Caddisfly behavioral responses to drying cues in temporary ponds: implications for effects of climate change

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Abstract: Aquatic organisms that live at high latitudes and elevations are especially vulnerable to climate-change-induced alterations in snowpack, snowmelt, and evaporation rates, all of which affect basin filling and drying dates. Extraordinarily early drying events in shallow ponds and wetlands at our study sites prompted us to conduct 2 mesocosm experiments to document how proximate cues of drying modify agonistic behaviors among larvae of the caddisfly, *Asynarchus nigriculus*. Larvae are mainly detritivores but can be extremely aggressive and engage in mob cannibalism, perhaps to obtain a dietary supplement that hastens escape from drying basins. In one experiment, we manipulated caddisfly density to simulate the effects of crowding during pond drying. In a 2nd experiment, we reduced water levels and manipulated a protein supplement that mimics the dietary benefits of cannibalism. We quantified the effects of those manipulations on aggressive behaviors that are precursors to cannibalism and on development time to pupation. Frequency and duration of agonistic encounters increased as a function of larval density and, independent of density, were higher in drying than nondrying treatments, especially in the absence of a protein supplement. Pupation occurred earlier in high- than low-density treatments and earlier with than without a protein supplement. In contrast, the timing of pupation was not accelerated in drying compared with nondrying treatments, which might reflect the extreme diel temperature fluctuations in drying ponds, hence suboptimal growth conditions. Our findings provide evidence that declining water levels and crowding serve as cues that enable caddisflies to adjust behavior and development in the face of habitat drying. Early drying events observed in recent years may exceed the limits of this flexibility and portend the demise of populations in temporary habitats that historically supported this species.

Key words: climate change, ponds, wetlands, drying, aggressive behavior, cannibalism, development time, alpine ponds

Global temperatures are projected to continue to increase during the next century, resulting in a dryer, warmer climate in many parts of the world (IPCC 2014). Climate-change effects have been documented in a wide range of standing and running freshwater habitats (e.g., Smol et al. 2005, Parker et al. 2008, Woodward et al. 2010). Negative effects are predicted to be especially strong in arid environments where organisms in intermittent streams (Stanley et al. 1997, Chessman 2015) and shallow standing waters (Sim et al. 2013) should be especially vulnerable. Rapid and dramatic changes also have occurred in shallow ponds and lakes at high latitudes and high elevations where low humidity, low water volumes, and high surface area-to-depth ratios make them especially vulnerable to changes in snowpack and timing of snowmelt (e.g., Barnett et al. 2005, Corcoran et al. 2009, Wissinger et al. 2016).

Animals in temporary habitats exhibit a wide array of adaptations for surviving desiccation (reviewed by Strachan et al. 2014a), and many should be especially responsive to interannual variation in weather and long-term changes in climate that affect basin hydroperiod. Individual responses to drying are triggered by a variety of cues, such as photoperiod, temperature, and heating degree-days, water chemistry, and wetting and drying events. Those cues, in turn, influence behaviors, aestivation, and life-cycle events including diapause, egg eclosion, larval pupation, emergence, and adult flight, which in concert facilitate survival and the eventual completion of development (Williams 1996, 2006, Wissinger 1999, Strachan et al. 2014b).

Some temporary-habitat specialists exhibit plasticity in their response to seasonal, interannual, and long-term changes in temperature and the duration of the wet–dry

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phases of pond hydroperiods (Baird et al. 1987, De Block et al. 2008, Stoks et al. 2014). However, for many organisms, the degree of flexibility is unknown. Moreover, studies documenting species-specific life history, behavioral responses such as movement to refuges, tolerance to changing conditions (O_2, temperature, crowding) as habitats dry, and the abilities to endure desiccation and recolonize (e.g., Walters and Post 2011, Chester and Robson 2011, Chessman 2013, 2015) will be needed to predict which species will be among the winners and losers in the face of a changing climate (Rosset and Oertli 2011).

The cues that trigger developmental and behavioral flexibility in aquatic invertebrates include increased temperature (e.g., Harper and Peckarsky 2006), decreased water volume or depth (e.g., Juliano and Stoffregen 1994), changes in food availability, and combinations of those cues (Johansson et al. 2001, De Block and Stoks 2004a, b, Jannot et al. 2008). However, developmental flexibility in response to changes in time constraints is not without cost. For example, smaller body sizes associated with early emergence reduce adult fitness (Loman and Claesson 2003, De Block and Stoks 2005). Moreover, animals exposed to desiccation can have lowered survival (Wickson et al. 2012 and reduced immune function (Gervasi and Foufopoulos 2008). Population-level and fitness outcomes associated with such costs can in turn influence community structure and ecosystem function (Meyer et al. 1999, Leberfinger et al. 2010).

In the central Rocky Mountains (western USA), long-term shifts in snowpack, snowmelt, and spring temperatures have led to increasingly erratic basin drying. Extraordinarily early drying of shallow ponds at our long-term study sites has led to cohort failures in a variety of aquatic invertebrates, including those of the caddisfly *Asynarchus nigriculus* (Trichoptera: Limnephilidae), a species for which such cohort loss has become increasingly frequent (Greig and Wissinger 2010). Larvae of this temporary-habitat specialist develop rapidly and synchronously during and after snowmelt and emerge in early summer just before the shallow, temporary basins they inhabit dry (see Wissinger et al. 2003 for detailed life-history data). Near the end of development, larvae are often crowded into increasingly smaller and shallower pools where it is easy to observe their frenetic foraging activities and aggressiveness toward conspecifics, behavior that includes cannibalism (Wissinger et al. 1996, 2004a). We have documented the population- and community-level consequences of *A. nigriculus* cannibalism (Greig and Wissinger 2010), but we have not previously quantified how proximate cues that signal impending drying affect aggressive behavioral interactions (including cannibalism) among larvae.

Our purpose was to quantify how crowding and decreased water level affect behavioral interactions among *A. nigriculus* larvae. We were interested in separating the response of larvae to decreased water levels per se from that caused by the crowding that occurs as the wetted areas of ponds shrink during drying. We separately manipulated those cues in 2 experiments conducted in mesocosms adjacent to drying ponds. In the 1st experiment, we varied the size of mesocosms to simulate the crowding that occurs in natural basins as they shrink in size (Fig. 1A, B). Cannibalism often has been observed as a response to an increase in density (Fox 1975, Polis 1981), and we hypothesized that agonistic interactions would increase as a result of crowd-

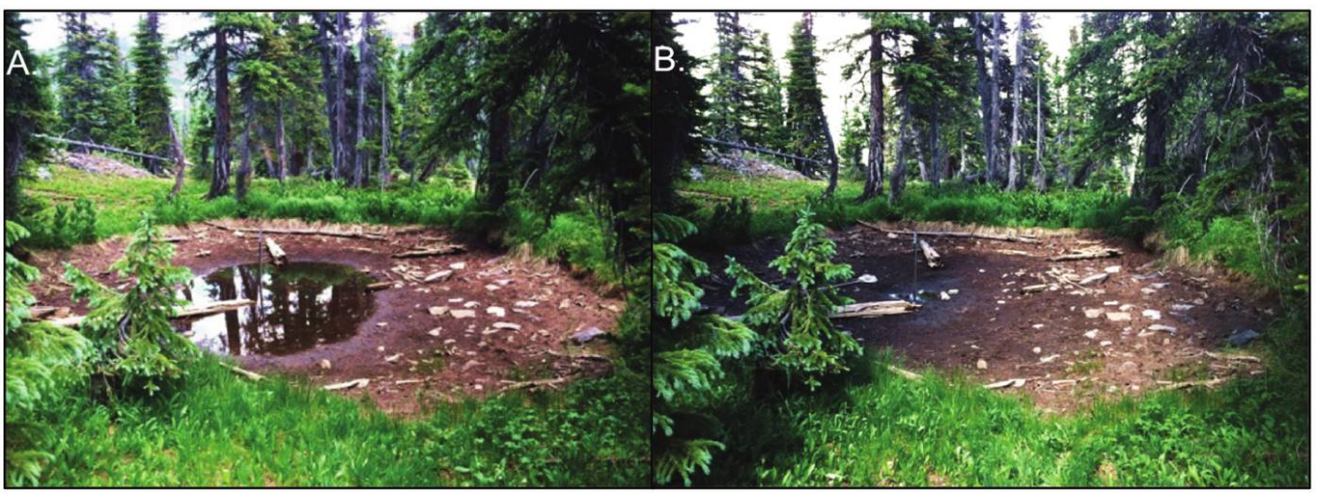

Figure 1. Photographs showing the difference in size of a temporary pond during drying at the Mexican Cut Nature Preserve on 27 June (A) and 30 June (B) 2012 (photo credit: JOL). Snowmelt fills the pond to the vegetated perimeter each spring. The entire cohort of *Asynarchus nigriculus* larvae in this and dozens of nearby similar ponds perished in 2012 when the ponds dried before larval development was completed.

