Note

# Keystone Individuals Alter Ecological and Evolutionary Consumer-Resource Dynamics

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abstract: Intraspecific variation is central to our understanding of evolution and ecology, but these fields generally consider either the mean trait value or its variance. Alternatively, the keystone individual concept from behavioral ecology posits that a single individual with an extreme phenotype can have disproportionate and irreplaceable effects on group dynamics. Here, I generalize this concept to include nonbehavioral traits and broader ecological and evolutionary dynamics. I test for the effects of individuals with extreme phenotypes on the ecology and evolution of a gall-forming fly and its natural enemies that select for opposite gall sizes. Specifically, I introduce a putatively keystone predator-attracting individual gall-maker, hypothesizing that the presence of such an individual should (1) increase gall maker population-level mortality, (2) cause consumer communities to be dominated by species that are most attracted to the keystone individual, (3) increase selection for traits conferring defense against the most common consumer, and (4) weaken patterns of stabilizing selection. I find support for both the ecological and evolutionary consequences of single individuals with extreme phenotypes, suggesting that they can be considered keystone individuals. I discuss the generality of the keystone individual concept, suggesting likely consequences for ecology and evolution.

*Keywords:* Eurosta, host-parasitoid, intraspecific variation, predator-prey.

## Introduction

Species interactions are central to our understanding of ecology and evolution (Benkman 2013; McPeek 2017). Ecologists often focus on the strength of species interactions in an effort to understand the structure of communities (Paine 1969; Chesson 2000), whereas evolutionary biologists aim to link species interactions to selection (Lande and Arnold 1983; McPeek 2017). A well-established rule in both ecology and evolution is that some species have much larger effects

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than others, with this tenet epitomized by the keystone species concept (Paine 1969; Power et al. 1996). Keystone species are those whose impact on their community or ecosystem is large and disproportionately large relative to its abundance (Mills et al. 1993; Power et al. 1996). While evidence suggests that species traits can affect ecological interactions and selection, less is known about the effects of individual trait variation.

Intraspecific trait variation is increasingly acknowledged as an important factor underlying ecological dynamics, including species interactions (Bolnick et al. 2011; Sih et al. 2012). While community ecologists typically consider differences in the population mean or variance of a trait (Bolnick et al. 2011), some have argued that the presence of a single individual with an extreme phenotype can affect biological patterns (Modlmeier et al. 2014). For example, recent work in behavioral ecology and evolution has emphasized the concept of the keystone individual, contending that certain individuals have extreme traits that cause them to have disproportionately large effects on group dynamics (relative to other individuals of the same species; Modlmeier et al. 2014). Notably, the effect of these extreme phenotypes is beyond the normal scaling between individual traits and an individuals impact on dynamics (Modlmeier et al. 2014). For example, the removal of a single dominant male prairie chicken caused an enormous decrease in group-level reproduction (Robel and Ballard 1974). However, to this point, the application of the keystone individual concept has been largely restricted to behavioral ecology (Modlmeier et al. 2014), despite probable utility for nonbehavioral traits and applications to more general ecological and evolutionary dynamics. In an ecological context, a keystone individual may then be an individual that has a large and irreplaceable (Modlmeier et al. 2014) effect on population, community, or ecosystem dynamics, with this effect likely being mediated by an extreme phenotype.

Keystone individuals may be more likely to structure some systems than others. Attack by consumers (predators and parasites) underlies many ecological patterns (Linde-

man 1942; Estes et al. 2011) and can impose strong selection on resource populations (McPeek 1997). For example, some resource individuals may have phenotypes that have large effects on the degree to which they—and those individuals around them—are affected by consumers (Van Buskirk and Schmidt 2000). The large effect of trophic dynamics and the often large variation in anti-consumer traits suggests that keystone individuals may be common in trophic systems (Modlmeier et al. 2014), a pattern we observe among keystone species (Paine 1966; Power et al. 1996).

One way that a keystone individual can affect trophic dynamics is through apparent competition. At the community scale, species that are easily consumed may increase the abundance of consumers or change consumer behavior such that nearby species are attacked more frequently (Holt 1977). We may extend this thinking to encompass intraspecific variation (Grosholz 1992): individuals that are easily identifiable or particularly attractive as prey may increase attack on the surrounding population (Balmer et al. 2009). In complex communities, if more than one consumer attacks a single resource species and consumers respond differently to a keystone individual, then the community of consumers attacking populations with and without keystone individuals are likely to diverge. In short, individual traits conferring susceptibility to consumption may increase attack rates on nearby individuals and alter the composition of the consumer community.

