

The contribution of parasitism to selection on floral traits in *Heuchera grossulariifolia*

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Abstract

Parasites are ubiquitous and have well-documented ecological consequences. In contrast, the extent to which parasites drive phenotypic evolution in hosts remains obscure. We use a recently developed statistical technique – selective source analysis – to analyse the strength of phenotypic selection acting on floral traits in the plant *Heuchera grossulariifolia* attributable to attack by the seed-parasitic moth, *Greya politella*. This analysis spanned 3 years and included two sympatric populations of the host plant *H. grossulariifolia* that differ in ploidy. Our analyses revealed that attack by *G. politella* contributed to phenotypic selection for flowering time and floral display size, favouring earlier flowering in the polyploid population, later flowering in the diploid population and increased floral display size in the polyploid population. Although selection imposed by parasite attack was generally quite weak, in one of the 3 years parasites generated a modestly strong selection gradient ($\beta = -0.059$) that explained 38.6% of total observed phenotypic selection for earlier flowering in the polyploid population. Together, our results demonstrate parasites can generate significant phenotypic selection, but that such selection may be sporadic across populations and time.

Introduction

Parasites have well-documented effects on the ecological dynamics of their hosts. For instance, it is well established that parasites can regulate host population densities directly (Hudson *et al.*, 1992) or indirectly by modifying interactions with competitors or predators (Hudson & Greenman, 1998; MacNeil *et al.*, 2003; Hatcher *et al.*, 2006). In addition to these localized effects, parasites can also alter host geographic ranges and promote or inhibit biological invasions (Mitchell & Power, 2003; Torchin *et al.*, 2003). These well-documented demographic consequences of parasitism create the potential for parasites to generate strong selection on host populations.

Understanding the strength of selection imposed by parasites on their host populations has important consequences for a wide variety of questions. For instance,

coevolutionary interactions between hosts and parasites generally favour increased sexual reproduction only when parasites exert very strong selection on host populations (Otto & Nuismer, 2004). Similarly, the degree to which parasites are locally adapted to host populations depends on the strength of parasite-mediated selection (Gandon & Michalakis, 2002). In a broader sense, the strength of selection imposed by parasites partially determines the extent to which ecological and evolutionary dynamics are coupled over ecological time scales (Thompson, 1998; Duffy & Sivars-Becker, 2007). If selection imposed by parasites is relatively weak, coevolution between hosts and parasites may not be an important ecological process. In contrast, if selection imposed by parasites is strong, ecological dynamics are likely to be fundamentally shaped by coevolution.

Despite the importance of estimating the strength of selection imposed by parasites on hosts, we have very few estimates from natural populations. The primary reason for this is that in addition to detecting selection in the host population – which is in and of itself a nontrivial undertaking – this selection must be statistically linked to

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differential parasite attack across host genotypes or phenotypes. Nevertheless, several empirical studies have been able to indirectly infer the existence of parasite selection in natural populations using studies of changes in genotype or clone frequencies over time (e.g. Dybdahl & Lively, 1998; Little & Ebert, 1999; Duncan & Little, 2007). Parasite selection has also been inferred by measuring performance of different host phenotypes thought to be involved in parasite resistance (e.g. Berenbaum *et al.*, 1986; Clayton *et al.*, 1999; Agrawal, 2005; Toju & Sota, 2006). Although these studies suggest the action of parasite-mediated selection, to our knowledge, none of them has tied selection in the host population to differential parasite attack of host phenotypes or genotypes in a statistically rigorous way in natural populations.

Here we use a recently developed statistical technique [selective source analysis (SSA), Ridenhour, 2005] to analyse the strength of phenotypic selection acting on flowering traits in the plant *Heuchera grossulariifolia* imposed by the seed-parasitic moth *G. politella*. The advantage of using the SSA technique is that phenotypic selection acting on plant traits can be statistically linked to differential attack by *G. politella*. Our analyses utilized data collected over 3 years from two sympatric populations of *H. grossulariifolia* that differ in ploidy. We used this data and our SSA analyses to address the following questions: (i) how strong is parasite-mediated phenotypic selection? (ii) what proportion of observed phenotypic selection is explained by differential parasite attack? (iii) how consistent is parasite-mediated selection across years and host populations?