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ing, which, in turn, would lead to increased cannibalism and increased growth rates among survivors. In the 2nd experiment, we varied water depth without changing larval density and manipulated a dietary supplement to test whether a combination of that particular drying cue and protein limitation affects aggression among larvae. We hypothesized that the threat of drying should increase aggressiveness among larvae and that protein supplementation should allay aggression, especially under drying conditions.

METHODS

Study system

We conducted this study at The Nature Conservancy's Mexican Cut Nature Preserve (MCNP; lat 41.695888, long −80.016244; elevation 3500 m) near the Rocky Mountain Biological Laboratory in the Elk Mountains of Colorado (USA). Multidecadal shifts in snowpack, snowmelt, summer precipitation, and air temperatures are well documented in this region (Clow 2010) as are the consequences of these shifts for high-elevation plants (Anderson et al. 2012, Boggs and Inouye 2012) and animals (Inouye and Barr 2006, Ozgul et al. 2010). *Asynarchus nigriculus* occurs throughout the central Rocky Mountains at subalpine and alpine elevations (Herrmann et al. 1986). The larvae are the biomass-dominant macroinvertebrate in short-duration temporary ponds and wetlands at our study site and throughout the region (Wissinger et al. 2003). High activity and high foraging rates of larvae typically facilitate rapid, synchronous development and emergence from vernal habitats (<60 d). During the past 2 decades, drying events that result in cohort failures of *A. nigriculus* subpopulations have become increasingly frequent in temporary habitats at our study sites. In 2012, snow depth was ~50 cm lower, snowmelt date 28 d earlier, and early summer precipitation ~12 cm less than the previous 10-y average across the region (Skordahl 2013), measures that reinforce long-term trends in those climate variables (Seager et al 2007). By early June 2012, it became clear that all *A. nigriculus* larvae in most temporary and many semipermanent ponds at MCNP would die from desiccation before completing larval development. Thus, we were able to use those larvae in the 2 mesocosm experiments described below without compromising the 25 y of longitudinal time-series data on the population dynamics of this species. The relatively short-term nature of the experiments (2 wk each in mid-June to early July) reflects the narrow window during which late-instar larval behaviors can be observed in the face of drying ponds in this rapidly developing species.

Larval density and aggression

We tested the hypothesis that *A. nigriculus* larvae respond to the high densities that occur as pond area shrinks during drying by becoming more aggressive and developing more rapidly. We created variation in larval density while controlling for the number of individuals (153 larvae per mesocosm). Three replicates of 3 different sizes of plastic mesocosms were arranged randomly in an array in an open meadow between 2 temporary ponds (MCNP ponds 7 and 8 in Wissinger et al. 1999). This manipulation mimicked the phenology in adjacent drying ponds—i.e., the same numbers of late-instar larvae were increasingly concentrated into a smaller and smaller area. The bottom surface areas of the containers (and densities) were as follows: 1.65 m^2 (~100 larvae/m^2), 0.79m^2 (~200 larvae/m^2), and 0.25 m^2 (~ 600 larvae/m^2). During drying in natural ponds the area of benthic substrates decreases geometrically (Fig. 1A, B), and larval densities can reach thousands of larvae/m^2. Thus, even the highest-density treatments in our experiment are conservative compared with those we observed in natural habitats. To separate crowding from other drying cues, we maintained constant water depth in each container by adding water from an adjacent pond as necessary.

We added ~1 cm depth of detritus (a mix of spruce [*Picea engelmannii*] litter and sedge–grass [*Carex aquatilis* and *Deschampsia cespitosa*]) to each mesocosm to mimic the substrates and subsidies in caddisfly source ponds, many of which have a thin veneer of organic substrate overlying bedrock. As ponds dry and shrink in size, the available area to forage decreases for a given number of larvae. We added rocks and underwater branches as surfaces for pupation and provided fine gravel so that caddisfly larvae had access to material to prepare pupal cases. Fourth- and 5th-instar caddisfly larvae (average dry mass = 6.9 mg; instar metrics for this species were reported by Wissinger et al. 2003) were collected from an adjacent pond that we knew, based on phenological data, would dry during the course of the experiment. The source pond is part of series of ponds connected by overland flow during snowmelt and hence part of a metapopulation of this caddisfly.

Mob cannibalism in *A. nigriculus* typically occurs as the culmination of a specific sequence of aggressive behaviors—the frenetic activity of late-instar larvae escalates into fighting and is followed by mobbing of individuals that are subsequently killed and consumed. In some instances, attackers become secondary victims in these mobs (Wissinger et al. 1996). To quantify the effects of density on these behaviors, we followed 1 randomly selected focal individual in each mesocosm and recorded all behaviors during 5-min trials. We conducted multiple trials/d on alternate days (4 replicates/d × 3 replicates × 3 treatments) during the last 2 wk of June. Observers were randomly assigned to record behaviors in different replicate containers each day between 1000 and 1200 h MDT. Behaviors observed were: 1) total time active, 2) en-

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counters with other individuals, 3) encounters that were aggressive (foreleg wrestling, biting, case grazing, case defense), 4) prolonged aggressive encounters, and 5) mobbing events (Table 1; modified from Wissinger et al. 1996).

Larval development times were recorded as time to pupation (number of days from the start of the experiment to pupation), indicated by sealed stone cases affixed to substrates. We removed pupae from rock and branch substrates daily. Pupae were transferred to emergence chambers, but mass mortality in those chambers prevented us from comparing emergence dates and adult body sizes as originally intended. We did not estimate larval mortality during the experiment because that would have required disrupting the mesocosms and handling each larva, hence potentially affecting larval behaviors. We terminated the experiment at the end of 2 wk because accelerating pupation rates began to cause densities to diverge among replicates.

All statistics were done in R (version 3.0.0; R Project for Statistical Computing, Vienna, Austria). We analyzed the effect of larval density on behaviors with 1-way analyses of variance (ANOVAs) and subsequent post hoc Tukey's Honestly Significant Difference tests when the overall analysis was significant. Residual vs fitted values and quantile plots indicated all dependent variables were normally distributed and met assumptions of the ANOVA. Two-way ANOVA indicated no effect of observers or time of day (over the 12-d experiment) on any of the behavioral variables ($p > 0.05$). Thus, behaviors were averaged across observers and observation times for the final analyses. We plotted the total number of pupae as a cumulative relative frequency curve for each treatment. Numeric integration under the curve of each replicate was analyzed with ANOVA to evaluate differences in pupation rates among treatments. Lower numeric integration values represented later pupation, and higher numeric integration values represented earlier pupation: i.e., treatments in which early pupating larvae made a greater contribution to the curve area resulted in a higher value. We used a χ^2 test to compare observed number of pupae in each treatment to values expected by random chance.

