Interactive effects of competition and social environment on the expression of sexual dimorphism

S. P. DE LISLE & L. ROWE

Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada

Abstract

The expression of sexual dimorphism is expected to be influenced by the acquisition of resources available to allocate to trait growth, combined with sex-specific patterns of resource allocation. Resource acquisition in the wild may be mediated by a variety of ecological factors, such as the density of interspecific competitors. Allocation may in turn depend on social contexts, such as sex ratio, that alter the pay-off for investment in sexual traits. How these factors interact to promote or constrain the expression and evolution of sexual dimorphism is poorly understood. We manipulated sex ratio and interspecific resource competition over the growing season of red-spotted newts (*Notophthalmus viridescens*) in artificial ponds. Fish competitors had a stronger effect on female than male growth, which effectively eliminated the expression of sexual size dimorphism. In addition, newt sex ratio influenced fish growth, leading to reduction in fish mass with an increase in female newt frequency. Fish also reduced the expression of male tail height, a sexually selected trait, but only in tanks with a female-biased sex ratio. This suggests males alter their resource allocation pattern in response to the strength of sexual selection. Our results demonstrate that ecologically and socially mediated interactions between sex-specific resource acquisition and allocation can contribute to variation in the expression of sexual dimorphism.

Introduction

Males and females often differ in key aspects of morphology, behaviour and life history, an outcome of sex-specific selection. Sexual dimorphisms have long been of interest to ecologists because of striking differences between the sexes in traits clearly related to ecological niche (Darwin, 1871; Selander, 1966; Shine, 1989; Dayan & Simberloff, 1994). Ecological theory predicts a role for resource competition in the evolution of such sexual dimorphisms, through limits on the niche space available for a single species to occupy (Schoener, 1977; Slatkin, 1984). A prediction from this body of work is that community structure will strongly influence the expression of sexual dimorphism, for example via

sexually asymmetric responses to a heterospecific resource competitor, and that the evolution of sexual dimorphism itself will have communitywide effects.

Further, because sexual selection is predicted to lead to the evolution of reaction norms that couple trait expression with resource availability (Rowe & Houle, 1996; Bonduriansky, 2007), competition is generally predicted to affect the expression of dimorphism in sexually selected traits by mediating the acquisition of resources that contribute to individual condition. Even symmetric (between the sexes) competition would be expected to influence the expression of such sexual dimorphisms because theory and data indicate consistent sex differences in the strength of condition-dependent expression of sexually selected traits (Rowe & Houle, 1996; Bonduriansky, 2007; Punzalan *et al.*, 2008). Thus, competition may generally influence the expression of sexual dimorphism by mediating the acquisition of resources available for the sexes to differentially allocate to trait growth.

Correspondence: Stephen P. De Lisle, Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON M5S 3B2, Canada. Tel.: 416 978 7590; fax: 416 978 5878; e-mail: s.delisle@utoronto.ca

Patterns of resource allocation may themselves be plastic and influenced by social conditions (e.g. Kasumovic *et al.*, 2013) that vary through space or time. Sexual dimorphism can then be seen as a complex reaction norm (Bonduriansky, 2007) where expression is determined by resource acquisition and allocation that are themselves ecologically mediated (Mikolajewski *et al.*, 2013). Surprisingly, despite a large body of work on the condition-dependent expression of sexual dimorphism, nearly all of this work has assumed implicitly that the strength of condition dependence (plasticity in allocation) is fixed.

We used a factorial mesocosm experiment to assess the interactive roles of interspecific competition and social environment in determining the expression of sexual dimorphism in red-spotted newts, *Notophtalmus viridescens*. Red-spotted newts are a common, pond-breeding salamander exhibiting a competitive mating system where males pursue and grasp females in premating struggles (Verrell, 1982). A key, sexually dimorphic trait in these struggles is tail height; males have taller tails than females and tail height is positively related to male mating success (Able, 1999; Gabor *et al.*, 2000; Bloch & Grayson, 2010). In addition, the intensity of intermale competition for mates increases with male frequency (Verrell, 1983). Newt tail height is phenotypically plastic and known to vary with season (Bloch & Grayson, 2010) and expression appears to be condition-dependent (Gabor *et al.*, 2000). Sexual size dimorphism is slight (females are usually larger) but can vary across populations (Caetano & Leclair, 1996). Newts compete with other vertebrate generalist predators for food (Morin, 1983; Bristow, 1991; Fauth & Resetarits, 1991) and reproduce in ponds spanning a wide gradient of ecological conditions, from ephemeral pools where newts are the dominant predator (Wilbur, 1997), to large permanent lakes occupied by fish (Hurlbert, 1969; Rafinesque, 1820; Caetano & Leclair, 1996; De Lisle personal observation). Sex ratio can vary dramatically through time in wild populations, from approximately 1 : 1 to strongly male biased (e.g. Gill, 1978) because of sex differences in pond arrival time (Bloch & Grayson, 2010), overwintering propensity (Massey, 1990; Grayson & Wilbur, 2009) and survival (Grayson *et al.*, 2011).

