to predict the mass of injured individuals. We examined the distribution of residuals from these predictions, and used deviations from the derived relationship to test size-class-specific models of how general body condition varied with injury. We applied Grubbs' Test (Grubbs, 1950) to each size class to identify and remove outliers ($n = 5$), and used a two-tailed t-test to determine whether the distribution of residuals for each size class significantly differed from 0.

We constructed models to predict two different response variables, the probability of injury at the level of the individual, and the proportion of individuals with injuries aggregated within each sampled habitat unit. For each model, we used binomial logistic regression (weighted by the number of individuals in each pool for habitat-level analysis), as both of our response variables were constrained between 0 and 1 (proportion of individuals injured and probability of injury). Our explanatory variables represented a suite of biotic and environmental factors: pool-specific salamander density (both mass/m² and individuals/m²; D), square root transformed distance from the tributary confluence (m ; d), standard deviation of SVL of salamanders within a habitat unit (SD_{SVL}), density of the largest size-class of individuals (> 70 mm SVL; individuals/m²; D_{SC3}), density of YOY steelhead (g/m²; D_{YOY}), density of 1+ steelhead (individuals/m²; D_{I+}), and individual coastal giant salamander SVL (mm; SVL ; only included in the individual-level analysis). At the individual level, we included the pool in which each salamander was found as a random factor in the model to account for pseudo-replication. We examined all combinations of explanatory variables to test for co-variation, resulting in pool-specific salamander density (mass/m²) being excluded from further analysis. Because we only had 31 data points at the habitat level, we limited the number of parameters in our models to $n/10 \approx 3$ (including intercept; Burnham and Anderson, 2002) for that analysis. We used Akaike's Information Criterion (Akaike, 1974) adjusted for small sample sizes (AICc) to compare

the degree of support for all combinations of explanatory variables at each level given that no a priori hypothesis was considered more or less probable (Anderson and Burnham, 2002). Such an approach is an acceptable way to explore behavioural data when relatively little is known of the system (Symonds and Moussalli, 2011). The results of this method can then be used to inform more traditional hypothesis tests in future studies, which are a more appropriate way to check for interactions among parameters.

Analyses were performed using *R* (v 2.15.3; R Core Team, 2013), with the AIC analysis package *AICcmodavg* (Mazerolle, 2013). We calculated Akaike weights (w_{Ak}) for each model (weight of support between 0 and 1, all w_{Ak} sum to 1), which can be interpreted as the probability that a given model is the best approximation (Symonds and Moussalli, 2011). To estimate a 95% confidence set of models (a subset of candidate models that we are 95% sure contains the best model in the original set), we selected the top models whose cumulative w_{Ak} just surpassed 0.95 (Burnham and Anderson, 2002). To compare the relative importance of individual variables, w_{Ak} for all models containing each variable were summed, resulting in a relative ranking of variable importance. The w_{Ak} was also used to calculate the weighted mean of variable coefficients across all models in which each variable was included.

Amphibians heal quickly (Yannas, Colt and Wai, 1996) and generate little scar tissue (Seifert et al., 2012, but see Ferguson and O'Kane, 2004), so the injuries we observed can be attributed to a narrow temporal window in each individual's ontogeny. If injuries or injury relics persisted for long periods, it could confound our analysis by attributing injuries to larger body-sizes when they may have been incurred at smaller body-sizes, or in other locations within areas we sampled. However, our estimates of injury could also be biased low if injuries inflicted are severe enough to result in death. However, we performed our analysis under the assumption that injury-induced mortality is low due to the lack of conspicuously unhealthy or dead salamanders in our study system. Both of these assumptions bear careful consideration if this methodology is used for other organisms.

