

LETTER

Predator personality structures prey communities and trophic cascades

Denon Start*  and Benjamin Gilbert

Department of Ecology and Evolutionary Biology, University of Toronto Toronto, ON, Canada M5S 3B3

*Correspondence: E-mail: denon.start@mail.utoronto.ca

Abstract

Intraspecific variation is central to our understanding of evolution and population ecology, yet its consequences for community ecology are poorly understood. Animal personality – consistent individual differences in suites of behaviours – may be particularly important for trophic dynamics, where predator personality can determine activity rates and patterns of attack. We used mesocosms with aquatic food webs in which the top predator (dragonfly nymphs) varied in activity and subsequent attack rates on zooplankton, and tested the effects of predator personality. We found support for four hypotheses: (1) active predators disproportionately reduce the abundance of prey, (2) active predators select for predator-resistant prey species, (3) active predators strengthen trophic cascades (increase phytoplankton abundance) and (4) active predators are more likely to cannibalise one another, weakening all other trends when at high densities. These results suggest that intraspecific variation in predator personality is an important determinant of prey abundance, community composition and trophic cascades.

Keywords

Copepod, *Daphnia*, *Epitheca canis*, food web, intraspecific variation, predation competition.

Ecology Letters (2017) 20: 366–374

INTRODUCTION

Trait variation is central to our understanding of how individuals interact, and how interactions determine community structure. Variation among species is particularly well studied with respect to trophic interactions (Brooks & Dodson 1965; Schmitz *et al.* 2000). Differences in traits of predator species are known to alter prey abundance and identity (Schmitz *et al.* 2000), ultimately influencing ecosystem function (Schmitz & Suttle 2001). For example, decades of research has shown that predator identity and abundance structure prey communities and often alter trophic cascades (Paine 1966; Schmitz *et al.* 2000). This research usually assumes that mean trait values adequately represent species interactions and their effects on community structure. However, using mean trait values or simply species identity, ignores considerable intraspecific trait variation (Benesh & Kalbe 2016), overlooking a potentially important determinant of community structure (Bolnick *et al.* 2011).

Intraspecific trait variation in a predator species can alter community structure and ultimately ecosystem processes. Intraspecific differences among populations have been shown to have large consequences on trophic dynamics (e.g. Morin 1983; Post *et al.* 2008). For example, Post *et al.* (2008) showed that trait variation among populations of a fish predator created differences in plankton communities, algal concentration and ecosystem processes. Within populations, intraspecific variation underpins evolution that can alter predator–prey dynamics (Cortez 2016), and even in the absence of evolution, nonlinear averaging can cause ecological dynamics to differ systematically when intraspecific variation is present (Bolnick *et al.* 2011). The sources and consequences of intraspecific variation are best understood from evolutionary and eco-evolutionary perspectives (Thompson 1988;

Fussmann *et al.* 2007; Schoener 2011). Fewer studies have addressed the ecological effects of intraspecific trait differences within communities, especially on higher order interactions (but see Johnson & Stinchcombe 2007; Crutsinger *et al.* 2009; Hughes & Stachowicz 2009). Understanding the consequences of differences among individuals on community processes is necessary for developing models of how and when the presence of intraspecific variation should alter dynamics (Bolnick *et al.* 2011).

Animal personalities are one type of intraspecific variation comprising groups of behavioural traits that vary consistently among individuals of a given species (Sih *et al.* 2004; Dingemanse *et al.* 2010). Animal personalities typically have genetic underpinnings and are heritable (Dochtermann *et al.* 2015), creating the potential for standing trait variation. For example, activity of larval odonates is heritable (Brodin & Johansson 2004), consistent across ontogeny (Brodin 2009) and can in turn alter predator activity and feeding rate (Araújo *et al.* 2011). Crucially, different personalities can be maintained both within or among populations, with differing consequences for community dynamics (Sih *et al.* 2012). In short, selection and gene flow can create populations composed of individuals with disparate personalities (Sih *et al.* 2012; Wolf & Weissing 2012), and we expect these differences to have important implications for species interactions.

Although intraspecific differences in animal personalities have clear implications for species interactions, their effects on higher order interactions remain poorly understood (Toscano & Griffen 2014; Belgrad & Griffen 2016). When differences in predator personality alter the rate at which they consume prey, they may influence the density, behaviour or identity of prey species (Royauté & Pruitt 2015), which should in turn have cascading effects on basal resources (Paine 1966; Schmitz *et al.* 2000). Because predators with active personalities can

consume larger numbers of prey (Sih *et al.* 2012; Royauté & Pruitt 2015), these individuals should produce larger trophic cascades. We expect these effects of personality to be particularly important when communities are strongly structured by predation (Schmitz *et al.* 2000), and when examining intraspecific variation in abundant species that interact strongly (Bolnick *et al.* 2011).

