

Predator-induced plasticity does not alter the pathway from evolution to ecology among locally adapted populations of *Daphnia*

Michelle Packer¹  · Matthew R. Walsh¹

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Abstract In the growing field of eco-evolutionary dynamics, evidence for an influence of rapid shifts in phenotype on ecological processes is accumulating, yet, the contributions of phenotypic plasticity versus genetic change to these observed ecological changes are unclear. In one of the best studied ecosystems in terms of eco-evolutionary dynamics, landlocked versus anadromous alewife (*Alosa pseudoharengus*) have caused strong evolutionary divergence in their key zooplankton prey (*Daphnia ambigua*). We previously showed that such evolutionary differences have cascading ecological effects on consumer-resource dynamics and primary production. Yet, these locally adapted populations of *Daphnia* also differ in trait plasticity, which may, in turn, modify the pathway from evolution to ecology. Here we compared *Daphnia* from lakes with landlocked versus anadromous alewife for differences in rates of population growth in the presence and absence of predator cues over the course of a 39-day experiment. We predicted that predator-induced shifts in life history traits would facilitate faster rates of population growth. Contrary to our expectations, predator cue exposure did not alter rates of population growth. We instead found that *Daphnia* from lakes with landlocked alewife ultimately attained higher population densities (and exhibited faster population growth) when compared with *Daphnia* from lakes with anadromous alewife. Based on our previous work, these population level responses were unexpected, as *Daphnia* from lakes with landlocked alewife exhibit slower rates of somatic growth and delayed maturation. We discuss our results in lieu of the known differences in plasticity and how the population growth patterns may be influenced by resource limitation.

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✉ Michelle Packer
michelle.packer@uta.edu

Matthew R. Walsh
matthew.walsh@uta.edu

¹ Department of Biology, University of Texas at Arlington, Arlington, TX 76019, USA

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Introduction

It is becoming increasingly clear that evolutionary diversification has the potential to influence ecological processes (Fussmann et al. 2007; Post and Palkovacs 2009; Schoener 2011; Reznick 2013; Hendry 2016a). A rapidly growing body of work has shown that phenotypic variation within or among populations can differentially alter the properties of populations, communities, and ecosystems (Schweitzer et al. 2004; Johnson and Agrawal 2005; Crutsinger et al. 2006; Whitham 2006; Steiner et al. 2007; Post et al. 2008; Harmon et al. 2009; Palkovacs and Post 2009; Bassar et al. 2010; Turcotte et al. 2011; Agrawal et al. 2012; Farkas et al. 2013). However, it is also well known that environmental changes can alter the expression of many phenotypic traits and that populations can often differ in phenotypic plasticity (Via and Lande 1985; Schlichting 1986; Hazel et al. 1987; West-Eberhard 1989; Ghalambor et al. 2007; Walsh and Post 2012). Yet, the relative importance of evolutionary genetic change versus phenotypic plasticity as agents of ecological change is largely unknown (Lundsgaard-Hansen et al. 2014). Phenotypic diversification is central to hypothesized ongoing feedbacks between ecological and evolutionary forces in the wild (eco-evolutionary interactions) (Fussmann et al. 2007; Post and Palkovacs 2009; Schoener 2011; Reznick 2013; Hendry 2016b). Thus, increased understanding of how organismal traits dictate changes in ecological properties is needed to dissect and ultimately predict the interplay between ecology and evolution.

Interactions between a dominant fish predator, the alewife (*Alosa pseudoharengus*), and their zooplankton prey (*Daphnia ambigua*) provide a model system to test for eco-evolutionary dynamics. Research has shown that lakes in Connecticut, USA exhibit significant heterogeneity in the form and intensity of predation imposed alewife (Brooks and Dodson 1965; Palkovacs and Post 2008; Post et al. 2008). Populations of anadromous and landlocked alewives differ in their duration of residence in freshwater, which influences the abundances of zooplankton. Adult anadromous alewives migrate into lakes to spawn each spring (~March–May), and young-of-the-year (YOY) alewives migrate from these lakes each fall. In these lakes, *Daphnia* are very abundant during the spring but are eliminated from the water column by YOY alewife predation by early summer each year (Post et al. 2008). Conversely, landlocked alewives are observed in freshwater year-round and this consistent presence of alewife maintains low densities of *Daphnia* (Post et al. 2008).