Our response variables, proportion of salamanders injured per pool and probability that an individual would be injured, included only the 2 larger size-classes of salamanders. Salamanders in the smallest size-class of *D. tenebrosus* showed no intra- or inter-specific aggression, suggesting that only larger *D. tenebrosus* and *O. mykiss* individuals injured the smallest size class (personal observation). Large individuals of both species predate on the smallest size-class of *D. tenebrosus* (Parker, 1993, 1994; Munshaw, unpublished data) and as both species are gape-limited predators, predation on larger individuals is not a viable feeding strategy. We therefore argue that injuries caused by aggressive interactions between larger individuals are due to resource competition or territorialism and not failed predation attempts. Additionally, the observed frequency of injury may be reduced in small individuals if predation attempts (by either large salamanders or steelhead) result in a higher rate of mortality or decreases the likelihood of escaping future predation attempts. Due to the proposed alternate mechanisms

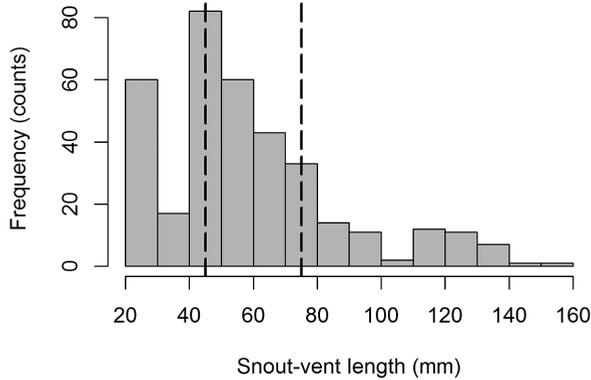


Figure 1. Histogram of salamander snout to vent length (SVL, mm) from Fox Cr. ($n = 354$). Vertical lines indicate divisions between size-classes as established in the literature.

of injury between the small and larger size-classes, size-class 1 salamanders were only included in the total salamander density estimates for each pool. Although we have ecologically-derived arguments for not including the smallest size-class in our main analysis, we have included the smallest size class in an otherwise identical parallel analysis and included the results in the online Supplementary Material.

Results

We captured a total of 354 *D. tenebrosus* individuals and 594 *O. mykiss* individuals in our census of 32 habitat units in Fox Cr. Over 85% of the steelhead individuals were YOYs ($n = 509$), and the distribution of salamander SVLs was heavily skewed towards smaller individuals (fig. 1). We captured 115 size-class 1 salamanders (4 injuries), 144 size-class 2 individuals (25 injuries), and 95 size-class 3 individuals (30 injuries). We removed one habitat unit from our analysis due to a lack of data; we found only a single salamander and were therefore unable to calculate SD_{SVL} for the unit. We found a significant relationship between natural log-transformed length and mass of uninjured individuals ($n = 296$; $\ln[\text{Mass}] = -9.66 + 2.88 * \ln[\text{SVL}]$; intercept SE = 0.10, SVL coefficient SE = 0.03, $P \ll 0.05$, $r^2 = 0.98$). Using this regression, we predicted the mass of injured individuals ($n = 59$) of each size class, and then examined the distribution of residuals for each size-class. One outlier was found and

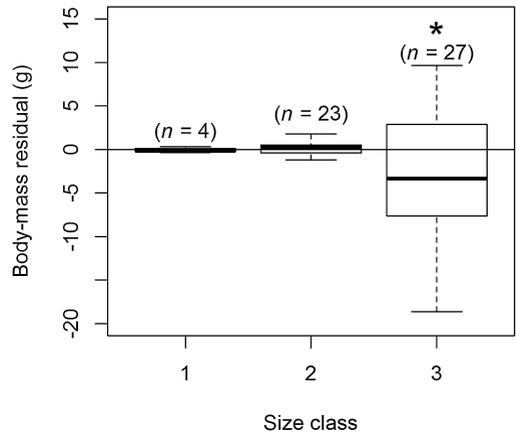


Figure 2. Predicted mass residuals (g) for each size-class of injured salamander based on a mass-length regression for uninjured individuals. Stars indicate size classes with residuals that differ significantly from 0.

removed from the analysis of size-class 2 individuals (one-sided Grubbs' test; $G = 3.23$, $P < 0.05$). We found that injuries only reduced mass in the largest size class (3). The distributions of residuals for injured size-class 1 and 2 individuals were not significantly different from 0 ($n = 4$ and 23, $t = 0.49$ and 1.16, $P = 0.66$ and 0.26, $\bar{x} = -0.07$ and 0.2 respectively), but injured size-class 3 individuals were an average of 3.73 g lighter than expected (fig. 2; $n = 27$, $t = -2.49$, $P < 0.05$, $\bar{x} = -3.73$).