Predator personality can also change the type of prey encountered and consumed, directly altering prey community composition, and through this change, trophic cascades (Peacor *et al.* 2011). In many communities prey fall along a predation competition continuum, where the most competitive species are efficient foragers that persist with low resources (Tilman 1980; Mittelbach 1981) and predation resistance species are well-defended but inefficient foragers (Werner & Hall 1988; Chase *et al.* 2002). The greater consumptive effect of active predators should reduce prey abundance, but can also select for well-defended prey species (Skelly 1995; Post *et al.* 2008). In other words, predator personality has the potential to selectively alter the prey community, which may alter the strength of trophic cascades and allow poorly competing species to persist.

While active predators should have disproportionately large effects on prey communities and trophic cascades, these patterns may be weakened or reversed by predator–predator interactions such as cannibalism (Rudolf 2007). Cannibalism increases with activity rate for at least two reasons. First, active predators encounter prey and each other at a higher rate (Dell *et al.* 2011), increasing the opportunity for cannibalism. Second, the increased metabolic demand of active predators (Brit-Friesen *et al.* 1989; Werner & Anholt 1993) can increase the need for cannibalism. High rates of cannibalism can reduce the abundance of predators, consequently increasing the abundance of prey, weakening trophic cascades (Rudolf 2007). In addition, if predators are satiated by cannibalism, they will consume fewer prey, reducing the strength of the trophic cascade on a per predator basis (Rudolf 2007). Thus, an active predator personality should have predictable impacts on prey communities and trophic cascades, but these impacts may be weakened or reversed by interactions among individual predators.

In this article, we used individual differences in personality observed within a predator population to test if these differences create divergent community dynamics when predators are considered in isolation or with the potential to interact. Specifically, we tested how predator personality and density interactively structure prey abundance, community composition and the strength of trophic cascades. We used a common and widespread dragonfly larvae (*Epiptera canis*), two zooplankton species and unicellular algae to examine trophic dynamics over multi-generational time scales. These species are the most common species found in many ponds at our field site, and are likely to have a disproportionate impact on food web dynamics. We first used a series of assays to test for differences in dragonfly activity rates and key components of our predicted trophic dynamics, such as a trade-off in predator tolerance and resource consumption among zooplankton species. We then created replicate mesocosms and determined how activity rate of the dragonfly predator influenced

zooplankton communities and algal abundance, while simultaneously measuring cannibalism rates. Our study addressed the above ideas, specifically testing if (1) active predators disproportionately reduce prey abundances, (2) predator-resistant zooplankton species have a higher relative abundance when active predators are present, (3) the combined effects of reduced prey abundance and changes in zooplankton community composition strengthen trophic cascades (increase algal abundance) when active predators are present and (4) cannibalism weakens the above hypotheses when multiple active predators are present. We show that natural variation in predator activity levels is sufficient to alter prey density and composition and, through these changes, alter trophic cascades.

METHODS

Study system and collection

We tested the above questions using a dragonfly predator, *Epiptera canis* (hereafter *Epiptera*), and a simple aquatic food chain. *Epiptera* larvae are common in fishless ponds throughout northeastern North America and are often the most abundant dragonfly (Anholt *et al.* 1991). Many odonates are cannibalistic (Van Buskirk 1989) and have heritable personality traits that are consistent across ontogeny (Brodin & Johansson 2004; Brodin 2009). We used two zooplankton species, a cyclopoid copepod (hereafter copepod) and *Daphnia catawba* Coker (hereafter *Daphnia*), as prey. Both species are abundant in ponds in southern Ontario, co-occur with *Epiptera*, and have largely overlapping ranges. Total zooplankton abundance, composed mainly of these species, averaged 90 individuals per litre when we collected zooplankton for our experiments (Start, unpublished data). Unicellular algae represented the basal resource of the system. Using a simplified system allows us to feasibly investigate multi-generational population and community dynamics.

We collected larvae, zooplankton and algae from a fishless pond at Koffler Scientific Reserve, Ontario, Canada between June 7 and 12, 2016. We collected *Epiptera* using dip nets and immediately transferred individuals to 9 cm Petri dishes filled with pond water. All larvae were fed *ad libitum* prior to the beginning of the experiment. We collected zooplankton using plankton nets (64 µm mesh) from the edges of the pond where most *Epiptera* larvae were found. We collected pond water and algae by filtering the water through the same plankton net immediately prior to initiating the experiment.

Estimating components of trophic dynamics

We first conducted a number of assays to estimate *Epiptera* activity phenotypes, individual predator responses to other predators, impacts of *Epiptera* on each prey species and impacts of zooplankton species on algae. These assays informed our interpretation of the subsequent mesocosm experiment.