Our previous work showed that intraspecific variation among alewife populations is correlated with evolutionary divergence in *Daphnia ambigua* (Walsh and Post 2011, 2012; Walsh et al. 2014a, b). This includes genetically-based differences in life history traits as *Daphnia* from lakes with anadromous alewife grow faster, mature earlier, and produce larger clutches of offspring than *Daphnia* from lakes with landlocked and no alewife (Walsh and Post 2011, 2012) (Fig. S1). Differences in the fish predator communities among lakes is also associated with evolutionary shifts in phenotypic plasticity (Walsh and Post 2011, 2012; Walsh et al. 2014a). Consequently, observed life history differences among *Daphnia* from lakes with anadromous, landlocked, and no alewives depend strongly upon environmental context. For instance, *Daphnia* experience strong, predictable increases in predation by anadromous alewife each year (Post et al. 2008). As predicted by theory (Levins 1968; Lively 1986; Scheiner 1993), *Daphnia* from lakes with anadromous

alewife respond to the presence of fish predator cues by modifying the expression of life history traits to a much greater extent than *Daphnia* from landlocked and no alewife lakes (Walsh and Post 2012) (Fig. S1). That is, *Daphnia* from lakes with anadromous alewife mature earlier and produce larger clutches than *Daphnia* from lakes with landlocked or no alewife. These observed life history differences are much greater in the presence of predator cues (Walsh and Post 2012).

We recently tested for a reciprocal influence of *Daphnia* evolution on consumer-resource dynamics (Walsh et al. 2012). This work showed that evolution of earlier maturation and high reproductive investment in *Daphnia* from lakes with anadromous alewife are associated with faster rates of population growth and faster declines in phytoplankton when compared with experimental units containing *Daphnia* from lakes with landlocked and no alewife (Walsh et al. 2012). These trends for zooplankton and phytoplankton abundances parallel those observed at the whole-lake scale. Such results clearly signal that the trait differences among our focal populations of *Daphnia* can alter ecological properties. However, this work utilized a simple environmental context whereby all treatments received non-limiting quantities of food. The known differences in plasticity in this system (Walsh and Post 2011, 2012; Walsh et al. 2014a) foreshadows that the pathway from the evolution of life history traits in individuals to changes in an ecological system may be influenced by population-specific responses to environmental cues.

Here we evaluated the pathway from evolution to ecology across contrasting environmental conditions using locally adapted populations of *Daphnia*. We first reared *Daphnia* from ‘anadromous’ and ‘landlocked’ lakes in a common garden for a period of two generations. We then assessed differences in rates of population growth when all populations were reared in the presence and absence of predator cues. This experiment also maintained a limited quantity of food throughout the duration of the experiments to allow for stress associated with resource limitation to increase as the populations increased in size (Walsh et al. 2014a). Based upon the results of our previous work (Walsh et al. 2012), we expected that *Daphnia* from lakes with anadromous alewife would display faster rates of population growth than *Daphnia* from landlocked lakes and that such differences would be larger in the presence of predator cues (Walsh and Post 2012).

Materials and methods

Focal lakes

We examined the ecological influence of *Daphnia* evolution using *Daphnia ambigua* from two ‘anadromous’ (Bride, Dodge) and two ‘landlocked’ (Long, Quonnapug) lakes. These lakes do not differ significantly in a variety of physical (i.e., size, depth) and biotic (productivity, alewife biomass) parameters that may confound the interpretation of the results of this study (Post et al. 2008).

Population growth experiment

This experiment utilized third generation lab-born individuals to eliminate previous environmental and maternal effects. All clones used in these experiments were established from sexually produced resting eggs (ephippia) collected from lake sediment. Sediment was collected in August–September 2009 using an Ekman Grab to provide viable clone

lines for future experiments as resting eggs remain viable and represent lake populations. In January 2015, we established >10 clones per lake by hatching ephippia in the lab. The first laboratory generation consisted of one female per clone reared in 90 ml jars containing COMBO media (Kilham et al. 1998) and an abundant supply of green algae (*Scenedesmus obliquus*, concentration >0.8 mg C l⁻¹ day⁻¹). The photoperiod and temperature for all phases of clone rearing and experimental trials was 12:12 h light:dark cycle and 18 °C respectively. For the second laboratory generation, ~20 neonates were collected from the second thru fifth clutch of each clone and reared under similar conditions to the first generation. During this phase of rearing, all beakers were monitored every other day and clones were transferred to fresh media and algae three times per week.