We predicted that resource competition with small sunfish (Bristow, 1991) would influence the expression of sexual size dimorphism via sex-specific effects on newt growth. We expected that female newts, with their larger gapes than males (see Fig. S1) would compete more strongly with sunfish, which have larger gapes than newts. Previous studies have demonstrated a reduction of sexual size dimorphism in some newt populations co-occurring with carnivorous fish (Caetano & Leclair, 1996), and greater female sensitivity to the abundance of large prey (Wilbur & Fauth, 1990). We also predicted that competition with fish

would reduce the expression of sexually selected tail height in male newts by reducing the resource pool available for males to allocate to tail growth. This effect on tail height is expected to depend on the sex ratio because male frequency changes the pay-off for investing in tail growth (Verrell, 1983). Finally, because newts in the wild can plastically change their phenotype and migrate out of the aquatic habitat, we designed our experiment to accommodate partial migration and predicted higher migration from environments with fish competitors. Our repeated measures experiment captured the entire growing season from the end of spring into the fall breeding season and allowed us to assess change in newt morphology both before and after partial migration of the population.

Materials and methods

Experimental design

Sixteen replicate experimental ponds were constructed using 2650-L circular polyethylene stock tanks (approximately 2.5 m diameter, 0.66 m deep; High Country Plastics, Caldwell, ID, USA) where we manipulated fish presence and newt sex ratio in a 2 × 2 factorial design. Tanks were arranged in a 4 × 4 grid in a field at the Koffler Scientific Reserve (King, Ontario Canada) and filled to a depth of approximately 53 cm on 11 May 2012 with filtered water from a nearby pond. We added 40 L of dry leaf litter, 110 g of aquatic macrophyte and 140 g of rabbit chow to each tank to provide substrate and nutrients. We repeatedly (3 X) inoculated the tanks with zooplankton and aquatic macro invertebrates (e.g. Crustacea, Ephemeroptera, Zygoptera, Coleoptera) collected from four nearby ponds, to provide prey for newts and sunfish. Our aim was to achieve high prey density to maintain newt urvival in the face of resource competition from fish. The high growth of newts in fishless tanks (see Results) suggest prey abundance was indeed high. Tanks were fitted with green 70% shade cloth lids to control temperature, evaporation, algal growth and prevent newt escape. Mesh-covered standpipes controlled maximum water level; depth stayed relatively constant over the course of the experiment. Because we were concerned about the possibility of shade gradients in two orthogonal directions, we assigned treatments to experimental units in a Latin square design (i.e. each treatment combination represented once in every row and column of the grid). We chose a Latin square at random from all possible 4 × 4 Latin squares, rejecting assignments in which treatments were not adequately interspersed (Hurlbert, 1984). On 13 June 2012, half the tanks received 4 juvenile pumpkinseed sunfish (*Lepomis gibbossus*; mean individual wet mass = 4.92 g ± 0.97 SD) collected from a nearby pond, the other 8 tanks were left fishless.

Approximately 240 aquatic adult newts were collected from three Southern Ontario ponds, photographed under standardized lighting on the dorsal side for individual identification from the spot pattern and measured. We anaesthetized each newt to measure body mass, body length, tail length and tail height (at the tallest point on the tail). Mass was measured by first gently patting each newt with a paper towel to remove excess moisture; linear measurements were taken to two decimal places with digital calipers. We repeated measurements on 30 individuals at a single time point to estimate the precision of our measurements. Individual newts were randomly assigned to a treatment/tank in a (M:F) 5 : 10 or 10 : 5 sex ratio, with a total density of 15 newts per tank; each tank received approximately equal numbers of individuals from each source pond. Levels of the sex ratio manipulation were designed to represent a release from male mating competition, and strong competition among males for mates, respectively, and are consistent with previous work that measured significant effects of sex ratio on newt behaviour (Grayson *et al.*, 2012). For logistical reasons, 128 newts were added to tanks on 7 June and the final 112 were added on 14 June, evenly distributed among tanks on both dates. Tanks were dip netted once a month over the course of the experiment, and captured newts were anesthetized, re-measured and returned to their assigned tank after regaining consciousness (usually within an hour of being anesthetized). On 19 July, after the first month of growth, we added floating bubblewrap mats (approximately 0.4 square meters) covered with leaf litter to provide terrestrial space for migrating newts. We checked tanks for migrants every 1–3 days, and individuals that were identified as migrants by phenotype (granular skin, reduced tail fin; Walters & Greenwald, 1977) and presence in the middle of the terrestrial space were measured and removed from the experiment. The experiment was ended on 23–25 October at which point all newts remaining in the tanks were removed and measured. The late end date was chosen to ensure that all individuals remaining in the tanks were of the aquatic phenotype and not preparing to migrate. Newts in the northern part of their range breed in the fall as well as spring (females can store sperm for extended periods; Sever, 2006); we observed amplexus occurring among residents at the conclusion of the experiment, and repeated measures of male tail height indicate an increase in breeding activity among residents in the fall (Fig. S2).