Our AICc model selection produced a set of 57 models at the individual level, and 14 models at the habitat level. Neither level of analysis

Table 1. Top and bottom ranked models for the set of models including 95% of all model support, at the individual (Injury) and habitat (Proportion Injured) levels of analysis. SD_{SVL} = standard deviation of salamander snout-vent lengths in a given pool, D_{SC3} = density of size-class 3 salamanders in a given pool ($\#/m^2$), SVL = snout-vent of the focal salamander (mm), D_{YOY} = density of young-of-the-year steelhead in a given pool ($\#/m^2$), D_{I+} = density of 1+ steelhead in a given pool ($\#/m^2$), d = square root of distance upstream (m), and D = salamander biomass density (g/m^2).

Level	Rank	AICc	Model	$\Delta AICc$	w_{Ak}
Individual	1	245.3	Injury $\sim SD_{SVL} + D_{YOY} + D_{SC3} + SVL + (1 Pool)$	0	0.195
	2	246.9	Injury $\sim D_{I+} + SD_{SVL} + D_{YOY} + D_{SC3} + SVL + (1 Pool)$	1.6	0.089
	3	247.1	Injury $\sim d + SD_{SVL} + D_{YOY} + D_{SC3} + SVL + (1 Pool)$	1.8	0.080
	⋮	⋮	⋮	⋮	⋮
	55	253.8	Injury $\sim D + D_{I+} + d + SD_{SVL} + D_{SC3} + SVL + (1 Pool)$	8.5	0.003
	56	253.8	Injury $\sim D + d + SD_{SVL} + D_{YOY} + SVL + (1 Pool)$	8.5	0.003
	57	253.9	Injury $\sim D + SD_{SVL} + D_{YOY} + D_{SC3} + (1 Pool)$	8.5	0.003
Habitat	1	92.6	Proportion Injured $\sim D_{YOY} + D_{SC3}$	0	0.527
	2	96.6	Proportion Injured $\sim D_{I+} + D_{SC3}$	4.0	0.071
	3	97.0	Proportion Injured $\sim d + D_{SC3}$	4.4	0.058
	⋮	⋮	⋮	⋮	⋮
	12	99	Proportion Injured $\sim d$	6.4	0.022
	13	99.4	Proportion Injured $\sim D + D_{YOY}$	6.8	0.017
	14	100.1	Proportion Injured $\sim D + D_{I+}$	7.5	0.013

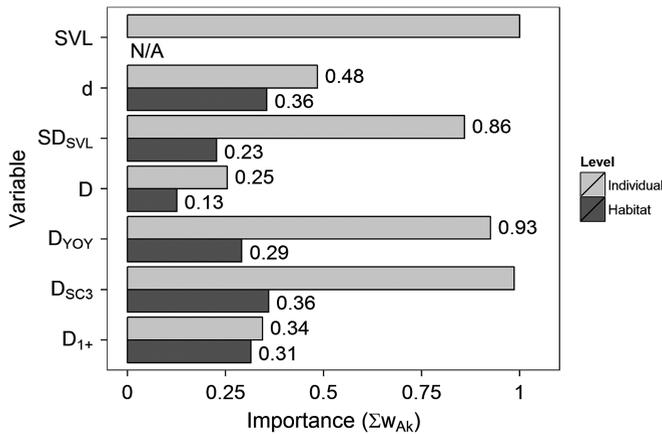


Figure 3. Model-averaged variable importance scores (sum of Akaike weights; $\sum w_{Ak}$) for individual-level (light bars) and habitat-level (dark bars) analyses. Importance computed by summing Akaike weights for every model in which each variable was present. SD_{SVL} = standard deviation of salamander snout-vent lengths in a given pool, D_{SC3} = density of size-class 3 salamanders in a given pool ($\#/m^2$), SVL = snout-vent of the focal salamander (mm), D_{YOY} = density of young-of-the-year steelhead in a given pool ($\#/m^2$), D_{I+} = density of 1+ steelhead in a given pool ($\#/m^2$), d = square root of distance upstream (m), and D = salamander biomass density (g/m^2).