Our experiment began by collecting 32 fourth generation lab-born individuals per clone. These individuals were equally divided (8 neonates per jar) between four 500-ml jars (that contained 400-ml of COMBO) that either did ('predator' = 2×) or did not ('non-predator' = 2×) receive fish chemical cues (see below for description of kairomones collection). Each treatment was replicated 2× for a total of 160 experimental units (4 lakes × 10 clones/lake × 2 treatments × 2 replicates = 160 jars) (Fig. 1). To evaluate rates of population growth under resource limitation, all jars received small quantities of green algae (concentration = 0.2 mg C l⁻¹ day⁻¹) that became increasingly limited as the populations grew over time. This low quantity of food was maintained by transferring all *Daphnia* in each jar to fresh media and algae (and predator cues when applicable) every 3 days. To assess population growth, we counted the number of *Daphnia* present in each container beginning on day 21 and every 6 days thereafter until the completion of the experiment on day 39 (approximately 3–4 generations) (4 counts per jar: day 21, 27, 33, 39). We also assessed the initial number of surviving individuals on day 9 of the experiment to potentially correct for small differences in the initial number of *Daphnia* per jar.

Kairomone collection

Stereochemicals known as kairomones have long been known to convey information in aquatic communities and specifically, kairomones from predators have been shown to induce plasticity in their prey (Stibor 1992; Tollrian 1994). We have previously shown that

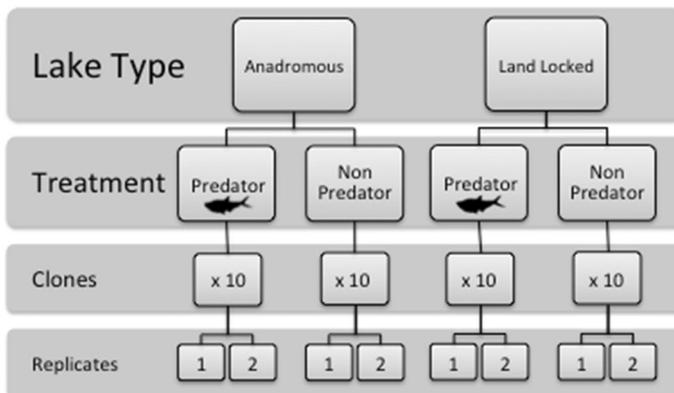


Fig. 1 Experimental design. Initially, eight individuals of each clone were placed in a 500-ml jar that either did or did not receive fish chemical cues. Each treatment was replicated twice for a total sample size of 160 experimental units (4 lakes × 10 clones/lake × 2 treatments × 2 replicates = 160 jars)

kairomone cues from fish predator communities induce divergent life history responses between *Daphnia* from lakes with anadromous and landlocked alewife (Walsh and Post 2012). We generated fish predator kairomones by collecting COMBO media that was conditioned by the presence of planktivorous fish from a tank containing 6 redbreast sunfish (*Lepomis auritus*) (~3-cm in total length) in 9-l of water. We used sunfish as our predator species because alewife exhibit very low survival in the lab. We have also shown that *Daphnia* respond comparably to the presence of alewife and sunfish kairomones (Walsh and Post 2012; Walsh et al. 2015, 2016). The sunfish were fed >200 *Daphnia ambigua* each morning of the experiment as injured *Daphnia* emit chemical cues that contribute to the magnitude of the phenotypic response to predation (Laforsch et al. 2006). Approximately 1 h later, media was removed from the aquaria and filtered using membrane filters (47 mm diameter, 0.45 μm mesh). This filtering helps to prevent the fish-conditioned media from providing supplemental nutrients. The concentration of kairomones that was used in this experiment was 0.66 fish/l.