Statistical analysis

We used a multivariate repeated measures linear model to assess the effects of sex ratio and fish on sex-specific growth over the course of the experiment. We treated averaged male and female mass within a tank as two dependent variables in the model. Body length changed little over the course of the experiment (growth in body length is asymptotic), and so mass is a more meaningful measure of size. We modelled the type of dependent variable (sex), fish presence, sex ratio, month and their interactions as fixed effects. We included initial average mass in a tank as a covariate as a 'baseline' measure (Littell *et al.*, 2006); this is analogous to treating growth as the dependent variable but has the advantage of greater power (Van Breukelen, 2006). We obtained equivalent results in an analysis with growth rate as the dependent variable. Sex and month were treated as repeated measures variables. This model structure allowed us to accommodate our multivariate data within the univariate framework of SAS Proc Mixed, taking advantage of the procedure's power in handling repeated measures linear models relative to traditional MANOVA. We modelled the covariance structure of the multivariate repeated measures data as the Kronecker product of two unstructured matrices (Galecki, 1994); this structure fit the data better then alternative structures based on AIC.

Because newt migration led to a change in density through time (see Results), we performed a similar analysis to that described above, but using only data from residents in the first month of the experiment, before migration began. This model included average body mass as the response variable and sex, sex ratio, fish presence, and their interactions as fixed effects, initial average mass as a covariate and accounted for correlated responses between males and females residing in the same tank. Finally, because migration had yet not occurred, we were also able to make use of the full data set of migrants and residents in month one and so repeated the above analysis with the addition of data from individuals that would go on to migrate (i.e. the full data set of 221 individuals, excluding 1 individual that was not recaptured in the first month).

We analysed mean male tail height in a tank at the conclusion of the experiment using a linear model with sex ratio, fish presence and the interaction as fixed effects, including body mass as a covariate. We performed orthogonal contrasts to test the effect of fish across sex-ratio treatments. Because density changed over the course of the experiment due to migration, we repeated this analysis using only data from the first month, before migration occurred. We also performed the same analysis as a repeated measures design using data from all time points and obtained equivalent results (see Fig. S2). We did not include individuals that would go on to migrate in any analysis of male tail height because this trait is directly affected by migration status.

Finally, we used a generalized linear mixed model with binomial error and logit link function to assess the effect of sex ratio, fish presence and sex on migration status (migrate or reside). Our model accounted for correlated responses between males and females migrating

from the same tank. All statistical analyses were performed using the mixed or GLIMMIX procedures in SAS v. 9.3 (Cary, NC, USA). We excluded one tank (male biased, fish present) from all analyses of newt morphology and migration because many small centrarchid fish (> 20) were discovered in this tank, likely accidentally introduced as eggs or larvae at the beginning of the experiment; all newts in this tank either migrated or died. We used the Kenwood-Rogers method to approximate degrees of freedom in models with repeated measures or random effects (Littell *et al.*, 2006).

Results

Survival was high in all tanks excluding the dropped outlier; 221 of the 225 newts either survived to migrate out of the experiment or were recovered alive at the end. Fish presence significantly increased migration probability (see Supporting Information). Three individuals from different tanks/treatments were found dead at the conclusion of the experiment, and the fate of the remaining individual was unknown. Nearly, all newts in all tanks were captured at all time points, and the repeatability of our measurements was high (intraclass correlation coefficients > 0.98 for all traits). No block effects were found in preliminary analyses, so we pooled blocks and treated the design as completely randomized for all analyses. Our analysis of morphology is based on the 51 males and 47 females that remained as residents at the conclusion of the experiment. Our assignment of individuals to the status of migrant or resident was confirmed by difference in phenotype at the conclusion of the experiment between the two groups; residents retained the aquatic phenotype (Fig. S3). Resident males also retained secondary sex traits (nuptial pads, swollen cloaca) at the conclusion of the experiment and increased tail size in the final two months (Fig. S2), indicating that the conclusion of our experiment coincided with the fall breeding season. All 32 fish survived the course of the experiment.

Resource acquisition: male and female growth

Males and females on average gained mass over the course of the experiment (month effect $F_{3,\ 13.7} = 15.69$, $P = 0.0001$; Fig. 1). Fish significantly reduced growth of both sexes (fish effect $F_{1,9.11} = 46.35$, $P < 0.0001$; Fig. 1), but this effect was stronger for female newts than for males, leading significant sex × fish ($F_{1,11} = 13.7$, $P = 0.0035$) and sex × fish × month interactions ($F_{3,12.7} = 5.91$, $P = 0.0094$). There was no significant main or interacting effect of newt sex ratio (Table 1). The same results were observed in the first month of the experiment, before newt migration began (fish effect $F_{1,11.4} = 34.7$, $P < 0.0001$, sex × fish interaction $F_{1,12} = 5.43$ $P = 0.0381$; Fig. 1, Table 2). Although this analysis is based on only those individuals that did not eventually migrate
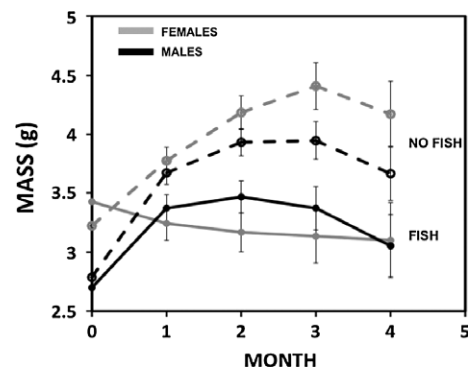

Fig. 1 Newt growth over the course of a 4-month mesocosm experiment. Solid lines are environments with fish, dashed lines are without. Black represents males, grey represents females. Fish reduced growth of males and females (main effect of fish: $P < 0.0001$), but more so for females than males (sex × fish interaction: $P = 0.0035$). Points represent least squares means with 95% confidence intervals from a multivariate repeated measures linear model. Initial body size (month '0') was included as a covariate in the model. Sex ratio and its interactions explained an insignificant portion of the variation and are not included in the figure.