Materials and methods

Natural-history background

Heuchera grossulariifolia (Saxifragaceae) is a rhizomatous, self-incompatible perennial distributed across eastern Washington, Idaho, and western Montana (Wolf *et al.*, 1990; Thompson *et al.*, 1997). Within this region, there have been at least two, and potentially up to nine, independent origins of autotetraploidy (Wolf *et al.*, 1990; Segraves *et al.*, 1999). Our study focusses on populations of *H. grossulariifolia* growing along a 1.6-km stretch of the main stem of the Salmon River approximately 27 km east of Riggins, Idaho, USA (45°25.352'N 116°02.158'W). The study site contains large numbers of spatially well-mixed diploid and tetraploid *H. grossulariifolia* with little evidence of microhabitat selection (Segraves *et al.*, 1999; Nuismer & Thompson, 2001). Plants growing within the study site flower between April and May and produce between 1 and 50 inflorescences, each of which can have up to 250 flowers. Although multiple species of insect parasite attack diploids and tetraploids at this site (Nuismer & Thompson, 2001), the focus of this study was the seed-parasitic moth, *G. politella* (Prodoxidae) (Davis *et al.*,

1992). This species oviposits into the flowers of both diploid and tetraploid *H. grossulariifolia* where, upon hatching, the larvae consume some fraction of the plant's developing seeds (Nuismer & Thompson, 2001). Although *G. politella* is an efficient and potentially important pollinator of another of its host species, *Lithophragma parviflorum* (Thompson & Pellmyr, 1992; Pellmyr *et al.*, 1996), it plays only a minor role in pollinating *H. grossulariifolia* at the Salmon River site (Merg and Thompson, in press).

General methodological approach

In order to determine if attack by *G. politella* affects plant fitness and contributes to phenotypic selection, we analysed data on plant fitness, plant traits and moth attack collected over a 3-year period (2001–2003). Data on plant fitness and plant traits were collected and analysed as part of a previous study (Nuismer & Cunningham, 2005). At the beginning of that study, we identified and individually marked diploid and tetraploid plants as described in Nuismer & Cunningham (2005). Our initial plan was to use these same individuals throughout the 3 years of the study, but because a substantial number of plants did not flower each year, we were forced to mark additional plants in order to maintain our desired sample size. Consequently, the number of plants used in each year of the study fluctuated slightly (2001: $n_{2x} = 128$, $n_{4x} = 151$; 2002: $n_{2x} = 147$, $n_{4x} = 177$; and 2003: $n_{2x} = 162$, $n_{4x} = 167$) and contained a different subset of individual plants.

Contribution of parasite attack to plant fitness

The intensity of attack by *G. politella* on diploid and tetraploid *H. grossulariifolia* was estimated for each year of the study, and on average across all years, based upon dissection of 10 floral capsules per plant. Specifically, for each marked plant, 10 floral capsules were collected at the end of the period of moth activity, dissected, and the number of moth eggs and larvae in each capsule determined. These data were used to compare the frequency of attack, the average proportion of capsules attacked per plant, and the average number of eggs and larvae found per capsule across the two ploidies. Statistical significance of differences in the frequency of attack were evaluated using *G*-tests; statistical significance of differences in the average proportion of capsules attacked and the average number of eggs and larvae per capsule were evaluated using 19 999 bootstraps and BCa confidence intervals (Efron & Tibshirani, 1993) to correct for non-normality. BCa confidence intervals are closely related to traditional percentile-based confidence intervals, but correct for skew and bias in the resampled distribution.

In order to evaluate the consequences of attack by *G. politella* for plant fitness, rather than simply use the

frequency of attack as in previous studies (Thompson *et al.*, 1997; Nuismer & Thompson, 2001), we estimated the average number of seeds consumed by larvae for both diploid and tetraploid *H. grossulariifolia*. This was accomplished during 2002 by marking individual flowers into which *G. politella* oviposited and collecting marked capsules 15–16 days later. After this amount of time, larvae have generally finished feeding but have not yet emerged from the floral capsule, allowing the average number of seeds consumed by each larvae to be determined by dissecting capsules and counting the number of larvae and the number of seeds destroyed by larvae (Thompson & Pellmyr, 1992; Pellmyr *et al.*, 1996). Multiplying the resulting estimate for the average number of seeds destroyed by each larva by the average number of eggs and larvae per capsule yielded an estimate for the average number of seeds consumed per capsule for each plant in the study.