We used an open-field activity test to assay individual larval activity rates. Open-field activity tests are used to test movement patterns including activity rate (Carducci & Jakob 2000)

and have revealed heritable patterns of activity rate in many organisms (Montiglio *et al.* 2013), including larval odonates (Johansson & Rowe 1999; Brodin 2009). We conducted activity assays on 102 individuals by placing a single larvae in a 9-cm Petri dish filled with filtered pond water. After 1 h, we recorded the position of each individual every 20 min for 3 h (10 observations). We calculated the minimum distance between each recorded position, using the total over the 10 observations as our measure of activity rate. To ensure that this behaviour was a repeatable trait of individual larvae, we repeated the assay using a subset of 25 individuals at the end of the subsequent mesocosm experiment (Brodin 2009). To avoid confounding activity rate with body size, we measured the head width (Johansson & Rowe 1999) of each individual using ImageJ software (0.316 ± 0.005 mm SE; ImageJ2, Bethesda, MD, USA). This ensured that any patterns were a result of activity rate, and not a spurious correlation between body size and activity. We determined whether the activity rate of a predator was changed by the presence of a conspecific by repeating the activity assay but with *Epiptera* either alone, or in the presence of a conspecific (10 replicates per treatment). This assay allows us to separate the effects of changes in *Epiptera* abundance from change in behaviour. Following activity assays we immediately introduced larvae to the mesocosm experiment (below).

We tested for differences in susceptibility to predation of each zooplankton species, and whether attack rate depended on predator activity rate. We tested susceptibility to predation by separately introducing 10 individuals of each prey species to 9 cm Petri dishes with filtered pond water (10 replicates per species). We randomly added one *Epiptera* to each Petri dish, then counted the number of prey remaining after 24 h. We had previously assayed all *Epiptera* for activity rate using the methods described above. Note that no prey died from causes other than predation, and that no new zooplankton were produced during the assay.

Our final assay tested the impacts of zooplankton on algal abundances. We introduced 10 individuals of each species to separate 9 cm Petri dishes filled with filtered pond water (10 replicates per species). We recorded initial algal abundance using the methods described below (Mesocosm experiment section), allowed zooplankton to graze for 24 h, then measured the change in algal abundance. We did not include a treatment with both zooplankton species as this would not allow us to distinguish their consumption rates, and because interference competition is not thought to be common among similarly sized zooplankton (MacIssac & Gilbert 1991; Peacor *et al.* 2011).

Mesocosm experiment

Our mesocosm experiment used several food web configurations of algae, zooplankton and one or two predators to test the impact of predator personality on prey abundance, community composition and algal abundance. We tested for differences in the strength of trophic cascades using four treatments: (1) algae only ($n = 10$); (2) algae and zooplankton ($n = 10$); (3) algae, zooplankton and a single predator ($n = 27$); (4) algae, zooplankton and two predators ($n = 35$).

These treatments allow us to separate the impact of zooplankton and predator density on algal abundance – our measure of the strength of a trophic cascade (Schmitz *et al.* 2000). The higher replication for treatments with predators was to capture the variation in responses that may arise from different predator personalities.

We set up the mesocosms in mid-June by filling 1 L cylindrical plastic containers (10.5 cm diameter \times 14 cm height) with filtered pond water. We added two 20 cm \times 5 cm strips of window screening to provide structure for *Epiptera* larvae (Johansson & Rowe 1999). *Epiptera* densities were in the range of natural densities, which can exceed three individuals per litre (Fig. S4). We introduced zooplankton to the mesocosms by taking 100 mL aliquots of water from a pooled zooplankton tank. By pooling all the zooplankton collected from the pond, we ensured that the two species of zooplankton were added to each container at naturally occurring relative abundances and in approximately equal abundances across replicates (copepods: 12 individuals \pm 2.6 SD; *Daphnia*: 47 individuals \pm 9.4; based on 10 random samples). After zooplankton acclimated for 1 week, we introduced predators (Peacor *et al.* 2011). To capture natural variation in predator personality, we randomly assigned individual predators to replicates of both predator treatments.

We monitored cannibalism, abundance of each zooplankton species and algal concentration throughout the experiment. We recorded cannibalism weekly, considering only dead individuals with obvious signs of chewing to have been cannibalised (*Epiptera* only consume live prey). We sampled zooplankton bi-weekly by mixing the water, then collecting 100 mL from the centre of each mesocosm. After counting the number of individuals of each species, we returned the water and zooplankton to the mesocosm. We monitored algal abundance bi-weekly using cell counts in 1 mL subsamples, with samples collected from the centre of each mesocosm after mixing the water. We enumerated algal cells by spreading each subsample on a Petri dish and counting cells with a compound microscope. We ran the experiment for 8 weeks, allowing plankton to reproduce *c.* 5 times and the algae to reproduce hundreds of times (Peacor *et al.* 2011), and for *Epiptera* to progress through several instars (Hopper *et al.* 1996). By allowing multiple generations during the experiment, we aimed to capture population and community dynamics, rather than simply recording the immediate consumption rate of predators.

Statistical analyses

We first used our assays to test if the presence of conspecifics altered activity rate, the susceptibility of each prey species to predation and prey consumption of algae. We tested whether body size predicted activity rate using a linear model (LM) and found no effect (Fig. S1; $R^2 = 0.01$, $P > 0.3$), so excluded body size from all subsequent analyses (Brodin 2009). We used a LM to test for the repeatability of activity rate, regressing activity rate after the experiment against activity rate prior to the experiment. To determine if the presence of a conspecific altered activity rate, we used data from the conspecific predator assay with the presence or absence of a

predator as a main effect. We next used a generalised linear model (GLM) with a Poisson distribution and a log link function to test for differences in prey consumption among predators differing in activity rate. We included zooplankton species and activity rate as main effects and estimated the number of zooplankton consumed in each replicate. Finally, we used data from the zooplankton–algae assay to test if algal abundance differed between zooplankton species.