Statistical analyses

We compared our populations and treatments for differences in population growth using repeated measures linear mixed models implemented with Restricted Maximum Likelihood (REML) (SPSS v.23). We evaluated changes in *Daphnia* abundances over the course of the experiment using a repeated measures approach whereby clone was entered as the within-subjects variable and sampling day was the repeated variable. These analyses included lake type (anadromous, landlocked), predator treatment (presence/absence of predator cues), sampling period (day 21, 27, 33, 39), and all interactions entered as fixed effects. We included clone (nested within lake) as a random effect. We also initially included lake (nested within lake type) as a random effect. Given that the experiments included only two lakes per lake type, we removed this term from the final models. The exclusion of lake did not alter the terms that were significant between the full and reduced models. These repeated measures analyses used an autoregressive covariance structure to account for the positive correlations in the abundance data over time. Assumptions of normality and heterogeneity of variances were confirmed via inspection of box plots and residuals.

Results

The abundances of both populations (anadromous and landlocked) of *Daphnia* significantly increased over the course of the experiment (Fig. 2; Table S1); *Daphnia* were 34% more abundant on day 39 versus day 21 of the experiment (see Fig. 2). The overall differences in *Daphnia* abundances between anadromous and landlocked lakes were not significant ($p > 0.05$) (Table 1, S1). Differences in *Daphnia* abundances between the predator treatments were also not significant ($p > 0.05$) (Table 1). However, differences in the abundances of *Daphnia* from anadromous and landlocked lakes varied strongly as a function of time, as we observed a highly significant ($p < 0.01$) ‘lake type versus sampling day’ interaction (Table 1; Fig. 2). *Daphnia* from anadromous lakes initially attained qualitatively higher abundances than *Daphnia* from landlocked lakes; the abundances of *Daphnia* from anadromous lakes were 11% higher by day 21. Yet, *Daphnia* from

Fig. 2 Variation in *Daphnia* abundances between anadromous and landlocked lakes. Closed circles—*anadromous* lakes, open squares—*landlocked* lakes. We observed a significant ($p < 0.01$) lake type \times day interaction. *Daphnia* from lakes with anadromous alewife were 11% more abundant on day 21 but *Daphnia* from lakes with landlocked alewife were >20% more abundant by the end of the experiment (i.e., day 39)

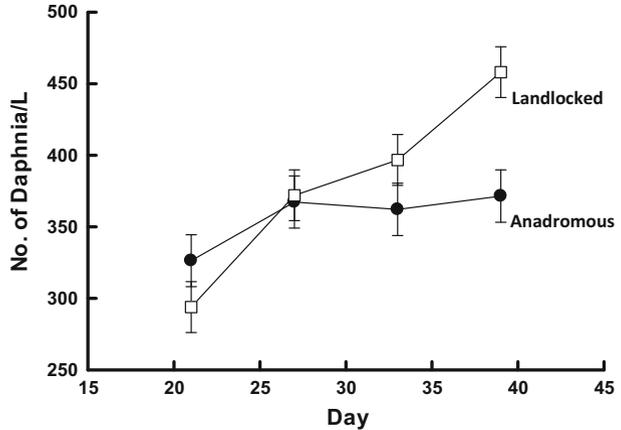


Table 1 Analyses of population growth

	Population size			Denom <i>df</i>
	<i>df</i>	F	<i>p</i>	
Fixed effects				
Lake type	1	1.2	0.28	38.2
Predator	1	0.53	0.47	42.7
Day	3	22.85	<0.001	185.2
Lake type \times predator	1	0.06	0.81	42.7
Lake type \times day	3	6.6	<0.001	185.2
Predator \times day	3	0.54	0.65	185.2
Lake type \times predator \times day	3	0.78	0.51	185.2
Random effects				
Lake (lake type)	1	0.59	0.56	
Clone (lake)	1	1.82	0.069	

Variation in the abundances of *Daphnia* over the course of the experiment were analyzed using linear mixed models with a repeated measures approach where clone (nested within lake) was entered as the within-subjects variable and sampling day was the repeated variable. These analyses included lake type (anadromous, landlocked), predator treatment (presence/absence of predator cues), sampling period (day 21, 27, 33, 39), and all interactions entered as fixed effects

Bold values represent statistically significant ($p < 0.05$) effects

landlocked lakes were $\sim 23\%$ more abundant than *Daphnia* from lakes with landlocked alewife by end of the 39-day experiment. All other interactions were not significant (Table 1).