The total fitness of each plant was then determined by subtracting the average number of seeds consumed by *G. politella* from the average seed set per capsule and multiplying the resulting quantity by the total number of capsules setting seed. The total number of capsules setting seed was determined by counting the number of capsules that reached maturity on each marked plant. Average seed set per capsule was determined by dissecting five floral capsules from each marked plant and counting the number of seeds (see Nuismer & Cunningham, 2005). Our method results in an estimate of total fitness for each plant in the study that explicitly incorporates the fitness consequences, resulting from variable levels of attack by *G. politella*.

Data on total seed set and moth attack were analysed both within each year and across all years using a full factorial two-way ANOVA where attack (as a binary variable; attacked individuals = 1, unattacked individuals = 0) and ploidy were factors used to explain total seed set. Due to non-normality in the total seed set data, the aforementioned bootstrapping procedure was used to determine the significance of the ANOVA. Bootstrapping was conducted within ploidy, however, to maintain the appropriate variance structure. ANOVA and bootstrap analyses were performed within each year and on average across all years using R (R Development Core Team, 2005).

Contribution of parasite attack to phenotypic selection

As part of a previous study (Nuismer & Cunningham, 2005), three floral traits were measured for each marked plant in each year of the study: average flowering date (AFD), maximum scape length (SL), and maximum floral display (MFD). We chose these three floral traits because each is likely to play at least some role in interactions with other species that utilize the flowers of *H. grossulariifolia* as a resource (e.g. floral parasites and pollinators).

It is possible, however, that other traits not included in our study experience stronger selection by *G. politella*. All data were collected over the course of the flowering period using daily observations of each marked plant. Observations were made on the majority of days where plants had open flowers. On each day that observations were conducted, all marked plants were observed and the number of open flowers and *G. politella* individuals recorded. On or near the date at which plants reached peak flower, the maximum SL of each plant was measured. AFD was calculated for each individual at the end of the flowering season using:

$$\text{AFD} = \sum_{i=1}^N \left(\frac{n_i x_i}{\sum_{i=1}^N n_i} \right), \quad (1)$$

where n_i is the number of flowers open on a particular plant on day i , x_i is the Julian date of day i and N is the last day the plant had an open flower (Nuismer & Cunningham, 2005). MFD was determined from daily surveys as the maximum number of flowers that were simultaneously open on an individual plant. When combined with the data on moth attack and plant fitness described in the previous section, this data allowed us to determine the extent to which parasite attack contributes to the phenotypic selection observed in Nuismer & Cunningham (2005).

In order to attribute selection to a particular source – in this case moth attack – special selection analyses must be used. Several methodologies have been designed to identify the origin of natural selection on particular traits (e.g. Stewart & Schoen, 1987; Iwao & Rausher, 1997; Scheiner *et al.*, 2000). A recent method for determining selective sources (SSA; Ridenhour, 2005) estimates traditional selection gradients (i.e. Lande & Arnold, 1983) and partitions these gradients into the contributions of particular sources. We used the SSA method to determine what portion of the selection gradients observed on floral traits by Nuismer & Cunningham (2005) could be attributed to differential parasite attack.

SSA partitions variance in fitness based upon two broad classes of traits: those intrinsic to the organism and those that are extrinsic. Primarily, Ridenhour (2005) discusses the use of specific trait values (e.g. ovipositor length of a moth) as the extrinsic selective sources. However, cases where multiple interactions between species, as is the case here when multiple moths visit a single plant, are discussed as well (Ridenhour, 2005). Accordingly, we chose three measures of attack by *G. politella* to represent the extrinsic factors important for *H. grossulariifolia* fitness: average number of parasite eggs and larvae per capsule, proportion of flowers attacked by parasites and whether a plant was attacked by a parasite or not (attacked = 1, not attacked = 0).