We used LMs to test the effects of predator personality on zooplankton abundance, community structure and algal abundance in mesocosms. We used final abundances and community composition in all analyses, although analysing data as a time series yielded similar results (Figs S5–S12). We first used a Poisson GLM to test for differences in total prey abundance, including treatment and activity rate as main effects. Similarly, we tested for effects of activity rate and treatment on algal abundance using a Poisson GLM. To test for differences in community structure, we tested the proportion of copepods in the entire community using a logistic GLM with a binomial distribution and treatment and activity rate as main effects. While personality types may interact in complex ways (Pruitt & Ferrari 2011), our experiment was designed to test for ecological consequences of predator personality rather than the interactions among personality types. We therefore summed the activity rates of individuals within a replicate to represent activity rate in mesocosms with two predators.

To discern the proximate cause of trophic cascades, we explored the effects of community composition and prey abundance on algal abundance in the mesocosms. We tested for these effects using a Poisson GLM to estimate algal abundance, including prey abundance and the relative abundance of copepods as main effects. We excluded the algae-only treatment for this test.

We then determined if activity rate predicted patterns of cannibalism and subsequent differences in zooplankton abundance, community structure and algal abundance. We first repeated all above analyses of mesocosms while excluding data from replicates where cannibalism occurred. We then conducted a number of GLMs using only data from the two-predator treatment as cannibalism was impossible in all other treatments. In particular, we used a logistic GLM with a binomial distribution to test for the effects of activity on cannibalism. We then tested the effect of activity rate and cannibalism on zooplankton abundance (Poisson GLM), the relative abundance of copepods (binomial GLM) and algal abundance (Poisson GLM). In all above analyses we used the full model with interactions, dropping non-significant interactive terms. We used log-likelihood ratios to test for significance of all models, with likelihoods determined from the maximum likelihood solution. Statistical analyses were conducted in R (version 3.1.1, 2014) using the base and ‘lme4’ packages (Bates *et al.* 2015).

RESULTS

Our assays showed that predators had highly variable activity rates, and assays repeated following experiments showed that predator personality was consistent through time (Fig. S3; $P < 0.001$, $R = 0.73$). Active predators consumed *c.* 50%

more *Daphnia* ($P < 0.001$), and *Daphnia* but not copepods were particularly sensitive to active predators (Fig. 1a; Species \times Activity interaction, $P = 0.03$). Copepods also consumed less algae (Fig. 1b; $P < 0.001$), creating a potential trade-off between susceptibility to predation and competitive ability. The presence of a conspecific did not alter activity rates of *Epitheca* (Fig. S2; $P = 0.44$).

We next tested the effect of activity rate on zooplankton abundance, community composition and cannibalism in the mesocosm experiment. Overall, greater *Epitheca* activity caused zooplankton to decrease by 65% and shift to copepod-dominated assemblages, and higher *Epitheca* activity rates also generated up to a threefold increase in algae. However, greater activity also increased cannibalism, which dampened the impact on zooplankton and the resulting shift in algal abundance. We outline the individual tests that support these conclusions below.

Zooplankton abundance dropped by *c.* 50% when one predator was present, and by *c.* 70% when two were present (Fig. 2a; $P < 0.001$). Active predators depressed zooplankton abundance more than inactive individuals (*c.* 60% difference in Fig. 2b; $P < 0.001$), particularly in the one-predator treatment (Fig. 2b; Treatment \times Activity Rate interaction, $P = 0.007$). This interaction caused two-predator treatments to have greater consumption when predators were inactive (left side of Fig. 2b), but not when predators were active (intersecting lines, Fig. 2b). This interaction disappeared when we excluded replicates where cannibalism occurred (red dashed line and points, Fig. 2b; $P > 0.4$).

The relative abundance of copepods increased with predator abundance from nearly absent to composing *c.* 40% of the community (Fig. 3a; effect of treatment, $P = 0.004$). Interestingly, the total abundance of copepods were also greatest when two predators were present ($P = 0.02$), increasing by 1.3 times in this treatment relative to the no predator treatment (Fig. S8). Similarly, the relative abundance of copepods increased when predators were active, particularly when one predator was present (Fig. 3b; Treatment \times Activity Rate

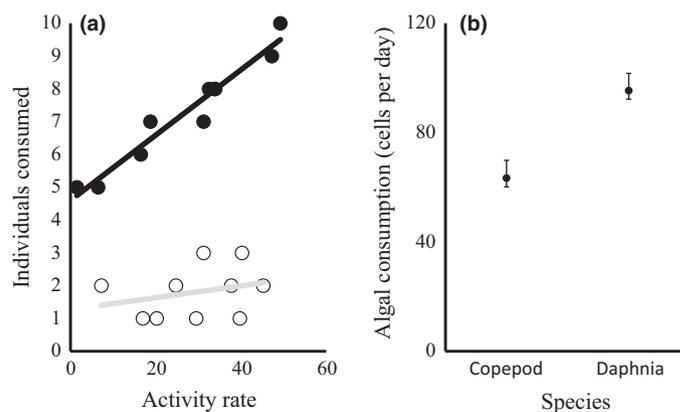


Figure 1 Results of two assays used to inform results of the mesocosm experiment. Fewer copepods (white circles, grey line) than *Daphnia* (black circles and line) were consumed in our assay (a), with *Daphnia* but not copepods being sensitive to differences in activity rate. Copepods consumed less algae than *Daphnia* in our assay (b). Error bars represent 1 SD.