Tests of simple main effects

Due to the significant lake type \times sampling day interaction, we performed tests of simple main effects to test for differences in *Daphnia* abundance between lakes with anadromous landlocked alewife on the first (day 21) and last sampling event (day 39) of the experiment.

Because these follow-up analyses include two additional tests of significance, we used Bonferroni correction to adjust our p values for multiple comparisons and considered p values <0.025 as being significant ($0.05/2 = 0.025$). Tests of simple main effects revealed non-significant differences in *Daphnia* abundances between anadromous and landlocked lakes on day 21 ($F_{1,37.8} = 2.11$, $p = 0.15$) but significant ($p < 0.025$, p value corrected for multiple comparisons) differences on day 39 ($F_{1,37.8} = 7.99$, $p = 0.007$).

Discussion

Here we evaluated locally adapted populations that vary in life history traits and trait plasticity (Walsh and Post 2011, 2012; Walsh et al. 2014a, b) for differences in population growth when reared in the presence and absence of predator cues. We previously showed that *Daphnia* from lakes with anadromous alewife mature earlier, produce larger clutches of offspring and in turn, exhibit faster rates of population growth than *Daphnia* from lakes with landlocked alewife (Walsh and Post 2011; Walsh et al. 2012). In contrast with this previous work, here we found that *Daphnia* from lakes with landlocked alewife were 23% more abundant than *Daphnia* from anadromous lakes after ~ 6 weeks of growth. Furthermore, exposure to predator cues did not alter these observed differences in population growth despite known differences in predator-induced life history plasticity (see Walsh and Post 2012; Walsh et al. 2016). Below we consider: (1) why the results of the current study generally differ from those observed in our earlier work (see Walsh et al. 2012) and (2) why we failed to detect an influence of predator cues on population processes?

We showed previously that the evolution of earlier maturation and increased reproductive outputs in *Daphnia* from lakes with anadromous alewife are associated with faster rates of population growth when compared with *Daphnia* from landlocked lakes in lab mesocosms (Walsh et al. 2012). This prior work was initiated with multiple clones of *Daphnia* and ample quantities of algae while we tracked dynamics over a single ‘boom-bust’ population cycle (Walsh et al. 2012). In the current study, we maintained low quantities of algae throughout the experiment. As a result, per capita resource availability declined as all populations grew but there is no evidence that resources were absent from experimental units; all populations maintained positive population growth (Fig. 2). Similar to the results of Walsh et al. (2012), *Daphnia* from lakes with anadromous alewife initially attained higher abundances than *Daphnia* from landlocked lakes (*Daphnia* from anadromous lakes were 11% more abundant by day 21). Yet, *Daphnia* from lakes with landlocked alewife exhibited significantly faster rates of growth thereafter (Fig. 2). Given that demand for resources likely increased as the populations increased in abundance, the observed difference in population growth between our focal populations indicate that *Daphnia* from lakes with landlocked alewife are better able to convert limited quantities of food into biomass when resources are low. An alternative possibility is that *Daphnia* from lakes with anadromous alewife versus landlocked lakes allocate resources differently between reproduction and growth/maintenance in the face of declines in per-capita resource availability. It is important to note that all assays were performed individually for each clone. The results are thus not influenced by clonal sorting or clonal selection and instead reflect population-level differences in how *Daphnia* cope with low quantities of food and/or increased density.

Our previous study on phenotypic responses to declines in resource quality at the individual level provides insight into the contrasting set of results between our previous

work (Walsh et al. 2012) and the current study. Lakes in the spring are characterized by abundant, high quality algae. *Daphnia* from lakes with anadromous alewife are only found in lakes during the spring (prior to the onset of anadromous alewife predation) and, in turn, have evolved to better exploit high resource levels but this comes at the expense of their performance under low resource quality conditions (Walsh et al. 2014a). That is, *Daphnia* from anadromous lakes exhibit higher fitness (i.e., early maturation, high reproductive output) when reared under high quality conditions (abundant food) but such differences disappear or reverse as food stress increases (Walsh and Post 2011; Walsh et al. 2014a). As a result, it appears that divergent phenotypic responses to resource stress among our focal populations may facilitate divergent population-level responses to declines in resources.