Water depth as a drying cue independent of density

We conducted a subsequent 2nd experiment in the 0.25-m^2 containers (described above) to evaluate whether larvae can detect decreasing water levels (or some associated variable, such as salinity or temperature) independent of the crowding associated with reduced pond area. All containers initially contained ~11 cm of pond water. We then reduced the water level to ~2 cm depth in 4 replicates of a "drying" treatment by removing water on alternate days over a 2-wk period to reflect a rate comparable to changes observed in natural basins. We compared larval behaviors in this drying treatment to those in a nondrying (~11 cm depth on all dates) treatment (4 replicates). Because larvae might detect chemical cues associated with drying, we measured total dissolved solids (TDS) daily in drying and nondrying treatments with a handheld TDS meter (HM Digital model TDS-3, Culver City, California). We could detect no differences among replicates or between treatments (always <10 mg/L), a result that is not surprising given the extremely low ionic concentrations at this remote, high-elevation site (snowmelt water on quartzite bedrock; for extensive water-chemistry data see Harte et al. 1985, Wissinger and Whiteman 1992). We also measured maximum and minimum daily temperature in the mesocosms because previous investigators have shown that water temperatures in drying habitats fluctuate more than in permanent habitats as a result of the exaggerated diel oscillations (30°C) in air temperatures at high elevations (Jannot et al. 2008).

We added 2 similarly sized rocks and 1 submerged spruce branch as substrates for pupation. We lined the

Table 1. Ethogram of measured and calculated behaviors of caddisfly larvae.

Behavior	Description
Recorded	
Time active	Time spent crawling or interacting during 5-min observations
Encounters	Physical encounters with another individual
Aggression	Aggressive physical encounters (proleg wrestling, case shaking, biting)
Prolonged aggressions	Aggressive physical encounters lasting >3 s
Mobbing	Cannibalistic mobbing events (involving ≥5 larvae)
Calculated	
Proportion of aggressive encounters	Proportion of total encounters that were aggressive
Time aggressive	Time spent engaging in aggressive encounters = number of short aggressions (×1 s) + number of prolonged aggressions (×3 s)

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bottom of each tank with 60 ± 10 g (mean dry mass ± SE) of spruce litter and 14.7 ± 2.4 g of mixed sedge–grass and added ~75 cm^2 of gravel and fine pebbles as pupal case material. We added fifty 4th-instar *A. nigriculus* larvae (average dry mass = 4.41 mg) to each mesocosm to achieve a density of ~200 larvae/m^2, comparable to densities sampled in the source ponds. We removed pupae daily and transferred them to separate pupation chambers.

Wissinger et al. (2004b) and Jannot et al. (2008) found that protein supplementation had a positive effect on fitness correlates including development time, adult body size, and larval survival. We tested whether protein supplementation affects larval aggression and cannibalism and whether supplementation interacts with drying in a factorial design. We replicated each of the 4 treatment combinations (drying × supplementation) 4 times. In each supplementation container, we applied a high protein–fat supplement (*Tubifex*: minimum crude protein 50%, crude fat 5%; Wardley, Secaucus, New Jersey) once weekly by evenly distributing 684.6 ± 11.7 mg of freeze-dried *Tubifex* worms on the detritus. We used the same focal animal and scanning behavioral protocols and response variables described above in the density experiment (Table 1).

We used 2-way ANOVA to test the separate and interactive effects of water level and protein supplementation on larval behavior. Residual vs fitted values and quantile plots indicated all dependent variables were normally distributed and met assumptions of ANOVA. We also used 2-way ANOVAs to test for observer bias and changes in larval behaviors over time (6 observations/d for each experimental unit). We conducted a paired-difference *t*-test to compare the diel fluctuation in temperature in drying vs nondrying treatments.

We plotted the total number of pupae as a cumulative relative frequency curve for each treatment. We analyzed the numeric integration under the curve of each replicate with ANOVA to evaluate differences in pupation rates among treatments. A lower numeric integration value indicates later pupation and a higher numeric integration value indicates earlier pupation. We used a χ^2 test to compare observed number of pupae in each treatment to values expected by random chance.

RESULTS

Effects of density on larval interactions and pupation

Density did not affect overall activity during focal animal observations (1-way ANOVA: $F_{2,6} = 2.12$, $p = 0.20$) because larvae were moving nearly all of the time under all experimental densities. However, the total number of encounters of the focal animal with other individuals increased with larval density (1-way ANOVA: $F_{2,6} = 9.04$, $p < 0.001$) and resulted in a significant difference in encounters between the highest and 2 lower densities (Fig. 2A). Encounters that escalated into aggression (1-way ANOVA: $F_{2,6} = 7.42$, $p = 0.02$) and duration of aggressive encounters (1-way ANOVA: $F_{2,6} = 10.39$, $p = 0.01$) also increased with larval density (Fig. 2B, C). The number of mobbing incidents among *A. nigriculus* larvae (39 in total) increased from low to high larval density, but this result was only marginally significant (1-way ANOVA: $F_{2,6} = 4.65$, $p = 0.06$).

By the end of the experiment, 323 pupae were recovered from the mesocosms (pooled across replicates within treatments): 45 at low density, 84 at intermediate density, and 194 at high density. The distribution of pupae observed across treatments could not be attributed to differences in the initial number of larvae (all treatments started with the same number), and this distribution was different than expected by random chance ($\chi^2_{2df} = 35.23$, 2-tailed $p < 0.0001$). The 1-way ANOVA based on numeric integration of the cumulative relative frequencies for each mesocosm indicated that pupation phenology differed among the 3 larval densities ($F_{2,6} = 24.93$, $p = 0.001$; Fig. 3). In summary, more larvae pupated, and they pupated earlier at high than at low densities.

Effects of decreasing water level on larval interactions and pupation

Drying and protein supplementation did not affect overall activity levels of *A. nigriculus* larvae (2-way ANOVA, drying: $F_{1,14} = 1.02$, $p = 0.33$; protein: $F_{1,14} = 0.32$, $p = 0.58$; drying × protein: $F_{1,14} = 0.01$, $p = 0.91$) or the total numbers of encounters among larvae (2-way ANOVA, drying: $F_{1,14} = 3.14$, $p = 0.10$; protein: $F_{1,14} = 2.45$, $p = 0.14$; drying × protein: $F_{1,14} = 0.27$, $p = 0.62$; Fig. 4A). However, the proportion of encounters that were aggressive was higher in drying than nondrying treatments and in treatments without protein added than those with protein added (Fig. 4B). The interactive effect of supplementation on the proportion of aggressive encounters among larvae was not significant (2-way ANOVA, drying: $F_{1,14} = 5.76$, $p = 0.04$; protein: $F_{1,14} = 4.92$, $p = 0.05$; drying × protein: $F_{1,14} = 0.68$, $p = 0.43$; Fig. 4B).

During focal animal trials, the total time that larvae spent interacting aggressively was higher in drying than nondrying treatments and higher without than with a protein supplement (Fig. 4C). That result was driven largely by the drying/no-supplement treatment, in which larvae spent much more time interacting aggressively with conspecifics compared with the other 3 treatments. This difference was reflected in the significant drying × protein supplementation interaction term (2-way ANOVA, drying: $F_{1,14} = 6.41$, $p = 0.03$; protein: $F_{1,14} = 6.29$, $p = 0.03$; drying × protein: $F_{1,14} = 4.95$, $p = 0.05$; Fig. 4C). We observed 5 mobbing events, all of which occurred in the drying/no-supplement treatment.