The partitioning of the fitness variance between intrinsic and extrinsic factors is accomplished through the use of regression techniques (or generalized linear

models) that conform to the guidelines of analysis set forth by Lande & Arnold (1983). Therefore, total seed set (fitness) was transformed to relative fitness and all other variables (traits) were transformed to units of phenotypic standard deviations. The intrinsic variables that we thought may be affected by moths were the same as those used in Nuismer & Cunningham (2005) and described above: SL, MFD and AFD. Our linear model for partitioning the variance therefore used our relative fitness measure as the dependent variable and the standardized versions of the three intrinsic (plant phenotypic traits) and three extrinsic (parasite attack traits) factors as independent variables.

After partitioning the variance in fitness according to the two source classes, we calculated the selection gradients based upon these sources. This process involves calculating the covariance of a fitness partition with the intrinsic traits (i.e. calculating a selection differential) and thereafter utilizing the phenotypic variances and covariances of our plant traits to transform the selection differentials into selection gradients (for specifics, see Ridenhour, 2005). Due to the non-normality of our data, and because of the statistical complexity of the SSA analysis performed here, the statistical significance of the SSA selection estimates was evaluated via bootstrapping. Bootstrapping was performed using *R*, and confidence intervals were calculated based on 19 999 bootstraps and the BCa method as above.

Results

Consequences of parasite attack for plant fitness

Dissections of floral capsules revealed that both diploid and tetraploid populations were regularly attacked by *G. politella* in each year of the study (Fig. 1). However, as observed in previous studies (Thompson *et al.*, 1997; Nuismer & Thompson, 2001), tetraploids are attacked more frequently, with this difference statistically significant in 2002 and 2003 and on average across years. In addition to suffering increased attack frequencies, tetraploids had a significantly greater proportion of their capsules attacked and a significantly greater number of eggs and larvae within each capsule in 2002 and 2003 and on average across years (Fig. 1).

In contrast to our results for the intensity of moth attack, our study of seed consumption by larval *G. politella* did not identify any significant differences across ploidies in the number of seeds consumed per larva ($F_{1,16} = 0.273$; $P = 0.61$). Consequently, we pooled the data for larval consumption across ploidies, yielding an estimate of 12.07 ± 3.04 seeds consumed per larva.

Our estimates for the effects of ploidy, parasite attack and their interaction on *H. grossulariifolia* total seed set yielded three important conclusions regarding the consequences of attack by *G. politella*. First, ploidy has a significant effect on total seed set only in 2001, when

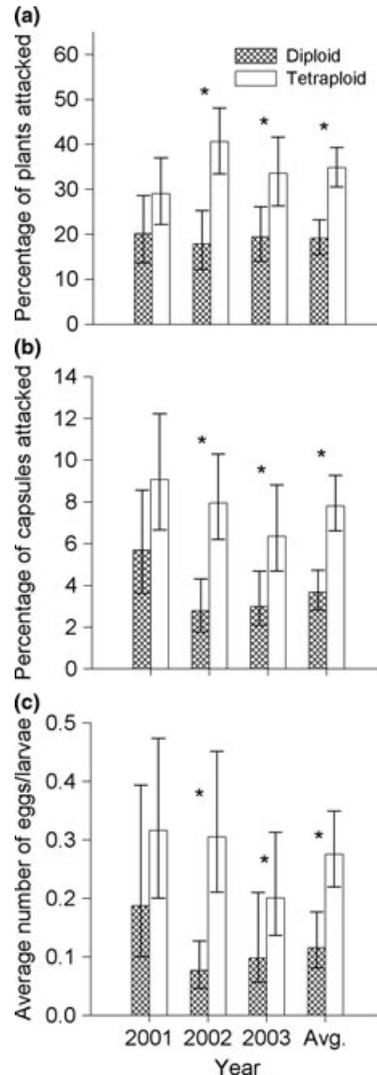


Fig. 1 The intensity of attack by *Greya politella* on diploid and tetraploid plants in each year of the study, and on average across years. Panels show the following: (a) the percentage of plants attacked, (b) the average proportion of capsules attacked and (c) the average number of eggs and larvae in each capsule. Asterisks indicate significant differences at the $P < 0.01$ level, based upon a G -test in panel A ($G^2 = 18.55, 7.91, 26.77$; d.f. = 1, 1, 1; $P < 0.0001$, $P < 0.005$, $P < 0.0001$ respectively), and 19 999 bootstraps in panels (b) and (c). Error bars represent 95% confidence intervals.