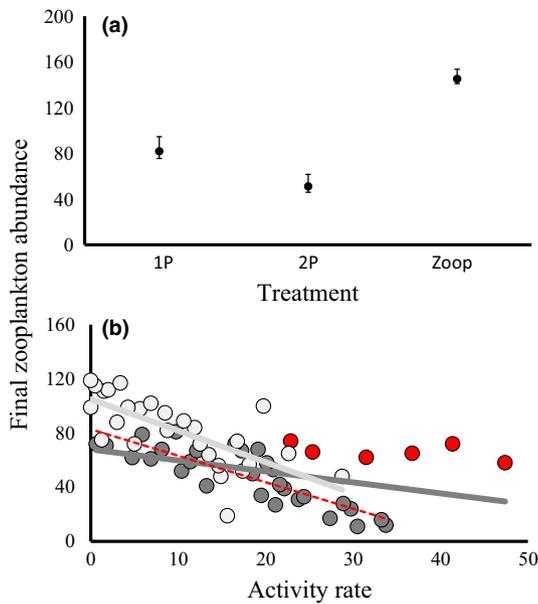


Figure 2 The abundance of zooplankton in the mesocosm experiment. Zooplankton were most abundant when predators were absent and least abundant in treatments with two predators (a; 1P = one predator, 2P = two predators, Zoop = zooplankton only). Error bars represent 1 SD. Active predators, measured as the total movement during the activity rate assay, depressed zooplankton numbers more than inactive predators (b). The effect of activity rate was greater in the one-predator treatment (b; light grey line and circles), a pattern that disappeared when replicates where cannibalism occurred (red points) were excluded from the analysis (dashed red line). Best fit lines are predicted values from a GLM.

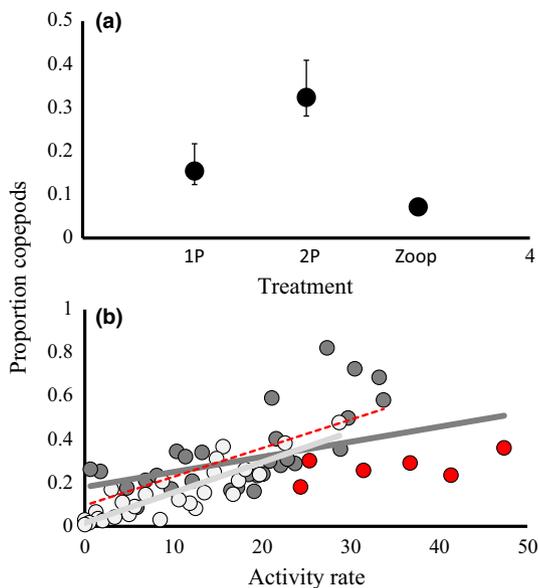


Figure 3 Patterns of copepod relative abundance. Copepods comprised a large proportion of the total zooplankton community when predators were present, particularly in the two-predator treatment (a; 1P = one predator, 2P = two predators, Zoop = zooplankton only). Error bars represent 1 SD. Active predators increased the relative abundance of copepods, particularly in the one-predator treatment (b; light grey line and circles), a pattern that disappeared when replicates where cannibalism occurred (red points) were excluded from the analysis (dashed red line). Best fit lines are predicted values from a LM.

interaction, $P < 0.001$), however this interaction disappeared when replicates where cannibalism occurred were excluded (red dashed line and points, Fig. 3b; $P > 0.45$).

Zooplankton reduced algae densities when predators were absent (Fig. 4a; 17 vs. 125 cells/mL), and predators counteracted this effect, causing a trophic cascade (Fig. 4a; two predator: 74 cell/mL, one predator: 51 cell/mL; $P = 0.027$). Active predators caused a greater increase in algal abundance (active predator: *c.* 100 cell/mL, inactive predator: *c.* 30 cell/mL, Fig. 4b; $P = 0.002$), particularly when only one predator was present (Fig. 4b; Treatment \times Activity Rate interaction, $P < 0.001$). The significant Treatment \times Activity Rate interaction was driven by cannibalism, as removing replicates where cannibalism occurred caused the interaction to disappear (red line, Fig. 4b; $P = 0.22$). The proximate cause of increased algal abundance was both fewer total zooplankton (Fig. 5b; $P < 0.001$) and an increased relative abundance of copepods (Fig. 5a; $P < 0.001$), a species which has little impact on algae (Fig. 1b).