As is typical in natural ponds, the number of larvae declined in all treatments during the experiment, in part

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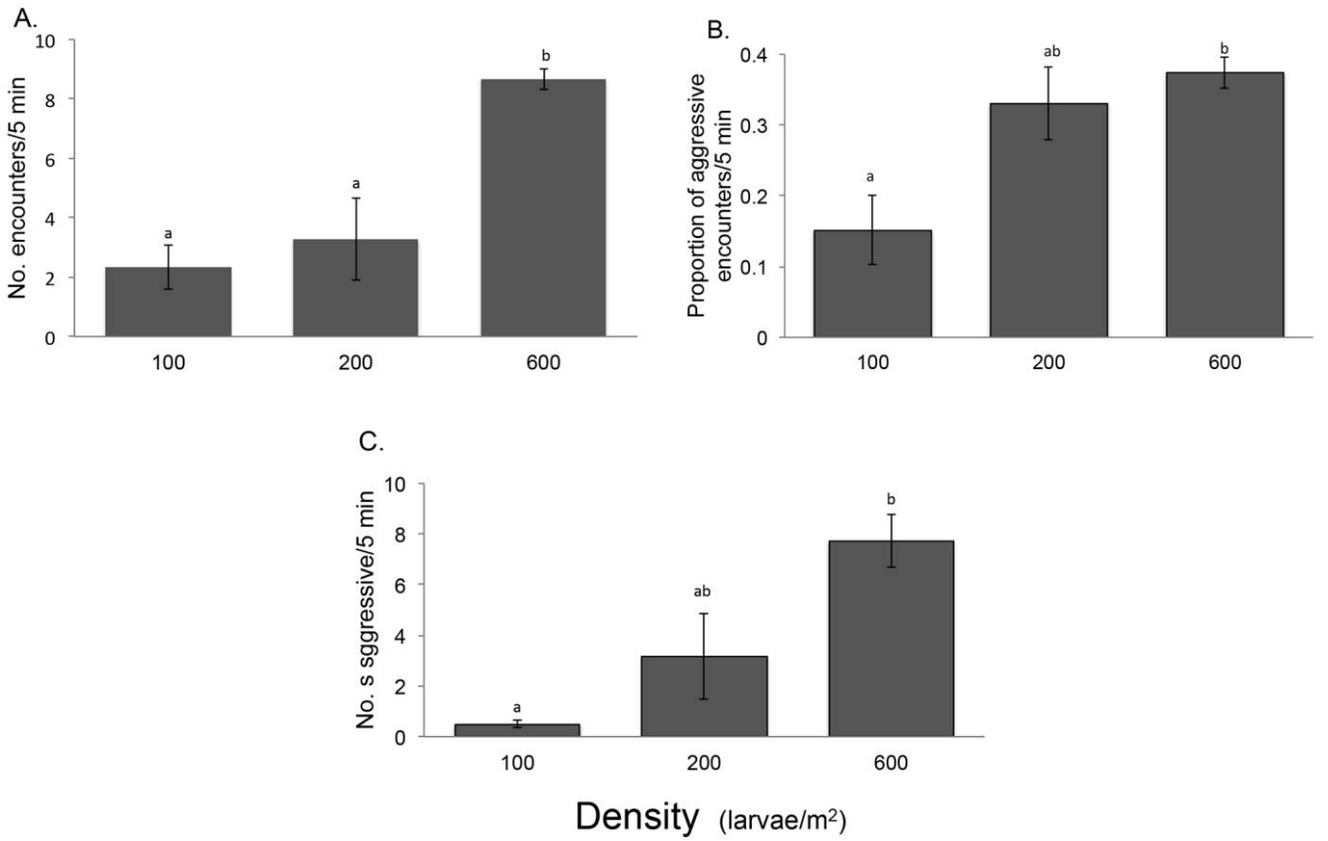

Figure 2. Mean (±1 SE) total number of encounters (A), proportion of total encounters that were aggressive (B), and number of seconds spent aggressively interacting with other individuals (C) observed per 5-min focal observation for each larval density treatment. Bars with the same letters are not significantly different.

as a result of pupation. At the end of the drying experiment, 154 *A. nigriculus* pupae had been removed (replicates were pooled within treatments; drying +/−protein: 22/11, nondrying +/−protein: 57/64). A χ^2 test revealed that the results were significantly different than expected by random chance. Fewer individuals pupated in the drying than the nondrying treatments, and protein supplementation did not affect the number of individuals that pupated (χ^2 test, all treatments: $\chi^2_{3df} = 52.49$, 2-tailed $p < 0.0001$; protein treatments: $\chi^2_{1df} = 1.361$, 2-tailed $p = 0.24$; drying treatments: $\chi^2_{1df} = 50.29$, 2-tailed $p < 0.0001$; Fig. 5A). Numeric integration of the cumulative relative frequencies to evaluate differences between the dates of pupation revealed no difference in the phenology of pupation among treatments (1-way ANOVA, $F_{1,14} = 0.30$, $p = 0.82$; Fig. 5B). Drying resulted in fewer individuals pupating by the end of the experiment but did not affect the timing of pupation.

Daily temperature fluctuations were greater in drying than nondrying treatments (paired-difference *t*-test, $t_{12df} = 2.4$, $p = 0.02$). On average, daily temperatures fluctuated 4°C more in drying than nondrying mesocosms, and in several instances toward the end of the experiment >10°C more in drying than nondrying treatments. On many days, daily fluctuations in drying treatments were >30°C (from <5 to >30°C).

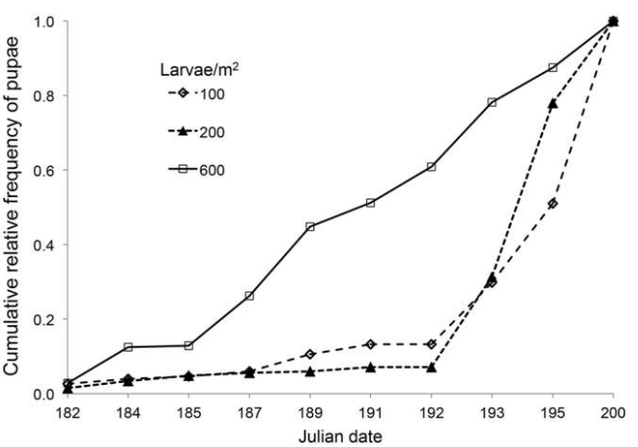

Figure 3. Cumulative relative frequency of pupae over time for each larval density treatment.