tetraploids set significantly more seed than diploids (Fig. 2). Second, attack by *G. politella* significantly reduced the total seed set of both diploids and tetraploids in 2001 and 2002. On average across all years, attack by *G. politella* reduced total seed set by 17.2% in diploids and 40.3% in tetraploids, demonstrating that parasite attack has significant negative fitness consequences in this system (Fig. 2). Third, there is a statistically significant interaction between attack and ploidy in 2003, demon-

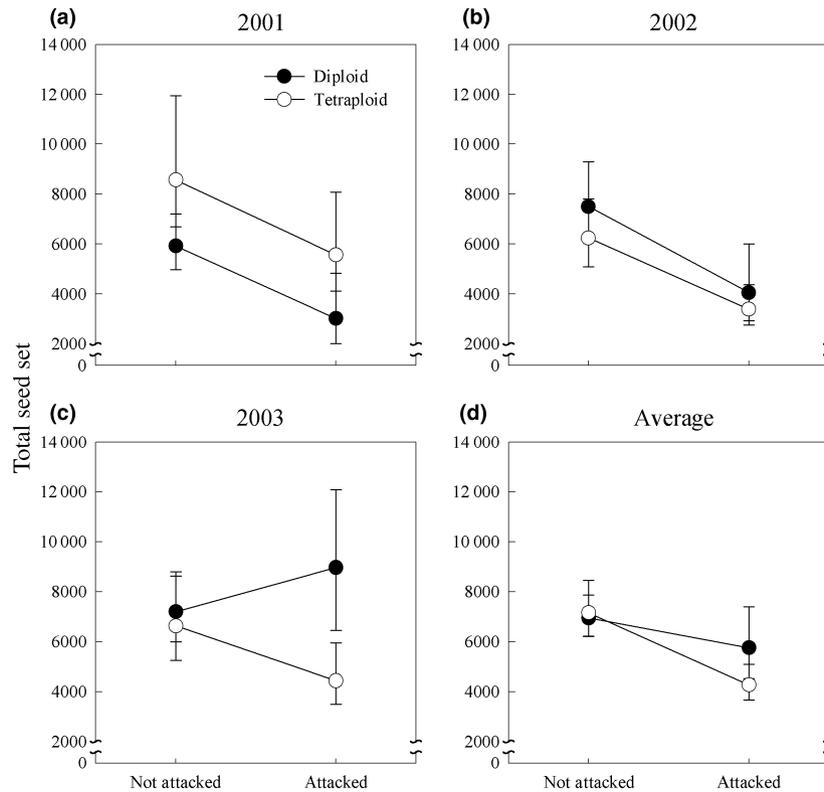


Fig. 2 The effect of attack by *Greya politella* on total seed set across ploidy and years. Each circle indicates the average total seed set for diploid and tetraploid *Heuchera grossularifolia* that were either not attacked or attacked by *Greya politella*. Error bars are the BCa 95% confidence intervals based on 19 999 bootstrap replicates. ANOVA results showed significant effects ($P < 0.05$) of attack on total seed set in 2001 and 2002 (panels a and b); ploidy alone had a significant effect in 2001 (panel a); the ploidy \times attack interaction was significant in 2003 (panel c). No other effects were significant.

strating that the consequences of parasite attack for plant fitness differed by ploidy in this year (Fig. 2).

Consequences of parasite attack for phenotypic selection

We tested the hypothesis that attack by *G. politella* contributes to phenotypic selection by performing an SSA (Ridenhour, 2005). Results of our SSA analysis are summarized in Table 1. As reported by Nuismer & Cunningham (2005), significant selection gradients exist for many of the focal traits during the 3 years of this study. However, attack by *G. politella* generated statistically significant phenotypic selection on only two of these three traits – MFD and AFD. Specifically, we found that differential parasite attack generated significant selection for larger MFD in the tetraploid population on average across years, earlier flowering in the tetraploid population in 2003 and earlier flowering in the tetraploid population on average across years, explaining 2.1%, 38.6% and 23.1% of the total observed selection gradients respectively (Table 1). In addition, differential parasite attack contributed to statistically significant

divergent selection for flowering time in 2003 and on average across years, favouring earlier flowering tetraploids but later flowering diploids. Although attack by *G. politella* did not cause significant selection on SL in the diploid or tetraploid population individually, it did contribute to divergent selection favouring shorter scapes in tetraploids and longer scapes in diploids on average across years (Table 1).