Daphnia from lakes with anadromous alewife respond to the presence of predator cues by altering the expression of life history traits to a greater extent than *Daphnia* from landlocked lakes (Walsh and Post 2012). We also recently showed that these differences in phenotypic plasticity are repeatable across studies (see Walsh et al. 2016). Yet, such differences in phenotypic plasticity at the individual level were not associated with differences in growth at the population level nor did exposure to predator cues significantly alter growth irrespective of population (Table 1). Given the established ecological importance of plasticity (Miner et al. 2005), such results were surprising. One potential explanation for the lack of connection between predator cues and population growth is simply that life history responses to predator cues are too small to be detected at the population level in the context of our experiment. For example, *Daphnia* from lakes with anadromous alewife responded to exposure to predator cues by maturing $\sim 3\%$ faster and producing $\sim 17\%$ more offspring (Fig. S1; Walsh and Post 2012). Perhaps such responses are not sufficiently strong to influence population growth. An alternative possibility is that the *Daphnia* became acclimated to exposure to environmental cues and phenotypic responses are lessened across multiple generations (Walsh et al. 2015).

A rapidly growing body of work has provided evidence that evolution may represent a significant agent of ecological change. This includes work demonstrating that genotypes or genetic diversity can impact aspects of populations, communities, or ecosystems (Schweitzer et al. 2004; Johnson and Agrawal 2005; Crutsinger et al. 2006; Whitham 2006; de Meester et al. 2007; Johnson and Agrawal 2007; Steiner et al. 2007; Altermatt and Ebert 2008; Weider et al. 2008; Hendry 2016b). Research using locally adapted populations of fish and insects has also shown that differences in life history, morphological, and behavioral traits have cascading consequences for community interactions and ecosystem function (Harmon et al. 2009; Palkovacs and Post 2009; Bassar et al. 2010; Farkas et al. 2013; Matthews et al. 2016). Far fewer studies, however, have isolated or considered the interplay between ecological context and the pathway from evolution to environmental properties (Lundsgaard-Hansen et al. 2014; Bassar et al. 2015; Matthews et al. 2016). Lundsgaard-Hansen et al. (2014) compared the ecological impacts of closely related ‘benthic’ and ‘limnetic’ species of Whitefish (*Coregonus* sp.) and found strong overall effects of evolution on ecosystem variables but also that diet-induced plasticity can significantly influence patterns of ecological change. Similarly, Bassar et al. (2015) compared the ecological importance of guppies (*Poecilia reticulata*) from populations that vary in the intensity of predation. As part of this work, the authors manipulated the size-structure of the experimental populations to mimic the known differences in demography in nature (i.e., more, smaller individuals found in sites with predators). They found that the phenotypic effects of guppies depend upon population size structure as, in some cases, the effects of guppy phenotypes on ecological processes were eliminated by a change in environmental context (i.e., size-structure) (Bassar et al. 2015). Turcotte et al. (2013)

experimentally demonstrated that the initial density of green peach aphids (*Myzus persicae*) altered the rate and direction of evolution and thereby the ecological consequences (population dynamics) of evolution.

Our results contribute to this growing body of work for two reasons. First, manipulations of predator cues and, presumably the induction of trait plasticity, did not alter observed differences in rates of population growth between our focal populations (Table 1). Such a result questions the importance of predator-mediated plasticity to population processes. Second, the influence of evolution on ecology differed between the results of our previous experiments (Walsh et al. 2012) and the patterns revealed in the current study. We argue that such differences stem from contrasting resource treatments between experiments and the known differences in resource-mediated trait plasticity in this system (see Walsh et al. 2014a). Though we caution that it is important for future studies to directly assess trait plasticity on individuals in addition to rates of population growth in the same study (ideally across multiple food treatments) to explicitly examine the connection between plasticity and ecological processes. Based upon the current set of results as well as several recent studies (Turcotte et al. 2013; Bassar et al. 2015) one theme that is emerging is that contrasting responses to parameters, such as population density and food availability, may significantly contribute to the influence of evolution on ecology and are likely key contributors to eco-evolutionary dynamics. Such results thus signal that the effects of evolution on ecology and eco-evolutionary feedback loops may be limited to a specific set of conditions.

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Author contributions MW designed experiments; MW MP collected data; MW and MP analyzed data; MW and MP wrote paper.

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