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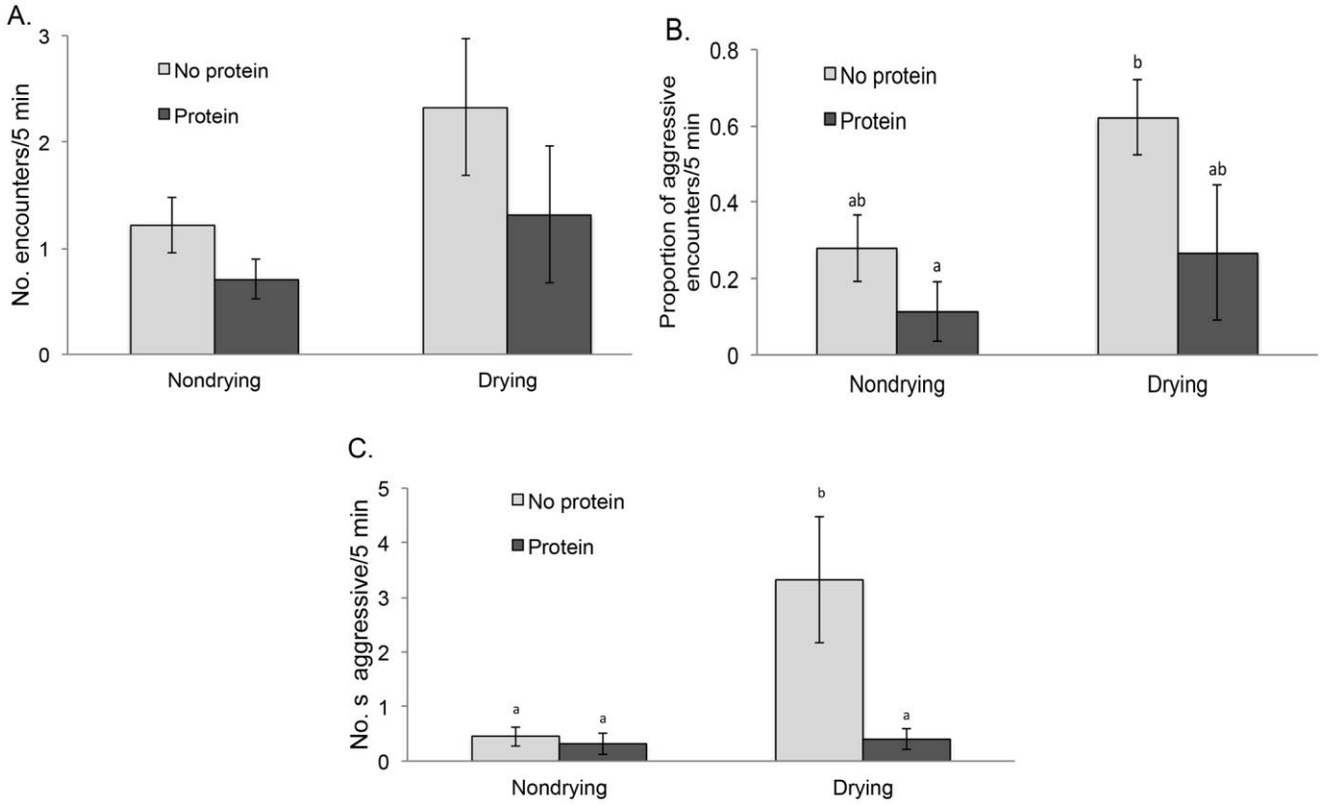

Figure 4. Mean (±1 SE) total number of encounters (A), proportion of encounters that were aggressive (B), and duration of aggressive encounters (C) during 5-min focal observations in drying and protein supplementation treatments. Bars with the same letters are not significantly different.

DISCUSSION

Early drying, crowding, and cannibalism

Crowding into smaller and smaller pool sizes as a consequence of habitat drying—and hence higher and higher densities—could be a cue detected by aquatic organisms that live in temporary habitats. We found that: 1) number of encounters, 2) proportion of encounters that escalated into aggressive behaviors (proleg wrestling, biting, case grazing, and case shaking to eject case-grazing conspecifics), 3) duration of sustained aggression, and 4) number of mobbings of caddisfly larvae increased with density. These results provide new evidence that the frequency and nature of aggressive behaviors in this species increase with crowding. Our study also provides quantitative evidence for previous anecdotal observations reported for natural ponds and experiments in which we studied population-level outcomes of cannibalism (Wissinger et al. 1996, 2004a).

Density-dependent aggression and cannibalism are well documented among carnivores (Fox 1975, Polis 1981), including aquatic invertebrates that live in temporary habitats (Johansson and Rowe 1999, De Block and Stoks 2004a, Rossi et al. 2011). In contrast, the caddisflies in our study usually obtain most of their nutrition from microbially colonized vascular plant detritus. Cannibalism in noncarnivores typically occurs between life stages that present minimal risk to the cannibals (e.g., larvae eating eggs; Richardson et al. 2010). Here, aggression and cannibalism occur between larvae of similar size, and we know from previous studies that potential costs of reciprocity are extremely high; e.g., attackers injured in cannibalistic mobs become secondary victims (Wissinger et al. 2004a). Cannibalism should evolve only if benefits (e.g., eliminate competitors, gain nutrition) outweigh costs (e.g., injury or death, disease transmission; Elgar and Crespi 1992, Nishimura and Isoda 2004. Thus, our results raise the question: what are the benefits of aggressive behaviors that escalate to cannibalism in this and other species that live in temporary habitats?

One hypothesis for the evolution of cannibalism in detritivores that live in temporary waters is that it provides a high-energy, high-protein food supplement that accelerates development. This "life-boat strategy" (sensu De Block and Stoks 2004a, b) should be especially important for noncarnivorous taxa. Comparison of the protein and energy contents of different aquatic food sources empha-

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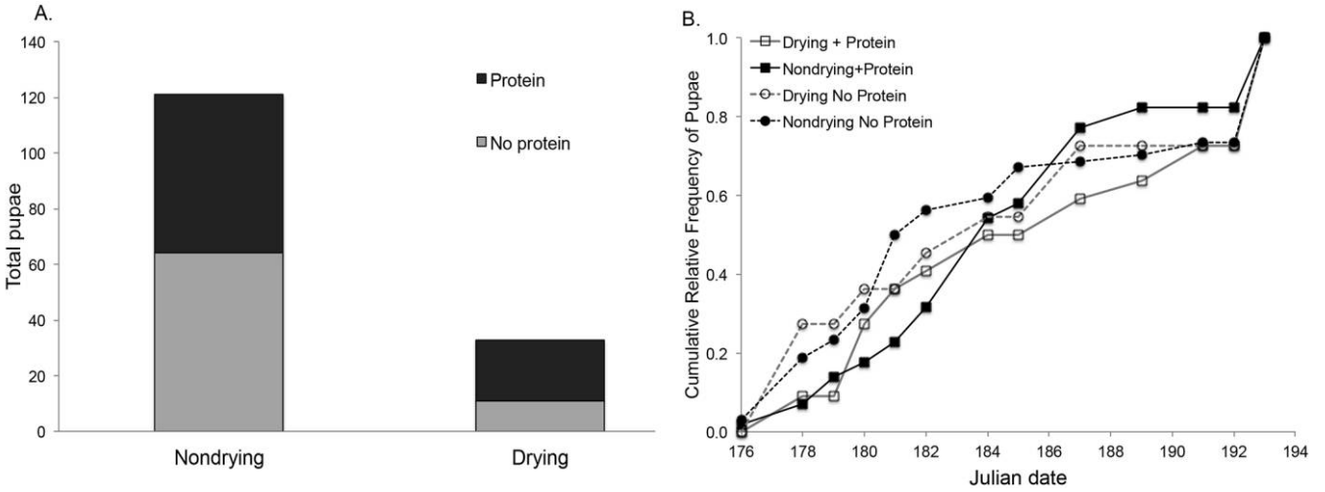

Figure 5. Total number of pupae (A) and cumulative relative frequency of pupae over time (B) in drying and protein treatments.

sizes that animal material (15–28 mg/kJ protein, 20–33 kJ/g gross energy) is a high-quality nutritional resource compared with detritus, even after microbial conditioning (1–20 mg/kJ protein, 5–10 kJ/g gross energy; Bowen et al. 1995, also see Cargill et al. 1985).

The behavioral responses to protein supplementation in the drying experiment are consistent with this hypothesis; i.e., agonistic behaviors (proportion of encounters that escalate into aggressive encounters, duration of aggressive interactions) were lower in treatments with than without an alternative protein supplement. Moreover, protein supplementation increased the number of larvae that pupated by the end of the experiment in drying and nondrying treatments. Thus, our results provide a behavioral explanation for outcomes of previous experiments in which nutrient supplementation accelerated pupation and led to emergence of larger adults (Wissinger et al. 2004b). Cannibalism in damselflies that live in temporary waters also increases with time constraints and food limitation and has multiple life-history consequences including accelerated larval development (De Block and Stoks 2004b).