supported a single top model: $\Delta AICc_{max} = 8.5$ and 7.5, and maximum $w_{Ak} = 0.2$ and 0.53 at the individual and habitat levels respectively (table 1). Individual size (SVL), density of size-class 3 individuals (D_{SC3}), and density of YOY steelhead (D_{YOY}) had the greatest variable importance at the individual level, and the latter two parameters had the greatest importance at

the habitat level (fig. 3). These variables were the only parameters whose coefficient estimates did not have confidence intervals including 0 (table 2). All 3 parameters had positive effects on injury probability (individual level; logit coefficients = 0.02, 3.46, and 1.68 respectively) and proportion of individuals injured (habitat level; excluding SVL , logit coefficients = 2.9

Table 2. Model averaged coefficients and 95% confidence intervals for factors predicting injury at the individual and habitat unit levels. Variable codes are defined in table 1. Stars indicate variables with confidence intervals that do not bound 0.

Level	Variable	Model-averaged estimate (95% CI)	Unconditional SE
Individual	<i>Intercept</i> *	-5.51 (-9.04, -1.98)	1.80
	<i>D</i>	0 (-0.04, 0.04)	0.02
	<i>D_{I+}</i>	1.48 (-1.22, 4.18)	1.38
	<i>D</i>	0.05 (-0.03, 0.12)	0.04
	<i>SD_{SVL}</i>	-0.07 (-0.14, 0.01)	0.04
	<i>D_{YOY}</i> *	1.68 (0.33, 3.04)	0.69
	<i>D_{SC3}</i> *	3.46 (0.49, 6.44)	1.52
	<i>SVL</i> *	0.02 (0.01, 0.03)	0.01
Habitat	<i>Intercept</i> *	-3.84 (-6.69, -0.99)	1.45
	<i>D</i>	-0.01 (-0.05, 0.03)	0.02
	<i>D_{I+}</i>	2.02 (-0.26, 4.3)	1.38
	<i>d</i>	0.05 (-0.01, 0.1)	0.03
	<i>SD_{SVL}</i>	-0.03 (-0.08, 0.03)	0.03
	<i>D_{YOY}</i> *	1.47 (0.33, 2.62)	0.59
	<i>D_{SC3}</i> *	2.9 (0.49, 5.32)	1.23

and 1.47 respectively) and had among the highest influences on injury in both analyses.

Discussion

Our results suggest that both density- and size-structured aggressive interactions are important in the coastal giant salamander population we studied. We found that only the largest size-class of injured individuals exhibited reductions in mass relative to uninjured individuals. We also found that densities of the largest size-class of salamander and YOY steelhead were good predictors of salamander injury at both the individual and the habitat scale, as well as individual size at the individual level (table 2). We found little support for models containing watershed position, and this parameter had little effect on the observed rate of injury at either level of analysis (fig. 3, table 2).

We found a strong relationship between injury on individual body condition for the largest size class, but found no relationship among size-class 1 and 2 individuals (fig. 2). This pattern suggests that injuries incurred at smaller sizes may not be severe enough to influence energy reserves and overall body condition, and so our results suggest that the negative fitness consequences of injury (as indexed by body condition) likely increase with body size. Alterna-