Discussion

Our results show that despite consistent negative fitness consequences of attack by the seed-parasitic moth, *G. politella*, phenotypic selection caused by differential parasite attack varies across years and populations of different ploidy. Specifically, our results show that the magnitude of parasite selection on flowering traits ranges from effectively 0 to 0.059. The largest of these values falls at approximately the 73rd percentile of the selection gradients compiled from the literature by Kingsolver *et al.* (2001), suggesting parasite-mediated selection is relatively modest for the traits we studied. In addition to being variable in magnitude, our results revealed

Table 1 Results of the selective source analysis for the three floral traits studied in *Heuchera grossulariifolia*: scape length (SL), maximum floral display (MFD) and average flowering date (AFD).

Trait	Selective source	Year											
		2001			2002			2003			Average		
		2x	4x	4x – 2x	2x	4x	4x – 2x	2x	4x	4x – 2x	2x	4x	4x – 2x
SL	SL	0.265	0.245	-0.019	0.304	0.309	0.005	0.246	0.318	0.072	0.241	0.274	0.033
	Moth	0.008	-0.025	-0.033	0.006	0.007	0.001	-0.001	-0.050	-0.048	0.006	-0.015	-0.021
	Total	0.272	0.221	-0.052	0.310	0.316	0.006	0.245	0.269	0.024	0.247	0.260	0.012
MFD	MFD	0.457	0.924	0.466	0.716	0.491	-0.225	0.705	0.675	-0.031	0.667	0.736	0.069
	Moth	0.012	0.021	0.009	0.002	0.015	0.014	0.003	0.002	-0.001	0.002	0.016	0.014
	Total	0.469	0.945	0.475	0.717	0.506	-0.212	0.708	0.676	-0.032	0.669	0.753	0.084
AFD	AFD	0.240	0.025	-0.215	0.138	-0.060	-0.197	-0.018	-0.094	-0.077	0.121	-0.083	-0.204
	Moth	0.004	-0.017	-0.021	-0.005	-0.018	-0.013	0.007	-0.059	-0.065	0.005	-0.025	-0.030
	Total	0.244	0.007	-0.237	0.133	-0.078	-0.210	-0.011	-0.153	-0.142	0.126	-0.108	-0.234

Selection on each floral trait is broken down into selection incurred due to moth attack and floral phenotype; these two sources sum to the total selection gradient. Within each year, entries are provided for the diploid population (2x), the tetraploid population (4x), and the difference between the two populations (4x – 2x). Bold entries indicate estimates significantly different from zero at the $P < 0.05$ level. Data used in the SSA consisted of 108 diploids and 141 tetraploids in 2001; 127 diploids and 169 tetraploids in 2002; and 154 diploids and 141 tetraploids in 2003.

populational differences in the direction of selection attributable to parasite attack, with parasite attack favouring earlier flowering and shorter scapes in the tetraploid population and later flowering and longer scapes in the diploid population.

These observations of divergent selection suggest that parasites may play an important role in the phenotypic diversification of populations, and potentially in sympatric speciation. This possibility is supported by our observation that attack by *G. politella* selected for divergent flowering times and scape lengths across the two host populations. Interestingly, this divergent selection acts to increase existing phenotypic differentiation between the two populations where tetraploids flower earlier and have shorter flowering scapes than diploids (Segraves & Thompson, 1999; Nuismer & Cunningham, 2005). The fact that parasites select for divergent flowering times is particularly relevant as divergence in this ecological trait is likely to also cause assortative mating, a situation particularly conducive to speciation (Dieckmann & Doebeli, 1999; Gavrillets, 2004). It is important to note, however, that although parasite attack contributes to divergent selection in multiple years, and on average across years, in only 1 year (2003) would removing parasites change the overall pattern of selection (Table 1).