Table 1 Results of multivariate repeated measures linear model with female and male body mass (tank means) as the dependent variable.

Source of variation	Num. d.f.	Den. d.f.	F	P
Sex	1	13.8	0.17	0.6827
Sex ratio	1	9.17	0.04	0.8546
Fish	1	9.11	46.35	**< 0.0001**
Month	3	13.7	15.69	**0.0001**
Sex × fish	1	11	13.7	**0.0035**
Sex ratio × sex	1	11.2	1.14	0.3089
Sex ratio × fish	1	9.09	0.01	0.9276
Sex ratio × sex × fish	1	11.3	0.74	0.4071
Sex × month	3	12.7	3.15	0.0626
Sex ratio × month	3	13.7	0.79	0.519
Sex ratio × sex × month	3	12.7	0.32	0.8131
Fish × month	3	13.7	8.09	**0.0024**
Sex × fish × month	3	12.7	5.91	**0.0094**
Sex ratio × fish × month	3	13.7	0.78	0.527
Sex ratio × sex × fish × month	3	12.7	0.67	0.5882
Initial size	1	18.3	217.61	**< 0.0001**

Bold values denote statistical significance ($P < 0.05$).

from tanks, we obtained equivalent results in an analysis of body mass of the full data set of both eventual migrants and residents in the first month of the experiment (fish effect $F_{1,11} = 34.1$, $P = 0.001$, sex × fish interaction $F_{1,12} = 6.90$ $P = 0.0221$, Table 3).

Table 2 Results of linear mixed model with body mass of residents (tank means) in the first month of the experiment as the dependent variable.

Source of variation	Num. d.f.	Den. d.f.	F	P
Sex	1	15.5	0.1	0.7593
Sex ratio	1	11.3	0.01	0.9411
Sex ratio × sex	1	11.6	0.17	0.6838
Fish	1	11.4	34.7	**< 0.0001**
Sex × fish	1	12	5.43	**0.0381**
Sex ratio × fish	1	11.2	0.99	0.3399
Sex ratio × sex × fish	1	11.6	0.09	0.7755
Initial mass	1	19	187.71	**< 0.0001**

Bold values denote statistical significance ($P < 0.05$).

Table 3 Results of linear mixed model with body mass of migrants and residents (tank means) in the first month of the experiment as the dependent variable.

Source of variation	Num. d.f.	Den. d.f.	F	P
Sex	1	15.1	0.52	0.4808
Sex ratio	1	12	0.91	0.3584
Sex ratio × sex	1	11.9	0.38	0.5484
Fish	1	11	34.1	**0.0001**
Sex × fish	1	12	6.9	**0.0221**
Sex ratio × fish	1	11.3	0.03	0.8762
Sex ratio × sex × fish	1	11.7	0.31	0.587
Initial mass	1	16.6	28.35	**< 0.0001**

Bold values denote statistical significance ($P < 0.05$).

Resource allocation: male tail size

The expression of male tail height at the conclusion of the experiment depended on the interaction between newt sex ratio and fish presence ($F_{1,9} = 11.44$, $P = 0.008$; Fig. 2), accounting for body size (mass covariate $F_{1,9} = 7.60$, $P = 0.02$). Fish had the effect of reducing newt tail height in environments where the sex ratio was female-biased (orthogonal contrast $F_{1,9} = 8.53$, $P = 0.017$). Fish had no effect on newt tail height in tanks with a male-biased sex ratio (orthogonal contrast $F_{1,9} = 1.01$, $P = 0.34$). There was no main effect of fish ($F_{1,9} = 1.39$, $P = 0.27$) or sex ratio ($F_{1,9} = 1.55$, $P = 0.24$). The same effects were observed in the first month of the experiment, before migration occurred; the effect of fish on size-corrected tail height depended on sex ratio (sex ratio × fish interaction $F_{1,9} = 7.50$, $P = 0.0229$), with a significant effect of fish in female-biased tanks (orthogonal contrast $F_{1,9} = 5.74$ $P = 0.0402$) but no fish effect in male-biased tanks (orthogonal contrast $F_{1,9} = 2.23$ $P = 0.17$). Sex ratio and fish effects were not significant.