tively, it is possible that smaller individuals experience a higher rate of injury-induced mortality and thus we observe a lower rate of injury in smaller individuals. However, this scenario is unlikely in our system due to a low occurrence of deceased individuals, and no significant effect of injury on mass of smaller individuals when we would expect to see a greater loss of mass if injury had particularly severe impacts on survival. It is also unlikely that we witnessed a low rate of injury among the smallest individuals due to high rates of successful predation upon them, as the occurrence of small individuals in the diets of large salamanders was low (1.8%; Munshaw, unpublished data). Another possibility is that individuals with lower body mass at a given length may be more prone to sustaining injuries, such as increased frequent foraging behaviour (in an effort to compensate for lower mass) leading to a higher frequency of intra-specific encounters. Injuries may impact fitness at two different time-scales. In the short term, fresh injuries may cause debilitation (e.g. loss of tail or limbs, infection), by decreasing a salamander's ability to compete for food resources, mates, or refugia to avoid predation (Krause, Steinfartz and Caspers, 2011). In the longer term, repair of injured tissues requires extra energy that likely represents a trade-off

with maintaining structures necessary for survival or reproduction (Fitzpatrick, 1976; Scott et al., 2007), which may be further exacerbated if debilitation reduces a salamander's ability to catch prey (e.g. damage to sensory organs).

Interactions between salamanders and trout are thought to be asymmetric, with trout negatively affecting salamander growth and survival through both competition and predation, the latter of which is expected to be uncommon (Rundio, Olson and Guyer, 2003; personal observation). The presence of multiple competing species has been shown to alter the distribution of salamanders within refugia (Kleeberger, 1984; Roudebush and Taylor, 1987), and negatively impact salamander populations by decreasing available resources within a habitat (Figiel and Semlitsch, 1990). We found that the density of YOY steelhead was positively correlated with rate of injury observed at both the individual and at the habitat level, suggesting that heterospecific interactions are likely to be important drivers of injuries in coastal giant salamanders. For example, a YOY density of $1.5/m^2$ (observed range: 1.16-2.53) increases the probability of injury from the baseline of 0.004 to 0.05 at the individual level, and increases the proportion of salamanders injured in a habitat unit from the baseline of 0.02 to 0.16 holding all other factors constant. This positive effect may be driven by behavioural responses between YOY steelhead and salamanders if they compete non-aggressively for refugia, or common food resources. Because *D. tenebrosus* reach large sizes relative to trout (Munshaw et al., 2013), there is no documented evidence of agonistic behaviour between steelhead and coastal giant salamanders, with the exception of relatively uncommon direct mutual predation (Parker, 1993, 1994; Munshaw et al., 2013). This suggests that the injuries we observed were not accrued through interspecific aggression with higher YOY densities, but most likely due to higher frequency intraspecific salamander interactions that in turn generate injuries. Larval coastal giant salamanders

have been shown to increase their use of refugia in the presence of chemical cues from predatory cutthroat trout (Rundio et al., 2003), which may lead to an increase in intraspecific encounters. We found a strong positive effect of 1+ steelhead on rates of injury, but our confidence intervals for the coefficients at both levels of analysis marginally bounded zero. This suggests a generally strong, but variable relationship of 1+ steelhead density and rate of injury where an increase of a single 1+ steelhead per square meter results in a 339% increase in the mean odds of injury at the individual level, and 654% increase at the habitat level. Although the density of both YOY and 1+ steelhead were positively linked to the probability of salamander injury, the large differences in body size and behaviour between the two size classes of steelhead likely result in different mechanisms of salamander injury. As with many stream-dwelling salmonids, juvenile steelhead feed primarily on drifting aquatic and terrestrial invertebrate prey, and 1+ steelhead are known to have a high degree of dietary overlap with giant salamanders (Atlas et al., 2013; Munshaw et al., 2013). Consequently, high densities of 1+ steelhead may intensify direct exploitation competition for prey with salamanders, leading to more aggressive encounters between individuals, or a higher frequency of salamander cannibalism attempts under prey-limited conditions (Wildy et al., 2001). Similarly, while it is unlikely that YOY steelhead represent a major exploitative competitor for larger giant salamanders, they do provide an abundant and energetically lucrative prey resource. If larger, more aggressive salamanders congregate in areas of locally high YOY abundance, the likelihood of aggression among salamanders may increase.