The hypothesis that cannibalism (and carnivory in general) can provide a nutritional boost to accelerate larval development of noncarnivores also could explain the many reports of animal material in the diets of late-instar detritivores (MacNeil et al. 1997), including detritus-shredding caddisflies (e.g., Anderson 1976, Giller and Sangpradub 1993). In the context of climate change, our results suggest that density-dependent aggression is a proximate mechanism by which temporary-habitat animals can respond to a shortening of the wet phase of basin hydroperiods. Cannibalism is well described for other groups of invertebrates that inhabit temporary habitats, including microcrustaceans (e.g., Rossi et al. 2011), odonates (e.g., Fischer 1961a, b, Fincke 1994), dytiscid beetles (Juliano and Lawton 1990, Culler and Lamp 2009), aquatic hemipterans (e.g., Klingenburg and Spence 1996), and mosquitoes (e.g., Sherratt and Church 1994). However, direct experimental tests that link the propensity for cannibalism (and intraguild predation) to threat of drying are lacking and would be a promising avenue for future research on the generality of cannibalism as a life-boat strategy in temporary waters.

We also observed a positive developmental response to increased larval density—i.e., pupation was earlier in high- than low-density treatments, despite the potential for intense intraspecific competition. This outcome may suggest that high densities of larvae signal deteriorating environmental conditions and, thus, stimulate accelerated development. The nutritional benefits associated with cannibalism also might underlie these results because higher levels of aggression and probability of cannibalism occurred in the high-density treatments. The number of mobs during our behavioral trials and anecdotal observations of cannibalism events between trials was low, but only a few observed incidences of cannibalism can have dramatic effects on growth and mortality when extrapolated in time and space (Fox 1975, Polis 1981). Whatever the mechanism, the time-of-pupation response indicates that this species responds behaviorally and developmentally to the changes in density that accompany pond drying.

Responses to decreasing water level

In many tests of the effect of drying on behavior and life-history traits of aquatic insects and amphibians, the effects of experimentally decreased water water levels are confounded by covarying changes in density levels (De Block and Stoks 2005, Gomez-Mestre et al. 2013; but see Wickson et al. 2012). Our study provides evidence that,

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independent of changes in density, the number of encounters between caddisfly larvae that escalate to aggressive interactions and the duration of those aggressive interactions are higher in drying than nondrying treatments. This difference was especially striking in drying treatments that did not receive a protein supplement. Many more larvae pupated by the end of the experiment in nondrying than in drying treatments, and that difference was most striking when larvae were given a protein supplement. Most of the pupae recovered from the mesocosms assigned to this experimental treatment died in emergence chambers, so we could not (as originally planned) directly measure the adult fitness consequences and tradeoffs associated with these behavioral and life-history outcomes (as in Stevens et al. 2000, De Block and Stoks 2005, Jannot 2009). However, in previous studies with this species, we showed that this same protein supplement had a positive effect on survival, emergence time, adult body mass, and female fecundity (Wissinger et al. 2004b). Those results combined with the behavioral data presented here support the hypothesis that, independent of density, much of the aggression among late-instar *A. nigriculus* larvae in drying pools is associated with obtaining a protein supplement (i.e., cannibalism) that subsequently accelerates development and ultimately affects adult fitness.

The puzzling lack of a developmental response to drying that we observed for *A. nigriculus* has been observed in a number of drying studies with aquatic invertebrates. For example, habitat drying resulted in little or no acceleration or an actual decrease in development of microcrustaceans and odonates (Fischer 1960, De Block and Stoks 2005) and mosquitoes (Juliano and Stoffregen 1994). This type of result is in contrast to an accelerated response of amphibian larvae to the threat of drying (e.g., Laurila et al. 2002, Loman and Claesson 2003). In some cases, the counterintuitive result for aquatic invertebrates can be attributed to a concomitant increase in density or food limitation (De Block and Stoks 2005). However, in our study and in a previous study with a different species of high-elevation caddisfly (*Limnephilus externus*) (e.g., Jannot et al. 2008), neither density nor food limitation is easily invoked as an explanation for the observed decelerating growth and development.

One explanation offered by Jannot et al. (2008) was that the expected growth response to the threat of desiccation is constrained by deteriorating growing conditions in shallow, drying ponds—specifically by the extreme diel temperature fluctuations at high elevations. Clear, shallow water, intense solar radiation, and low humidity at high elevations lead to rapid heating and evaporation of ponds during the day and rapid cooling at night (Dillon et al. 2006). At low temperatures, insects decrease activity levels and foraging rates (De Block and Stoks 2003, Van Doorslaer and Stoks 2005). Modest increases in temperature accelerate aquatic insect development (Ward and Stanford 1982, Sweeney 1984), but at extremely high temperatures, metabolic rates increase and digestion and growth efficiencies decrease (e.g., Gallepp 1977, Iversen 1979). Thus, at high elevations, suboptimal physiological temperatures at night (too cool) and during the day (too warm) may constrain the ability of caddisflies to increase growth rates in drying basins. Because growth is often coupled with development time prior to metamorphosis (e.g., Rowe and Ludwig 1991, Lytle 2002), a reduction in growth should increase time to pupation. Testing whether the negative developmental response to drying in this and previous studies in drying ponds reflects a tradeoff or coupled response to other life-history and fitness correlates would be fruitful topics for future studies (e.g., Rudolf and Rodel 2007, Shama and Robinson 2009).

Coda: climate change and limits to flexibility

Shallow, temporary aquatic habitats are extremely vulnerable to the effects of climate change because even slight changes in temperature, evaporation, and precipitation can have dramatic effects on when and for how long they hold surface water (Sim et al. 2013, Tuytens et al. 2014). The results presented here combined with those of other studies provide evidence that animals living in those habitats may detect cues related to habitat drying and respond with an attempt to complete life cycles in deteriorating environments. That flexibility notwithstanding, during the course of our mesocosm experiments, we observed the desiccation of hundreds of thousands of caddisfly larvae and innumerable other temporary pond specialists (SAW, personal observation). These extraordinarily early drying events exceed limits of organismal flexibility (also see Smol and Douglas 2007, Wickson et al. 2012). When intermittent streams are adjacent to permanent reaches (e.g., Murphy et al. 2010, Robson et al. 2013) or temporary ponds are part of a cluster of basins that include relatively permanent waters, recolonization from dispersal after extreme drying events can be rapid (e.g., Brendonck et al. 2014). However, for populations in isolated temporary waters, complete cohort failures are likely to result in local extirpation. The focal animal in our study is the only macrodetritivore in subalpine temporary ponds in this region, and in the absence of functional redundancy (as in Boersma et al. 2014), local extinctions should lead to the loss of the multiple ecosystem processes (e.g., Klemmer et al. 2012) associated with breakdown of vascular plant detritus by this species.

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LITERATURE CITED

Anderson, J. T., D. W. Inouye, A. M. McKinney, R. I. Colautti, and T. Mitchell-Olds. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proceedings of the Royal Society B: Biological Sciences 279:3843–3852.

Anderson, N. H. 1976. Carnivory by an aquatic detritivore, *Clistoronia magnifica* (Trichoptera: Limnephilidae). Ecology 57:1081–1085.

Baird, D. J., L. R. Linton and R. W. Davies. 1987. Life-history flexibility as a strategy for survival in a variable environment. Functional Ecology 1:45–48.

Barnett, T. P., J. C. Adam, and D. P. Lettenmaier. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303–309.

Boersma, K. S., M. T. Bogan, B. A. Henrichs, and D. A. Lytle. 2014. Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. Freshwater Biology 59:491–501.

Boggs, C. L., and D. W. Inouye. 2012. A single climate driver has direct and indirect effects on insect population dynamics. Ecology Letters 15:502–508.

Bowen, S. H., E. V. Lutz, and M. O. Ahlgren. 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. Ecology 76:899–907.

Brendonck, L., M. Jocqué, K. Tuytens, B. Timms, and B. Vanschoenwinkel. 2014. Hydrological stability drives both local and regional diversity patterns in rock pool metacommunities. Oikos 124:741–749.

Cargill, A. S., K. W. Cummins, B. J. Hanson, and R. R. Lowry. 1985. The role of lipids as feeding stimulants for shredding aquatic insects. Freshwater Biology 15:455–464.