Consumers can create strong selection for defensive phenotypes of resources. Consumer species often select for specific resource phenotypes, causing divergent selection regimes among populations differing in attack rates (McPeek 1997). For example, Van Buskirk and Schmidt (2000) showed that predators reduced survival of poorly defended newts, but when predators were absent, well-defended newts grew more slowly. Applying the keystone individual concept, we may then predict that the presence of an individual that attracts consumers will augment selection for anti-consumer traits in the rest of the population (a consumer-attracting keystone individual). However, populations are frequently attacked by several species. In complex communities, where multiple consumers attack a single resource, trade-offs often exist between defending against one consumer or another (Weis and Abrahamson 1985; Mikolajewski et al. 2010; Start and Gilbert 2016). In evolutionary terms, different consumers can impose opposing selective forces, together creating stabilizing selection favoring intermediate phenotypes (Weis and Abrahamson 1985). We may then predict that a consumer-attracting keystone individual will shift consumer community composition, ultimately increasing selection for defensive traits and in so doing also weakening stabilizing selection. In sum, the presence of a keystone individual may affect the ecological (trophic) interactions of its neighbors, ultimately altering selection.

In this article, I test how the presence of a putatively keystone individual affects trophic interactions and selection. I introduce a single individual with an extreme consumer-attracting phenotype to populations of a gall-forming fly (*Eurosta solidaginis,* hereafter *Eurosta*) and then measure attack rate by a guild of parasitoid enemies and bird predators (Weis and Abrahamson 1985). Earlier work has shown that galls found high on the stem are more likely to be attacked by birds, suggesting that these individuals may be particularly conspicuous and serve to attract bird predators (Confer and Paicos 1985). Research in this system has also shown that a parasitoid wasp (*Eurytoma* gigantean, hereafter *Eurytoma*) and bird predators attack small and large galls, respectively, thus selecting for the opposite phenotype (Weis and Abrahamson 1985). When both enemies are present, their joint effect is to produce stabilizing selection on gall size, although selection often has a directional component favoring the gall size attacked by the rarer enemy (Weis and Abrahamson 1985). Selection can thus vary from entirely directional when only one enemy is present to stabilizing with or without a directional component when both enemies are present (Weis and Abrahamson 1985). I use this experiment to test the above ideas by hypothesizing that (1) total mortality will be greater when a predator-attracting individual is present in a population; (2) the height of a putatively keystone individual on the stem will shift community composition of enemies, causing relative increases in bird attack rates; (3) increased bird attack in those populations will shift selection gradients to favor small galls that are more susceptible to parasitoid attack but less susceptible to bird attack; and (4) strong directional selection resulting from high bird attack rates in populations with a keystone individual will weaken stabilizing selection.

## Methods

### Study System

*Solidago altissima* (hereafter goldenrod) is a common old-field plant in eastern North America (Root 1996). Goldenrod is attacked by *Eurosta*, a fly whose larvae cause the development of a spherical stem gall (Uhler 1951). Adult female flies emerge from galls, mate, and lay eggs just below the apical meristem in late May in Southern Ontario, with galls appearing 3 weeks later and growing along with the plant for another month (Weis and Abrahamson 1985). The height of a gall is determined by the height of the goldenrod plant when eggs are laid, with eggs that are laid later or those laid on tall (possibly superior host) plants producing galls higher on the stem (Craig et al. 2000). Galls are then attacked by a suite of enemies, including bird predators (downy woodpeckers and chickadees), two *Eurytoma* wasps, and a *Mordelistenna* beetle (Weis and Abrahamson 1985). Note that

birds create a hole in the gall, but the gall typically remains otherwise intact. Crucially, these enemies impose opposing selection on gall size. Birds and *Eurytoma* preferentially attack large and small galls, respectively, with each enemy imposing directional selection favoring the gall sizes they do not attack (Weis and Abrahamson 1985; Start and Gilbert 2016). When both enemies are present, selection favors intermediate gall sizes (i.e., stabilizing selection), with the optimum gall size depending on the relative attack rate of birds and *Eurytoma* (Weis and Abrahamson 1985; Start and Gilbert 2016).