The size-structure of a population has the potential to directly influence rates aggressive interactions, as aggression among size-classes is well-documented in salamanders (Mathis, 1990; Formanowicz and Brodie, 1993; Wildy et al., 2001) and can influence individual activity and spatial distribution (Roudebush and Taylor,

1987; Brunkow and Collins, 1998). Previous work examining aggression between salamanders has found that larger salamanders exhibit agonistic behaviour towards both smaller and equal size individuals (Wiltenmuth, 1997), suggesting that the injuries observed in this study may be attributable to increasing aggression within size-classes as size increases. Our results support this hypothesis, as we found that injury rate is strongly linked to the density of salamanders in the largest size-class (size-class 3), but less so to overall salamander density (fig. 3, table 2). A density of the largest size-class of $0.3/\text{m}^2$ (observed range: 0 to 0.61) results in an increase at the individual level from the baseline probability of 0.004 to 0.01 (a 180% increase), and an increase at the habitat level from 0.02 to 0.05 (a 132% increase). In Fox Creek, the smaller size-classes (1 and 2) make up a large portion (73% numerically) of the *D. tenebrosus* population (fig. 1). Consequently, salamander density within a given habitat unit is largely driven by numerous small salamanders, which the literature suggests are not as likely to initiate aggressive encounters with larger sized individuals. This numerical bias towards smaller salamanders may also be driven by factors such as differences in predation risk, rate of survival, detectability, or resilience to injury, all of which merit further investigation. We recognize that the distribution of salamanders within a given stream likely exhibits temporal variability over years, seasons, potentially even days, and so our study represents a single snapshot of the overall variability of this system. However, the between-pool spatial variability in individual density among our 32 stream reaches likely captures some portion of that variability, making our findings more robust to the fluid nature of population dynamics within a stream.

Using a field-based census of a population of coastal giant salamanders, we identified correlates of injury as a potential proxy for aggressive behaviour among *D. tenebrosus* individuals. Our results suggest that YOY steelhead (and to a lesser degree 1+ steelhead) are posi-

tively linked to the frequency of injury in giant salamanders, despite low rates of mutual predation (Parker, 1993, 1994). Similarly, we suggest that aggressive encounters among salamanders within the largest size-class also drive injury frequency higher. If aggressive encounters among salamanders and the resulting injuries have fitness impacts at the individual level, aggression among *D. tenebrosus* may scale to affect local population growth rates. For example, a mean sized salamander from this study (59 mm SVL) in a pool of average YOY, 1+ steelhead, and size-class 3 densities (as observed in this study) has a 32% chance of being injured. As salamander size and density of both predators increase, the probability of injury increases and the cumulative impacts to individual fitness may manifest at the population level. Given these rates, our study suggests that aggressive encounters could be an important component of density-dependent population growth. Although our results suggest strong correlates of aggression-induced injury in a cryptic stream salamander species, the specific mechanisms of aggression remain untested. Injuries of the nature observed in this study may be attributable to random encounters between salamanders when foraging or to purposeful contests for resources, as well as rare aggressive heterospecific encounters or environmentally inflicted injuries (e.g. shifting river stream alluvium). Game theory predicts that a wide range of factors including motivation to engage in conflict (Hofmann and Schildberger, 2001), previous history of aggression (Hsu, Earley and Wolf, 2007), length territorial ownership (Johnsson, Nöbberlin and Bohlin, 1999), and habitat resource quality (Hugie and Dill, 1994) may influence an individual's likelihood of engaging in aggressive interactions, all of which may influence the rates and correlates of injury we examined in this study. Additional work is needed to address both the mechanisms driving aggressive interactions between conspecifics, but also the influence of heterospecific interactions with steelhead. In this way, future work can determine whether direct causal-

ity or common environmental drivers result in the correlated population metrics we observed. We have also demonstrated a useful method for determining environmental correlates of injury in a cryptic species, a potentially useful tool for pilot-studies or preliminary investigations into the more detailed mechanisms and factors affecting injury and aggression among and within species.

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