Migration

Of the 221 newts surviving our experiment, 123 transitioned to the terrestrial adult form and were removed
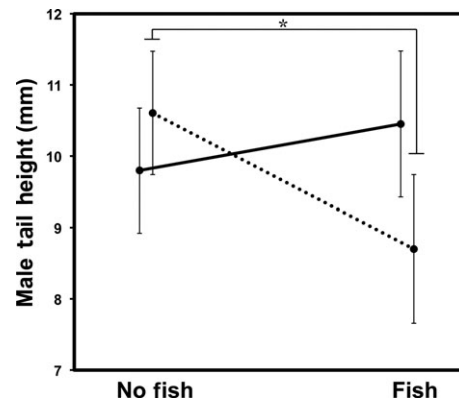

Fig. 2 Male tail height (controlling for body size) at the conclusion of a 4-month mesocosm experiment. Dotted line is a female-biased sex ratio; solid line is a male-biased sex ratio. The effect of fish on the expression of male tail height depended on sex ratio (sex ratio × fish interaction: $F_{1,9} = 11.44$, $P = 0.008$). Asterisk indicates a significant ($F_{1,9} = 8.53$, $P = 0.017$) effect of fish in tanks with a female-biased sex ratio based on orthogonal contrasts; there was no significant effect of fish in male biased tanks. Points represent least squares means and 95% confidence intervals from a linear model.

from the experiment. Individuals that would go on to migrate or reside generally did not differ in phenotype at the beginning of the experiment (Figs S3–S5), although migrant males were slightly heavier than residents (Fig. S5A). Fish presence significantly increased the probability of an individual migrating from a tank ($F_{1,11.59} = 13.13$, $P = 0.0037$; Fig. 3). There was no significant difference between the sexes in migration probability, and no significant main or interaction effects of sex or sex ratio (Table 4).
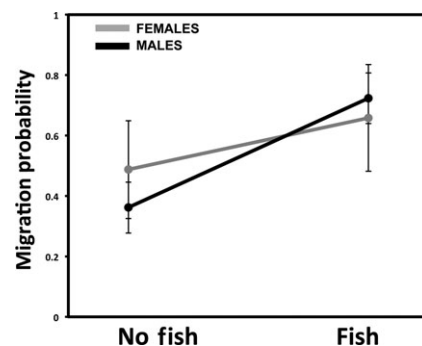

Fig. 3 Probability of an individual newt transitioning to the terrestrial form. Grey is females; black is males. Fish significantly increased migration probability ($P = 0.0037$). The sex × fish interaction was not significant ($P = 0.17$) but illustrates that there were no consistent sex differences in migration propensity. There was no main effect of sex, and no main or interacting effects of sex ratio (Table 4). Points represent least squares means and 95% confidence intervals from a logistic linear model.

Table 4 Results of a generalized linear model with proportion of individuals migrating as the dependent variable.

Source of variation	Num. d.f.	Den. d.f.	F	P
Sex	1	11.81	0.14	0.7414
Sex ratio	1	11.59	0.64	0.4393
Fish	1	11.59	13.13	**0.0037**
Sex × sex ratio	1	11.81	0.1	0.752
Sex × fish	1	11.81	2.12	0.1714
Sex ratio × fish	1	11.59	0.95	0.3501
Sex × sex ratio × fish	1	11.81	0.88	0.3657

Bold values denote statistical significance ($P < 0.05$).

Discussion

Our results from a four-month mesocosm experiment indicate that sunfish, a resource competitor, generally reduced the expression of sexual size dimorphism in red-spotted newts. Fish competitors reduced growth of both sexes, but a strongly female biased response led to a reduction in sexual dimorphism in mass in the presence of fish. Fish also reduced growth of male tail height, a sexually selected trait, but only in tanks with a female-biased sex ratio. These results together indicate that ecological and social conditions can effect the expression of sexual dimorphism by mediating sex-specific acquisition and allocation of resources. Finally, we found that fish presence influenced individual life history strategies, with newts more likely transition to the terrestrial form when housed with fish (Fig. 3). Although newt density changed over the course of the experiment as a result of migration, the same effects of fish on the expression of sexual dimorphism were observed in the first month of the experiment, before migration occurred, indicating these effects are not an outcome of changes in newt density.

Resource acquisition: male and female growth

Female growth was more sensitive than male growth to competition with fish, resulting in the elimination of female-biased sexual size dimorphism in high competition tanks (Fig. 1). These data demonstrate that the expression of sexual size dimorphism can depend on local ecological conditions. Although past work in other systems has implicated a role for plasticity in generating interpopulation variation in sexual size dimorphism (Madsen & Shine, 1993; Fairbairn, 2005), these studies have not identified the ecological agents affecting this variation. Consistent with our results, in surveys of five newt populations in Quebec, Caetano & Leclair (1996) reported a reduction in sexual size dimorphism associated with increasing fish abundance. Wilbur and Fauth (1990) found that females were sensitive to manipulations of vertebrate prey (tadpole) communities, whereas males were not, suggesting that females are

more sensitive to the presence of large prey than males. In our experiment, it is noteworthy that ecologically relevant sexual dimorphism is relatively minor in newts (Fig. S1), but nonetheless appears to affect a strong sex-specific effect of resource competition.