Chessman, B. C. 2013. Identifying species at risk from climate change: traits predict the drought vulnerability of freshwater fishes. Biological Conservation 160:40–49.

Chessman, B. C. 2015. Relationships between lotic macroinvertebrate traits and responses to extreme drought. Freshwater Biology 60:50–63.

Chester, E. T., and B. J. Robson. 2011. Drought refuges, spatial scale and the recolonization of invertebrates in non-perennial streams. Freshwater Biology 56:2094–2104.

Clow, D. W. 2010. Changes in the timing of snowmelt and stream flow in Colorado: a response to recent warming. Journal of Climate 23:2293–2306.

Corcoran, R. M., J. R. Lovvorn, and P. J. Heglund. 2009. Long-term change in limnology and invertebrates in Alaskan boreal wetlands. Hydrobiologia 620:77–89.

Culler, L. E., and W. O. Lamp. 2009. Selective predation by larval *Agabus* (Coleoptera: Dytiscidae) on mosquitoes: support for conservation based mosquito suppression in constructed wetlands. Freshwater Biology 54:2003–2014.

De Block, M., M. McPeek, and R. Stoks. 2008. Life history plasticity to combined time and biotic constraints in *Lestes* damselflies from vernal and temporary ponds. Oikos 117:908–916.

De Block, M., and R. Stoks. 2003. Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. Journal of Evolutionary Biology 16:986–999.

De Block, M., and R. Stoks. 2004a. Cannibalism-mediated life history plasticity to combined time and food stress. Oikos 106:587–597.

De Block, M., and R. Stoks. 2004b. Life history responses depend on timing of cannibalism in a damselfly. Freshwater Ecology 49:775–786.

De Block, M., and R. Stoks. 2005. Pond drying and hatching date shape the tradeoff between age and size at emergence in a damselfly. Oikos 108:485–494.

Dillon, M. E., M. R. Frazier, and R. Dudley. 2006. Into thin air: physiology and evolution of alpine insects. Integrative Comparative Biology 46:49–61.

Elgar, M. A. and B. J. Crespi. 1992. Ecology and evolution of cannibalism. Pages 1–12 *in* M. A. Elgar and B. J. Crespi (editors). Cannibalism: ecology and evolution among diverse taxa. Oxford University Press, Oxford, UK.

Fincke, O. M. 1994. Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. Oecologia (Berlin) 100: 118–127.

Fischer, Z. 1960. The influence of some changes of environment on the development of *Daphnia magna* Straus and the larvae of the dragonfly *Lestes nympha* Selys. Polskie Archiwum Hydrobiologii 7: 125–142.

Fischer, Z. 1961a. Cannibalism among the larvae of the dragonfly *Lestes nympha* Selys. Ekologia Polska Seria B 7:33–39.

Fischer, Z. 1961b. Some data on the Odonata larvae of small pools. International Revue des gesamten Hydrobiologie und Hydrographie 46:269–275.

Fox, L. R. 1975. Cannibalism in natural populations. Annual Review of Ecology, Evolution, and Systematics 6:87–106.

Gallepp, G. W. 1977. Responses of caddisfly larvae (*Brachycentrus* sp.) to temperature, food availability, and current velocity. American Midland Naturalist 98:59–84.

Gervasi, S. S., and J. Foufopoulos. 2008. Costs of plasticity: responses to desiccation decrease post-metamorphic immune function in a pond-breeding amphibian. Functional Ecology 22:100–108.

Giller, P. S., and N. Sangpradub. 1993. Predatory foraging behavior and activity patterns of larvae of two species of limnephilid cased caddis. Oikos 67:351–357.

Gomez-Mestre, I., S. Kulkarni, and D. R. Buchholz. 2013. Mechanisms and consequences of developmental acceleration in tadpoles responding to pond drying. PLoS ONE 8:e84266.

Greig, H. S., and S. A. Wissinger. 2010. Reinforcing abiotic and biotic time constraints facilitate the broad distribution of a generalist with fixed traits. Ecology 91:836–846.

Harper, M. P., and B. L. Peckarsky. 2006. Emergence cues of a mayfly in a high altitude stream ecosystems: implications for

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All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

consequences of climate change. Ecological Applications 16:612–621.

Harte, J., G. P. Lockette, R. A. Schneider, H. Michaels, and C. Blanchard. 1985. Acid precipitation and surface water vulnerability on the western slope of the high Colorado Rockies. Water, Air, and Soil Pollution. 25:313–320.

Herrmann, S. J., D. E. Ruiter, and J. D. Unzicker. 1986. Distribution and records of Colorado Trichoptera. Southwestern Naturalist 31:421–457.

Inouye, D., and B. Barr. 2006. Consequences of abrupt climate change for hibernating animals and perennial wildflowers at high altitude in the Colorado Rocky Mountains, USA. Pages 166–168 *in* M. F. Price (editor). Global change in mountain regions. Sapiens Publishing, London, UK.

IPCC (Intergovernmental Panel on Climate Change). 2014. Summary for policy makers. Pages 1–32 *in* C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, and L. L. White (editors). Climate change 2014: impacts, adaptation, and vulnerability. Part A: global and sectoral aspects. Contribution of Working Group II to the 5th Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Iversen, T. M. 1979. Laboratory energetics of larvae of *Sericostoma personatum* (Trichoptera). Holarctic Ecology 2:1–5.

Jannot, J. E. 2009. Life history plasticity and fitness in a caddisfly in response to proximate cues of pond drying. Oecologia (Berlin) 161:267–277.

Jannot, J. E., S. A. Wissinger, and J. R. Lucas. 2008. Diet and developmental time constraints alter life-history trade-offs in a caddisfly (Trichoptera: Limnephilidae). Biological Journal of the Linnean Society 95:495–504.

Johansson, F., and L. Rowe. 1999. Life history and behavioral responses to time constraints in a damselfly. Ecology 80:1242–1252.

Johansson, F., R. Stoks, L. Rowe, and M. De Block. 2001. Life history plasticity in a damselfly: effects of combined time and biotic constraints. Ecology 82:1857–1869.

Juliano, S. A., and J. H. Lawton. 1990. The relationship between competition and morphology. II. Experiments on co-occurring dytiscid beetles. Journal of Animal Ecology 59: 831–848.

Juliano, S. A., and T. L. Stoffregen. 1994. Effects of habitat drying on size at and time to metamorphosis in the tree hole mosquito *Aedes triseriatus*. Oecologia (Berlin) 97:369–376.

Klemmer, A. J., S. A. Wissinger, H. S. Greig, and M. L. Ostrofsky. 2012. Nonlinear effects of consumer density on multiple ecosystem processes. Journal of Animal Ecology 81: 770–780.

Klingenberg, C. P., and J. R. Spence. 1996. Impacts of predation and intracohort cannibalism in the water strider *Gerris buenoi* (Heteroptera:Gerridae). Oikos 75:391–397.

Laurila, A., S. Karttunen, and J. Merilä. 2002. Adaptive phenotypic plasticity and genetics of larval life histories in two *Rana temporaria* populations. Evolution 56:617–627.

Leberfinger, K., I. Bohman, and J. Herrmann. 2010. Drought impact on stream detritivores: experimental effects on leaf litter breakdown and life cycles. Hydrobiologia 652:247–254.

Loman, J., and D. Claesson. 2003. Plastic response to pond drying in tadpoles *Rana temporaria*: tests of cost models. Evolutionary Ecology Research 5:179–194.

Lytle, D. A. 2002. Flash floods and aquatic insect life-history evolution: evaluation of multiple models. Ecology 83:370–385.

MacNeil, C., J. T. A. Dick, and R. W. Elwood. 1997. The trophic ecology of freshwater *Gammarus* (Crustacea: Amphipoda); problems and perspectives concerning the functional feeding group concept. Biological Reviews 72:349–364.