More active predators were more likely to be involved in cannibalistic interactions (Fig. 6a; $P = 0.014$). However, the individual that survived a cannibalistic interaction was not predicted by activity rate ($P > 0.6$) and was predicted by body size ($P = 0.03$). Cannibalism caused measurable impacts on zooplankton and algae in the two-predator treatment – when cannibalism occurred, zooplankton abundance was 1.5 times higher (Fig. 6b; $P < 0.001$), copepod relative abundance increased by 1.5 times (Fig. 6c; $P = 0.006$) and algae

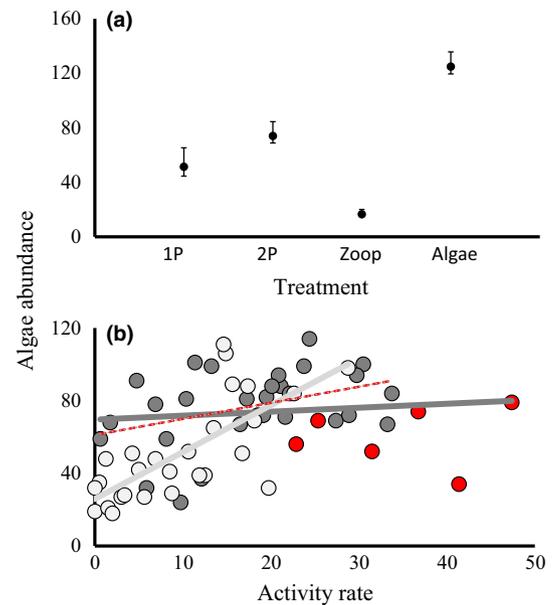


Figure 4 Algal abundances across and within treatments. Algae were most abundant in the absence of zooplankton and were found at greater abundance in treatments with zooplankton when predators were also present (a; 1p = one predator, 2P = two predators, Zoop = zooplankton, Algae = algae-only treatment). Error bars represent 1 SD. Active predators increased algal abundances more so than inactive individuals, particularly in the one-predator treatment (b; light grey line and circle), a pattern that disappeared when replicates where cannibalism occurred (red points) were excluded from the analysis (dashed red line). Best fit lines are predicted values from a GLM.

abundance fell by 21% (Fig. 6d; $P < 0.001$). Using total activity rate to predict predator impacts also illustrated the effects of cannibalism; removing two-predator treatments in which cannibalism occurred caused predator activity to have

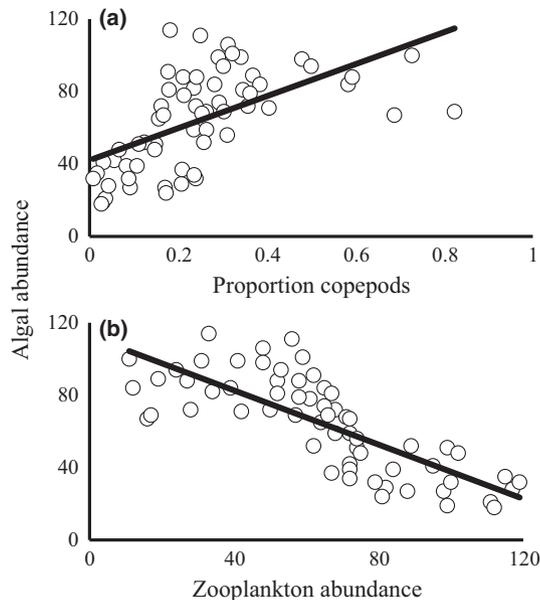


Figure 5 The impact of zooplankton communities on algal abundance. Both fewer total zooplankton (b) and a higher relative abundance of copepods (a) increased algal abundance. Best fit lines are predicted values from a GLM.