We have interpreted the interaction between newts and sunfish as one of interspecific resource competition, based on the reduced growth of newts in the presence of fish, the shared food types and similar gapes between the two species at the size classes used in this experiment, and the very high newt survival. Similar reduction of newt growth, even with high survival, could also occur if newts change their foraging strategy in the presence of predators to minimize predation risk (Mcnamara & Houston, 1992). However, newts do not appear to alter foraging strategies in response to sunfish presence (Kesler & Munns, 1991), and sunfish do not generally prey on newts (Hurlbert, 1970). Finally, fish grew less in female- than in male-biased tanks, with a near 10% reduction in fish mass in tanks with a female-biased sex ratio in the last two months of the experiment (sex ratio x month interaction $P = 0.0816$; Fig. 4), providing another line of evidence supporting competition between females and fish that is inconsistent with alternative hypotheses, for example changes in newt growth as a result of chemically induced behaviour. Although this trend is not statistically significant, we note that our power was low to measure an effect of newts on fish, and that the large observed effect size is in the predicted direction. Thus, our data suggest resource competition between newts and sunfish that is asymmetric with respect to newt sex. These results are also consistent with the prediction that the
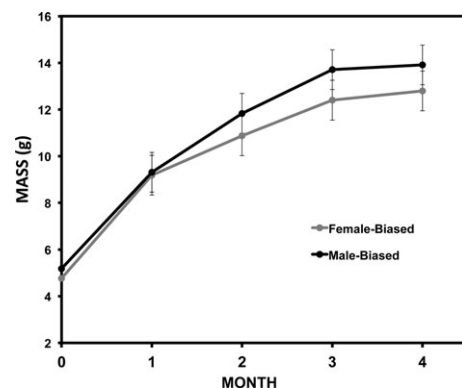

Fig. 4 Results of a repeated measures linear model with average fish mass in a tank as the dependent variable. Newt sex ratio, month and their interaction were included as fixed effects in the model, with month treated as the repeated measures variable and tank as the subject. There was a trend towards a sex-ratio effect (sex ratio $F_{1,6} = 2.58$ $P = 0.1593$; sex ratio × month $F_{3,18} = 2.63$ $P = 0.0816$). We modelled the covariance structure as compound symmetric based on AIC. Points represent least squares means and 95% confidence intervals. $n = 8$ tanks.

evolution of sexual dimorphism can have community-wide effects (Schoener, 1977), here manifested as an effect of sex-ratio variation of a top predator on a resource competitor.

Resource allocation: male tail size

Fish reduced the expression of size-corrected male tail height when sex ratio was female-biased, but not when male-biased (Fig. 2). These results suggest that allocation to these dimorphic traits depends on male frequency. Newts can sense sex ratio via chemical cue (Dawley, 1984) and have been shown to modify behaviour in response (Rohr *et al.*, 2003, 2005; Grayson *et al.*, 2012). Sex ratio has strong effect on male-mating strategy, with more physical struggles when male-biased (Verrell, 1983), indicating that sexual selection on male tail height, which aids males in these struggles (Able, 1999), likely increases with male frequency. Our results suggest that males change allocation to tail size in response to resource availability and the pay-off for investment in this sexually selected trait. Such plasticity in the strength of condition-dependent expression could be adaptive for newts because the strength of sexual selection likely varies dramatically through the breeding season as the sex ratio and distribution of male phenotypes change (e.g. Bloch & Grayson, 2010). Males that increase relative allocation of resources to tail growth in response to an increase in the strength of sexual selection would gain a temporary mating advantage in comparison with a fixed condition-dependent expression strategy.

The observed effect size of fish on tail height is biologically nontrivial. Able (1999) found a significant reduction in male-mating success after surgically removing 2 mm of tail, creating a body-size-controlled effect on tail height very similar to our observed effect size of fish in female-biased tanks (Fig. 2). Bloch and Grayson (2010) found that males with tails of < 8.1 mm, a value within the confidence limits of our estimate of tail height in female-biased tanks with fish, did not successfully obtain mates in their survey of a Virginia population.

Migration

Adult newts in many populations, including those in Ontario, exhibit partial migration and can overwinter either on land or in the water (Sever, 2006). The transition to the terrestrial environment is accompanied by a distinct change in phenotype, with a reduction in tail height and an increase in skin desiccation tolerance (Walters & Greenwald, 1977; Grayson & Wilbur, 2009). Newts in our experiment were more likely to transition to the terrestrial form when housed with fish, consistent with the intraspecific density dependence in migration observed by Grayson and Wilbur (2009).

We expected to see a main effect of sex on migration probability, based on the results of Grayson and Wilbur's (2009) experiment where males were less likely to transition to the terrestrial form than females. Although our experiment lacked the power of Grayson and Wilbur's design, it is noteworthy that we did not observe even a consistent trend of a sex difference in migration probability (Fig. 3). The high quality of environmental conditions within our mesocosms may have contributed to the lack of a sex difference in migration rates. All newts except females in tanks with fish grew substantially, in contrast to the experiment of Grayson and Wilbur (2009) where newts in most enclosures lost body mass. Given that evidence suggests newt migration decisions are based in part on environmental quality, where individuals in higher quality (e.g. low density) environments are more likely to remain resident (Grayson & Wilbur, 2009; Grayson *et al.*, 2011), it is possible that difference in resource availability between our tanks and Grayson and Wilbur's (2009) enclosures may in part account differences in sex-specific migration in these two experiments.