*Trait Survey*

In an effort to identify extreme phenotypes, which are most likely to have large effects on ecological dynamics and act as keystone individuals (Modlmeier et al. 2014), I first aimed to describe intraspecific trait variation in *Eurosta*. I surveyed intraspecific trait variation of *Eurosta* galls at Koffler Scientific Reserve by randomly selecting 647 galls and then measuring their height and horizontal diameter (hereafter size), both traits that are thought to underlie patterns of attack by enemies (Abrahamson et al. 1989). While gall size and possibly height are partly heritable (Start and Gilbert 2016), both traits are also partly determined by the environment (Craig et al. 2000) and plant genotype, resulting in nutritional and plant height differences (Abrahamson et al. 1989). Traits were uncorrelated ($P > .65$ using a linear model) but were used to identify trait values for the subsequent experiment.

*Focal Individual Experiment*

I used a simple experimental approach to test for the effects of traits of putatively keystone individuals on ecological interactions and selection. I began by identifying and demarcating 20 patches (2 m × 2 m) that contained goldenrod and were greater than 15 m from any tree (galls near trees suffer extremely high bird mortality; Confer and Paicos 1985). All patches were in the same field and placed haphazardly, with a minimum edge-to-edge distance of 8 m separating each patch. I then randomly assigned each patch to contain a focal individual either high or low on a goldenrod stem in the center of the patch (10 replicates per treatment). I expected galls positioned high on stems to attract greater bird predation (Confer and Paicos 1985), acting as keystone individuals. Because bird predators also prefer large galls, I used galls varying from 17 to 28 mm in diameter. To impose treatments, I collected focal individual galls from elsewhere at Koffler Scientific Reserve and then, using glue, affixed them to the upper (130 cm) or middle (85 cm) portion of a goldenrod stem in the center of each patch. High and low focal gall positions represent the highest

1% of galls and mean gall height, respectively (from trait survey data; fig. A1), with all high galls being >15 cm higher than the next highest gall in the population. After imposing treatments in late June, I allowed surrounding (nonfocal) galls to be attacked by their parasitoid enemies and bird predators until the following April. In April, I collected nonfocal galls and then measured their maximum horizontal gall diameter. Finally, I dissected each nonfocal gall to determine its content, scoring galls containing *Eurosta* larvae as survivors, those with large holes as having been killed by birds, those containing other larvae as having been killed by the corresponding parasitoid (e.g., *Eurytoma*), and empty galls showing no signs of habitation as early larval death (Abrahamson et al. 1989).

*Statistical Analyses*

I used a series of linear models (LMs) to test for the effects of putatively keystone individuals on species interactions and selection. I first standardized all independent variables by subtracting the mean and dividing by the standard deviation. I then began by testing for differences in mortality and attack rates among nonfocal galls. I used a generalized linear mixed model (GLMM) with a binomial distribution and logit link function to test for differences in the rate of mortality, including treatment (high or low focal individual) and focal gall size as main effects and plot as a random effect. I used the same model to independently test for differences in attack rates of each enemy (*Eurytoma gigantea*, *Eurytoma obtusiventris*, *Mordellistena* spp., and birds) and early larval death. When analyzing patterns of parasitoid attack, I excluded galls that had been attacked by birds because some parasitoids may have been consumed, biasing estimates of parasitoid attack rate when bird predation differs among populations (Start and Gilbert 2016). Because focal gall size had no effect in any model, I did not include this variable in subsequent selection analyses. In all cases, I began with the fully interactive model before removing nonsignificant interaction terms to arrive at the final model.