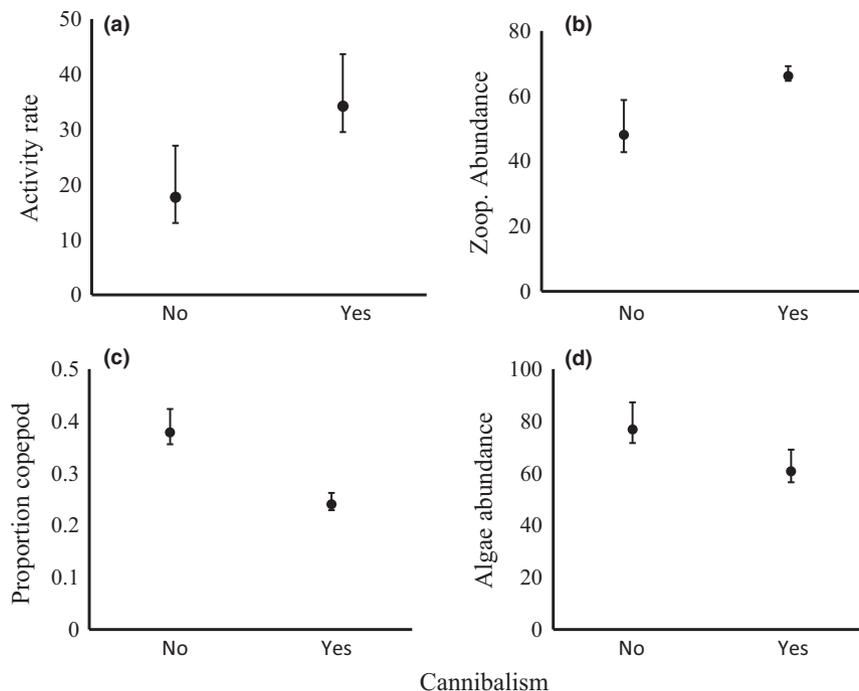


Figure 6 The effects of activity rate on cannibalism and the subsequent impacts on zooplankton and algae. Cannibalism was more likely to occur when the mean activity rate of both predators was high (a). Cannibalism increased the abundance of zooplankton (b) and reduced the relative abundance of copepods (c). Cannibalism also reduced the abundance of algae (d). Error bars represent 1 SD. Note that we switched the explanatory and response variable in panel (a) for presentation only.

consistent impacts on zooplankton abundance, algae abundance and zooplankton composition, regardless of predator density (Figs 2b, 3b and 4b).

DISCUSSION

Our study demonstrates how intraspecific differences in predator personality that naturally occur within populations can affect community composition and trophic interactions over multiple generations. Predators with active personalities decreased the abundance of both prey species more than inactive predators (Fig. 2b; Royauté & Pruitt 2015). Both prey species saw declines, but copepods increased in abundance relative to *Daphnia* (Fig. 3), indicating that the former is less susceptible to predation (Fig. 1a). While copepods are less susceptible to predation (Fig. 1a), they have a smaller impact on algae abundance (Fig. 1b) and are competitively inferior when predators are absent (Figs 3 and S8). Reduced prey abundance together with shifts in prey community composition increased the abundance of algae (Fig. 5a and b), resulting in active predators creating stronger trophic cascades than inactive individuals (Fig. 4). These patterns of prey abundance, community composition and the strength of trophic cascades are consistent across predator densities, but in all cases weaker when both predators are active (dark grey line in Figs 2b, 3b and 4b). The weakening of these patterns at higher predator density is seemingly caused by increased cannibalism when predators are active (Fig. 6). Following cannibalism, predator density is effectively reduced, allowing increased prey abundance (Fig. 6b and c) and ultimately

decreased algal abundance (Fig. 6d). The interactive effect of personality and density suggests that variation in personality may not simply average out in its effect on community dynamics, at least at high densities, as high-activity individuals are more likely to suffer from cannibalism. More generally, intraspecific differences in animal personality influence prey abundance and community composition (Sih *et al.* 2004; Royauté & Pruitt 2015) and, in so doing, mediate the strength of trophic cascades.

An important component of our trophic cascade arose through the effect of intraspecific differences among predators on prey community structure (Araújo *et al.* 2011; Sih *et al.* 2012). The high prey mortality associated with active predators translated into shifts in community composition towards predator resistant prey (Fig. 3b). These shifts likely occurred because, despite an unchanging predator density, active individuals imposed a greater selective force owing to higher rates of prey consumption (Fig. 1a; Brodin 2009). Similar shifts in community composition have been attributed to interspecific variation or population-level differences among predators (Morin 1983; Post *et al.* 2008). Large shifts in zooplankton communities are frequently observed following the replacement of invertebrates with fish as the top predator in ponds (Vanni 1987; Mittelbach 1988). More subtly, Post *et al.* (2008) observed among species shifts in body size and other life-history traits of zooplankton in lakes where the dominant fish predator was either resident or anadromous. While shifts in prey community composition are commonly attributed to differences among predator species or populations, our study highlights that different behavioural phenotypes of a single predator population can also drive such shifts.

Our results suggest that predator personality not only creates differences in prey community composition, but may mediate prey species coexistence. We found that predator-resistant copepods were out-competed by *Daphnia* in the absence of predators (Fig. 3a; Steiner & Leibold 2004). This result, along with the weaker effect of predators on copepods in our predation assay (Fig. 1a) and the greater impact of *Daphnia* on algae (Fig. 1b), suggests that these species may exist along a predation competition continuum (Werner & Anholt 1993; Kneitel & Chase 2004). Because predator personality regulates the impact of predators (Figs 1–3; Sih *et al.* 2012; Royauté & Pruitt 2015), variation in predator personality may promote coexistence of multiple species who trade-off between predation and competition (Abrams 1999). This type of trade-off has been well documented, including in zooplankton communities (Chase *et al.* 2002), but has not been attributed to predator personality or intraspecific variation in a predator population. Together, our results suggest that intraspecific differences could alter species interactions, allowing for the coexistence of multiple prey types.