Conclusions

Our results illustrate that ecological and social factors that affect resource acquisition and allocation can interact to determine the expression of sexual dimorphism and that sexual dimorphism can have communitywide effects. Sexually asymmetric interspecific competition can lead to rapid changes in the expression of sexual size dimorphism, and the effect of competition on the expression of sexually selected traits can depend on male frequency. Our experiment and recent work by others (e.g. Cothran & Jeyasingh, 2010; Cothran *et al.*, 2012; Kasumovic *et al.*, 2013) highlight interesting future directions for the study of condition-dependent sexual dimorphism. Most studies of the condition-dependent expression of sexually selected traits have assumed implicitly that the strength of the relationship between condition and trait expression is not plastic. Yet the strength of sexual selection and the cost of sexually selected traits likely varies through time or space in many wild populations (Punzalan *et al.*, 2010; Siepielski *et al.*, 2011), and so phenotypic plasticity in the strength of condition-dependent expression of sexually selected traits may be common. The population-genetic consequences may be non-trivial if plasticity in the reaction norms of sexually selected traits can, as suggested by our results, temporarily reduce the genetic covariance between a trait and condition. This could, for example, have the effect of temporarily reducing the efficacy of sexual selection as a mechanism of reducing mutation load (Whitlock & Agrawal, 2009), or equivalently, reduce the genetic benefits of female mate choice (Rowe & Houle, 1996).

Acknowledgments

References

Able, D.J. 1999. Scramble competition selects for greater tailfin size in male red-spotted newts (Amphibia: Salamandridae). *Behav. Ecol. Sociobiol.* **46**: 423–428.

Bloch, A.M. & Grayson, K.L. 2010. Reproductive costs of migration for males in a partially migrating, pond-breeding amphibian. *Can. J. Zool.* **88**: 1113–1120.

Bonduriansky, R. 2007. The evolution of condition-dependent sexual dimorphism. *Am. Nat.* **169**: 9–19.

Bristow, C.E. 1991. Interactions between phylogenetically distant predators: *Notophthalmus viridescens* and *Enneacanthus obesus*. *Copeia* **1991**: 1–8.

Caetano, M.H. & Leclair, R.J. 1996. Growth and population structure of red-spotted newts (*Notophthalmus viridescens*) in permanent lakes of the Laurentian Shield, Quebec. *Copeia* **1996**: 866–874.

Cothran, R.D. & Jeyasingh, P.D. 2010. Condition dependency of a sexually selected trait in a crustacean species complex: importance of the ecological context. *Evolution* **64**: 2535–2546.

Cothran, R.D., Stiff, A.R., Jeyasingh, P.D. & Relyea, R.A. 2012. Eutrophication and predation risk interact to affect sexual trait expression and mating success. *Evolution* **66**: 708–719.

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. J. Murray, London.

Dawley, E.M. 1984. Identification of sex through odors by male red-spotted newts, *Notopthalmus viridescens*. *Herpetologica* **40**: 101–105.

Dayan, T. & Simberloff, D. 1994. Character displacement, sexual dimorphism, and morphological variation among british and irish mustelids. *Ecology* **75**: 1063–1073.

Fairbairn, D.J. 2005. Allometry for sexual size dimorphism: testing two hypotheses for Rensch's rule in the water strider *Aquarius remigis*. *Am. Nat.* **166**(S4): S69–S84.

Fauth, J.E. & Resetarits, W.J.J. 1991. Interactions between the salamander Siren intermedia and the keystone predator *Notophthalmus viridescens*. *Ecology* **72**: 827–838.

Gabor, C.R., Krenz, J.D. & Jaeger, R.G. 2000. Female choice, male interference, and sperm precedence in the red-spotted newt. *Behav. Ecol.* **11**: 115–124.

Galecki, A.T. 1994. General class of covariance structures for two or more repeated factors in longitudinal data analysis. *Commun. Stat. Theory Methods* **23**: 3105–3119.

Gill, D.E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecol. Monogr.* **48**: 145–166.

Grayson, K.L. & Wilbur, H.M. 2009. Sex- and context-dependent migration in a pond-breeding amphibian. *Ecology* **90**: 306–312.

Grayson, K.L., Bailey, L.L. & Wilbur, H.M. 2011. Life history benefits of residency in a partially migrating pond-breeding amphibian. *Ecology* **92**: 1236–1246.

Grayson, K.L., De Lisle, S.P., Jackson, J.E., Black, S.J. & Crespi, E.J. 2012. Behavioral and physiological responses to sex ratio bias in a pond-breeding amphibian. *Front. Zool.* **9**: 24.

Hurlbert, S.H. 1969. The breeding migrations and interhabitat wandering of the vermilion-spotted newt *Notophthalmus viridescens* (Rafinesque). *Ecol. Monogr.* **39**: 465–488.

Hurlbert, S.H. 1970. Predator responses to the vermilion-spotted newt (*Notophthalmus viridescens*). *J. Herpetol.* **4**: 47–55.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**: 187–211.