Our SSA demonstrates parasite attack contributes much more strongly to phenotypic selection in tetraploids than in diploids. Specifically, we found significant selection gradients attributable to *G. politella* only in the tetraploid population. The strongly asymmetric contribution of parasite attack to observed patterns of selection in diploid and tetraploid *H. grossulariifolia* is not surprising given the large discrepancy that exists in the intensity of attack by this parasite across ploidy. Specifically, the

intensity of attack by *G. politella* has repeatedly been shown to be greater on tetraploid populations (Thompson *et al.*, 1997; Nuismer & Thompson, 2001). Results reported here are consistent with these previous studies, showing that tetraploids are 1.82 times as likely to be attacked, have 2.13 times more flowers attacked and 2.39 times as many larvae in each flower (Fig. 1). It seems likely that this approximately twofold difference in overall attack rates explains much of the difference in the strength of parasite selection we observe.

We chose the three floral traits we have studied because each is likely to play at least some role in interactions with other species that utilize the flowers of *H. grossulariifolia* as a resource (e.g. floral parasites and pollinators). It is possible, however, that other traits not included in our study experience stronger selection by *G. politella*. For instance, numerous studies have shown that attack rates by parasites depend on the concentrations of toxic defensive compounds in the host (e.g. Berenbaum & Zangerl, 1998; Mauricio, 2001; Agrawal & Van Zandt, 2003). Such chemical defences may play an important role in the interaction studied here as well, but we currently have no information on chemical defences in the developing seeds of *H. grossulariifolia*. Similarly, other traits such as seed coat thickness, length of seed coat spines and floral morphology may all play a role in defence against attack by *G. politella*. A potentially insightful method for determining whether important traits have been excluded from the analysis would be to calculate a quantity akin to the opportunity for selection (Crow, 1958; Arnold & Wade, 1984). One such quantity would be the covariance between host relative fitness and various measures of parasite attack (e.g. proportion of capsules attacked). If a single trait explained 100% of the variation in moth attack, this measure would equate

to the classical opportunity for selection, and thus would define the maximum possible selection differential that could be ascribed to parasite attack. Our analysis of this quantity showed it to be significant in many cases where no significant selection gradients were observed, suggesting that there may be other traits which explain variation in parasite attack, but which have not been included in our analysis.

Although our results suggest *G. politella* contributes to phenotypic selection in *H. grossulariifolia*, there are two important caveats to the interpretation of this result. First, SSA is a correlative technique, as are all regression-based methods of detecting phenotypic selection (e.g. Lande & Arnold, 1983; Rausher, 1992; Mauricio & Mojonner, 1997; Kingsolver *et al.*, 2001; Stinchcombe *et al.*, 2002). Thus, our results do not conclusively demonstrate that differential attack by the seed-parasitic moth, *G. politella*, causes observed patterns of variation in relative fitness. It is possible, for instance, that individual moths preferentially attack plants that set less seed, or that small-scale spatial variation leads to increased moth densities in regions where plants set fewer seeds. However, neither of these possibilities – which could lead to a spuriously attributing the observed patterns of phenotypic selection to moth attack – seem particularly likely. The first possibility requires a seed parasite prefers plants offering reduced resources whereas the second requires a seed parasite have greater population densities in regions where plants produce fewer seeds. Both conditions seem biologically improbable, although might occur if, for instance, more vigorous plants tend to produce more seeds and are better defended against parasitism. The second major caveat to our results is that we have used total seed set as our measure of lifetime fitness and thus have ignored potentially important contributions of male function and vegetative reproduction.

Taken together, our results show that phenotypic selection by parasites may be highly variable across host populations and time, emphasizing the potential importance of temporal variability in coevolutionary interactions (e.g. Nuismer *et al.*, 2003). In our study, the strength of selection varied considerably across years, even though parasitism caused strong and fairly consistent fitness losses in the host populations. This decoupling of fitness consequences and selection emphasizes the importance of using statistical techniques to evaluate the contribution of hypothesized sources of phenotypic selection in a statistically rigorous way (e.g. Iwao & Rausher, 1997; Scheiner *et al.*, 2000; Ridenhour, 2005). Only by using such techniques will we be able to develop a general understanding of the strength of parasite-driven phenotypic selection in the wild.

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