Changes in prey abundance are often considered the proximate mechanism determining the strength of trophic cascades, yet changes in prey community composition may have underappreciated effects. Active predators drove a consistent shift in communities towards increased relative abundance of copepods (Fig. 3b) which have a lesser impact on algae than *Daphnia* (Fig. 1b). A back-of-the-envelope calculation using these data (Figs 1b and 3) suggests that the shift in

community composition accounts for *c.* 20% of the effect of predators on algae. The wealth of examples demonstrating that predators alter prey community composition (Lindeman 1942; Paine 1966; Morin 1983; Schmitz *et al.* 2000), along with the commonness of predation competition trade-offs (Kneitel & Chase 2004), suggest that this mechanism may be widespread (Peacor *et al.* 2011). Given that many studies of trophic cascades treat species within a trophic level as equal, exploring how prey community composition affects trophic cascades could offer new insights into the biology underlying shifts in prey and resource abundances.

High predator densities may reduce trophic cascades indirectly through behavioural modification of predators, or directly through interference or cannibalism (Johnson & Sih 2005). In our system, active predators consistently reduced prey communities and increased algae abundance, but these effects were tempered by intraspecific interactions when predator activity was particularly high (reduced slope for two-predator treatment in Figs 2b, 3b and 4b). Our results suggest that cannibalism is the proximate mechanism reducing the effect of predator personality on trophic cascades, as cannibalism increased when both predators were active, and differences among density treatments disappeared when mesocosms that experienced cannibalism were removed from the analysis (red dashed line in Figs 2b, 3b and 4b). In other words, cannibalism caused prey to increase in abundance (Fig. 6b), caused communities to shift towards high *Daphnia* abundance (Fig. 6c) and ultimately reduced the strength of trophic cascades (Fig. 6d). Interestingly, a *post hoc* analysis of the two-predator treatments showed an additional effect of the variation in predator traits on trophic cascades, where more variable pairs had larger impacts on zooplankton and resulted in greater algal abundances (Figs S13 and S14). The shift in cannibalism as more extreme, active individuals encounter each other, along with the intriguing suggestion that more variable predators are more efficient at consuming prey than similar predators, suggests that populations consisting of variable personalities may produce distinct community dynamics.

Interspecific interactions among predator species also frequently dampen trophic cascades through intraguild predation (Finke & Denno 2005), yet the consequences of interspecific interactions are likely distinct from those generated by intraspecific differences. Theory posits that intraguild predation can only persist when the ‘top’ predator is a poorer competitor for prey species (Holt and Polis 1997), causing predation of the intermediate predator to have a disproportionately positive impact on prey (Claessen *et al.* 2004). Cannibalism, on the other hand, does not necessarily cause the loss of individuals with a greater impact on prey – as in our study it may even be unrelated to consumptive impact. In this case, the loss of individuals to cannibalism does not change the mean consumption rate per predator (Figs 2b, 3b and 4b). However, energetic gains by large individuals following cannibalism may accelerate emergence (Polis 1981), further decreasing within-pond densities and generating stronger positive feedbacks on prey species. These feedbacks generated by cannibalism frequently induce population cycles or even chaos but, unlike with intraguild predation, cannot cause the extinction of the ‘intermediate’ predator without collapsing the

entire food chain (Claessen *et al.* 2004). The density-dependent nature of cannibalism, and the link between cannibalistic interactions and activity rate without greater survival of high-activity individuals, suggests that activity rate may experience distinct evolutionary pressures that depend on local densities (Polis 1981). In sum, cannibalism and intraguild predation have qualitatively similar short-term consequences on prey, but their effects manifest through different mechanisms and the magnitude these effects on prey density and community composition differs (Claessen *et al.* 2004).

By considering animal personality in the context of food web dynamics, our work has helped to elucidate the importance of intraspecific variation in community ecology (Bolnick *et al.* 2011). We have demonstrated that predator personality creates differences not only in the abundance of prey communities but also in their composition (Royauté & Pruitt 2015), and that these differences determine the strength of trophic cascades. We further suggest that intraspecific variation in one species can allow for the coexistence of the species with which it interacts (Pruitt *et al.* 2012). Finally, we show that while the effects of personality on trophic cascades have a consistent direction, personality also influences the strength of trophic cascades by increasing cannibalism at the top trophic level (Rudolf 2007). These far reaching effects of behaviour were driven by naturally occurring frequencies of predator personalities and highlight their potential importance in natural communities (Sih *et al.* 2012). The commonness of varied animal personalities and the omnipresence of intraspecific variation suggests that these types of dynamics are likely to be widespread in nature.

ACKNOWLEDGEMENTS

We would like to thank Shannon McCauley for helping to identify larvae and for her constant and helpful input and advice. We thank several undergraduate students who helped to collect larvae. We also thank the staff members of the Koffler Scientific Reserve for their hospitality and technical support. Research funding was provided by NSERC (B.G.) and personal funding was awarded by both Ontario Graduate Scholarships and the Koffler Scientific Reserve (D.S.).

AUTHORSHIP

DS conceived of the study, and collected and analysed the data. DS/BG wrote and approved the manuscript.

COMPETING INTERESTS

We have no competing interests.

DATA ACCESSIBILITY

Data will be made accessible through Dryad.

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SUPPORTING INFORMATION

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Editor, Andrew Sih

Manuscript received 30 August 2016

First decision made 3 October 2016

Second decision made 4 December 2016

Manuscript accepted 19 December 2016