Kasumovic, M.M., Hall, M.D., Try, H. & Brooks, R.C. 2013. Socially cued developmental plasticity affects condition-dependent trait expression. *Behav. Ecol.* **24**: 429–434.

Kesler, D.H. & Munns, W.R.J. 1991. Diel feeding by adult red-spotted newts in the presence and absence of sunfish. *J. Freshw. Ecol.* **6**: 267–273.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D. & Schabenberger, O. 2006. *SAS for Mixed Models*, 2nd edn. SAS Institute Inc., Cary, NC.

Madsen, T. & Shine, R. 1993. Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution* **47**: 321–325.

Massey, A. 1990. Notes on the reproductive ecology of red-spotted newts (*Notophthalmus viridescens*). *J. Herpetol.* **24**: 106–107.

Mcnamara, J.M. & Houston, A.I. 1992. Risk-sensitive foraging: a review of the theory. *Bull. Math. Biol.* **54**: 355–378.

Mikolajewski, D.J., Wohlfahrt, B., Joop, G. & Beckerman, A.P. 2013. Sexual size dimorphism and the integration of phenotypically plastic traits. *Ecol. Entomol.* **38**: 418–428.

Morin, P.J. 1983. Competitive and predatory interactions in natural and experimental populations of *Notophthalmus viridescens dorsalis* and *Ambystoma tigrinum*. *Copeia* **1983**: 628–639.

Punzalan, D., Cooray, M., Rodd, F.H. & Rowe, L. 2008. Condition dependence of sexually dimorphic colouration and longevity in the ambush bug *Phymata americana*. *J. Evol. Biol.* **21**: 1297–1306.

Punzalan, D., Rodd, F.H. & Rowe, L. 2010. Temporally variable multivariate sexual selection on sexually dimorphic traits in a wild insect population. *Am. Nat.* **175**: 401–414.

Rafinesque, C.S. 1820. *Annals of Nature or Annual Synopsis of New Genera and Species of Animals Plants, etc, Discovered in North America* **1**: 1–16.

Rohr, J.R., Madison, D.M. & Sullivan, A.M. 2003. On temporal variation and conflicting selection pressures: a test of theory using newts. *Ecology* **84**: 1816–1826.

Rohr, J.R., Park, D., Sullivan, A.M., McKenna, M., Propper, C.R. & Madison, D.M. 2005. Operational sex ratio in newts: field responses and characterization of a constituent chemical cue. *Behav. Ecol.* **16**: 286–293.

Rowe, L. & Houle, D. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. Biol. Sci.* **263**: 1415–1421.

Schoener, T.W. 1977. Competition and the Niche. In: *Biology of the Reptilia*, vol. 7 (C. Gans, D.W. Tinkle, eds), pp. 35–136. Academic Press, New York.

Selander, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* **68**: 113–151.

Sever, D.M. 2006. 'The false breeding season' of the Eastern newt, *Notophthalmus viridescens*. *Bull. Chicago Herpetol. Soc.* **41**: 149–153.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* **64**: 419–461.

Siepielski, A.M., DiBattista, J.D., Evans, J.A. & Carlson, S.M. 2011. Differences in the temporal dynamics of phenotypic selection among fitness components in the wild. *Proc. Biol. Sci.* **278**: 1572–1580.

Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* **38**: 622–630.

Van Breukelen, G.J.P. 2006. ANCOVA vs. change from baseline had more power in randomized studies and more bias in nonrandomized studies. *J. Clin. Epidemiol.* **59**: 920–925.

Verrell, P.A. 1982. The sexual behavior of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). *Anim. Behav.* **30**: 1224–1236.

Verrell, P.A. 1983. The influence of the ambient sex ratio and intermale competition on the sexual behavior of the red-spotted newt, *Notophthalmus viridescens* (Amphibia: Urodela: Salamandridae). *Behav. Ecol. Sociobiol.* **13**: 307–313.

Walters, P.J. & Greenwald, L. 1977. Physiological adaptations of aquatic newts (*Notophthalmus viridescens*) to a terrestrial environment. *Physiol. Zool.* **50**: 88–98.

Whitlock, M.C. & Agrawal, A.F. 2009. Purging the genome with sexual selection: reducing mutation load through selection on males. *Evolution* **63**: 569–582.

Wilbur, H.M. 1997. Experimental ecology of food webs: complex systems in temporary ponds. *Ecology* **78**: 2279–2302.

Wilbur, H.M. & Fauth, J.E. 1990. Experimental aquatic food webs: interactions betweeen two predators and two prey. *Am. Nat.* **135**: 176–204.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Head width in red spotted newts (*Notophthalmus viridescens*), a gape-limited predator.

Figure S2 Change in tail height, accounting for body size, of resident males over the course of the experiment.

Figure S3 ANCOVAs with tail height as the dependent variable, body length as a covariate and migratory status as a fixed effect.

Figure S4 ANCOVAs with mass as the dependent variable, body length as a covariate and migratory status as a fixed effect.

Figure S5 Body size distributions of migrants and residents at the beginning of the experiment.

Data deposited at Dryad: doi:10.5061/dryad.g0q15