Meyer, J. L., M. J. Sale, P. J. Mulholland, and N. L. Poff. 1999. Impacts of climate change on aquatic ecosystem functioning and health. Journal of the American Water Resources Association 35:1373–1386.

Murphy, N. P., M. T. Guzik, and J. W. Wilmer. 2010. The influence of landscape on population structure of four invertebrates in groundwater springs. Freshwater Biology 55:2499–2509.

Nishimura, K., and Y. Isoda. 2004. Evolution of cannibalism: referring to costs of cannibalism. Journal of Theoretical Biology 226:293–302.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population growth in response to environmental change. Nature 466:482–485.

Parker, B. R., R. D. Vinebrooke, and D. W. Schindler. 2008. Recent climate extremes alter alpine lake ecosystems. Proceedings of the National Academy of Sciences of the United States of America 105:12927–12931.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12: 225–251.

Richardson, M. L., R. F. Mitchell, P. F. Reagel, and L. M. Hanks. 2010. Causes and consequences of cannibalism in noncarnivorous insects. Annual Review of Entomology 55:39–53.

Robson, B. J., E. T. Chester, T. G. Matthews, and B. D. Mitchell. 2013. Disturbance and the role of refuges in Mediterranean climate streams. Hydrobiologia 719:77–91.

Rosset, V., and B. Oertli. 2011. Freshwater biodiversity under climate warming: identifying the winners and losers in temperate standing waterbodies. Biological Conservation 144: 2311–2319.

Rossi, V., G. Benassi, F. Belletti, and P. Menozzi. 2011. Colonization, population dynamics, predatory behavior and cannibalism in *Heterocypris incontruens* (Crustacea: Ostracoda). Journal of Limnology 70:102–108.

Rowe, L., and D. Ludwig. 1991. Size and timing of metamorphosis in complex life cycles—time constraints and variation. Ecology 72:413–427.

Rudolf, V. H. W., and M.-O. Rodel. 2007. Phenotypic plasticity and optimal timing of metamorphosis under certain time constraints. Evolutionary Ecology 21:121–142.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. P. Huang, N. Harnik, A. Leetmaa, and N. C. Lau. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184.

Shama, L., and C. T. Robinson. 2009. Microgeographic life history variation in an alpine caddisfly: plasticity in response to seasonal time constraints. Freshwater Biology 54:150–164.

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Sherratt, T. N., and S. C. Church. 1994. Ovipositional preferences and larval cannibalism in the Neotropical mosquito *Trichoprosopon digitatum* (Diptera: Culicidae). Animal Behavior 48:645–652.

Sim, L. L., J. A. Davis, K. Strehlow, M. McGuire, K. M. Trayler, S. Wild, P. J. Papas and J. O' Connor. 2013. The influence of changing hydroregime on the invertebrate communities of temporary seasonal wetlands. Freshwater Science 32:327–342.

Skordahl, M. 2013. Schofield Pass (737) site information and reports. US Department of Agriculture, Natural Resources Conservation Service, National Water and Climate Center, Colorado Snow Survey, Denver, Colorado. (Available: http://www.wcc.nrcs.usda.gov/)

Smol, J. P., and M. S. V. Douglas. 2007. Crossing the final ecological threshold in high Arctic ponds. Proceedings of the National Academy of Sciences of the United States of America 104:12395–12397.

Smol, J. P., A. P. Wolfe, J. B. Birks, M. S. V. Douglas, V. J. Jones, A. Korhola, R. Pienitz, K. Ruhland, S. Sorvari, D. Antoniades, S. J. Brooks, M. Fallu, M. Hughes, B. E. Keatley, T. E. Laing, N. Michelutti, L. Nazarova, M. Nyman, A. M. Paterson, B. Perren, R. Quinlan, M. Rautio, E. Saulnier-Talbot, S. Siitonen, N. Solovieva, and J. Weckstrom. 2005. Climate-driven regime shifts in the biological communities of arctic lakes. Proceedings of the National Academy of Sciences of the United States of America 102:4397–4402.

Stanley E. H., S. G. Fisher, N. B. Grimm. 1997. Ecosystem expansion and contraction in streams. BioScience 47:427–435.

Stevens, D. J., M. H. Hansell, and P. Monaghan. 2000. Developmental tradeoffs and life histories: strategic allocation of resources in caddisflies. Proceedings of the Royal Society of London Series B: Biological Sciences 267:1511–1515.

Stoks, R., A. N. Geerts, and L. De Meester. 2014. Evolutionary and plastic responses of freshwater invertebrates to climate change: realized patterns and future potential. Evolutionary Applications 7:42–55.

Strachan, S. R., E. T. Chester, and B. J. Robson. 2014a. Freshwater invertebrate life history strategies for surviving desiccation. Spring Science Reviews 3:57–75.

Strachan, S. R., E. T. Chester, and B. J. Robson. 2014b. Microrefuges from drying for invertebrates in a seasonal wetland. Freshwater Biology 59:2528–2538.

Sweeney B. W. 1984. Factors influencing life-history patterns of aquatic insects. Pages 56–100 *in* V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger, New York.

Tuytens, K., B. Vanschoenwinkel, A. Waterkeyn, and L. Brendonck. 2014. Predictions of climate change infer increased environmental harshness and altered connectivity in a cluster of temporary pools. Freshwater Biology 59:955–968.

Van Doorslaer, W., and R. Stoks. 2005. Growth rate plasticity to temperature in two damselfly species differing in latitude: contributions of behaviour and physiology. Oikos 111:599–600.

Walters, A. W., and D. M. Post. 2011. How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. Ecological Applications 21:163–174.

Ward, J. V., and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. Annual Review of Entomology 27:97–117.

Wickson, S., E. T. Chester, and B. J. Robson. 2012. Aestivation provides flexible mechanisms for survival of stream drying in a larval trichopteran (Leptoceridae). Marine and Freshwater Research 63:821–826.

Williams, D. D. 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. Journal of the North American Benthological Society 15:634–650.

Williams, D. D. 2006. The biology of temporary waters. Oxford University Press, New York.

Wissinger, S. A. 1999. Ecology of wetland invertebrates: synthesis and applications for conservation and management. Pages 1043–1086 *in* D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). Invertebrates in freshwater wetlands of North America: ecology and management. John Wiley and Sons, New York.

Wissinger, S. A., A. J. Bohonak, H. H. Whiteman, and W. S. Brown. 1999. Habitat permanence, salamander predation, and invertebrate communities. Pages 1043–1086 *in* D. P. Batzer, R. B. Rader, and S. A. Wissinger (editors). Invertebrates in freshwater wetlands of North America: ecology and management. John Wiley and Sons, New York.

Wissinger, S. A., W. S. Brown, and J. E. Jannot. 2003. Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (U.S.A.). Freshwater Biology 48:255–270.

Wissinger, S. A., C. Eldermire, and J. C. Whissel. 2004a. Role of larval cases in reducing aggression and cannibalism among caddisflies in temporary wetlands. Wetlands 24:777–783.

Wissinger, S. A., B. Oertli, and V. Rosset. 2016. Invertebrate communities in alpine ponds. In D. P. Batzer and D. Boix (editors). Invertebrates in freshwater wetlands: an international perspective on their ecology. University of California Press, Oakland, California (in press).

Wissinger, S. A., G. B. Sparks, G. B. Rouse, W. S. Brown, and H. Steltzer. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. Ecology 77:2421–2430.

Wissinger, S. A., J. Steinmetz, J. S. Alexander, and W. Brown. 2004b. Larval cannibalism, time constraints, and adult fitness in caddisflies that inhabit temporary wetlands. Oecologia (Berlin) 138:39–47.

Wissinger, S. A., and H. H. Whiteman. 1992. Fluctuation in a Rocky Mountain population of salamanders: anthropogenic acidification or natural variation? Journal of Herpetology 26:377–391.

Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2093–2106.

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