In order to gauge the potential for selection, I tested for differences in gall size preference by estimating attack rates of each species using a GLMM with a binomial error distribution, gall size as a main effect, and plot as a random effect. I next aimed to link any differences in species interactions to patterns of directional and nonlinear selection on gall size among treatments using phenotypic selection analyses (Lande and Arnold 1983). I first calculated relative fitness by dividing an individual's survival by the mean survival measured in the entire experiment (i.e., relativizing across all plots; Lande and Arnold 1983). I then used separate models to estimate significance values and selection coefficients, because coefficients from GLMMs are not directly

analogous to selection, and LMs of transformed binary data violate statistical assumptions and so cannot be assessed for significance (Start and Gilbert 2016). I tested for significant selection coefficients by regressing survival against standardized gall size using a GLM with a logit link function for each plot separately and all data together, including plot as a random effect in the global model. I then used LMs with relative fitness as the response variable to estimate selection coefficients. To estimate nonlinear selection coefficients, I repeated the above analyses, estimating relative fitness while including standardized squared gall size in the models (Lande and Arnold 1983) and then doubling coefficients to find the magnitude of nonlinear selection (Stinchcombe et al. 2008). Note that galls experiencing early larval death were excluded from all selection analyses because mortality owing to small gall size cannot be separated from small gall size resulting from the cessation of growth following abortion (Start and Gilbert 2016).

Last, I tested for treatment-level differences in selection on gall size of nonfocal individuals. I used an LM to estimate directional selection coefficients using treatment as a main effect. I repeated this analysis separately for stabilizing/disruptive selection coefficients. I used log-likelihood ratios to test for significance of all models, with likelihoods determined from the maximum-likelihood solution. All analyses were conducted in R (R Development Core Team 2015) using the base and lme4 packages (Bates et al. 2015). Data are available in the Dryad Digital Repository: http://dx.doi .org/10.5061/dryad.t6j7p (Start 2018).

## Results

Focal individuals affected attack rates and selection. In a given plot, *Eurosta* was twice as likely to die ($P < .001$; fig. 1*A*) and three times more likely to be attacked by birds ($P < .001$; fig. 1*B*) when the focal individual was high on the goldenrod stem (i.e., keystone individual present). Conversely, the height of the focal individual did not affect rates of early larval death or attack by any parasitoid, including *Eurytoma* (all $P > .6$; fig. 1*B*). Similarly, focal gall size had no effect on mortality or attack rate by any enemy (all $P > .4$). Overall, the presence of a focal individual high on the stem increased attack by some enemies, augmenting mortality.

Birds and *Eurytoma* preferentially attacked large (effect size $= .16$) and small (effect size $= -.56$) galls, respectively (both $P < .001$; fig. 2*A*), while other parasitoids had no bias (both $P > .45$, with the magnitude of effect sizes $< .08$; fig. 2*A*). Globally, these preferences caused selection to favor large galls ($\beta = .15$, $P < .001$), but selection also had a significant stabilizing component ($\gamma = -.68$, $P = .008$; fig. A2). The directional selection coefficient was always in

favor of large galls but was much higher when focal galls were low on the stem (mean $\beta = .24$) than when focal galls were high on the stem (mean $\beta = .08$; significant difference between treatments: $P = .012$; fig. 2*B*, 2*C*). Stabilizing selection did not differ between treatments ($P > .65$; high gall: $\gamma = -.41$, $P = .27$; low gall: $\gamma = -.62$, $P = .051$). In short, focal individual traits altered patterns of linear but not nonlinear selection on gall size.

## Discussion

Realistic but extreme phenotypes of a single individual affected ecological and evolutionary dynamics across resource populations and consumer communities, suggesting a role for keystone individuals (Modlmeier et al. 2014). *Eurosta* populations near focal individuals high on the stem (hereafter keystone individuals) were twice as likely to die (fig. 1*A*). From a community ecology perspective, individuals with extreme phenotypes altered consumer communities, causing a threefold increase in bird predation, but parasitoid attack was unaffected (fig. 1*B*). Changes in mortality and consumer communities weakened selection for larger galls when keystone individuals were present (fig. 2), without affecting stabilizing selection. I suggest that *Eurosta* with extreme phenotypes can be keystone individuals, affecting ecological and evolutionary dynamics.

Keystone individuals increased consumer-induced mortality, with likely consequences for population dynamics. The presence of a keystone individual doubled mortality of the surrounding *Eurosta* population (fig. 1*A*). This pattern of attack is analogous to the intraspecific extension of apparent competition (Holt 1977), with the presence of an individual of one phenotype increasing the likelihood of attack for individuals with different (less susceptible) phenotypes. Intraspecific apparent competition has been documented (Yamaguchi and Kishida 2016), for example, in coinfections by two strains of the same pathogen, where coinfection increases immune function (effectively a predator) and hence clearance rates (Balmer et al. 2009). While this and other examples exist, to my knowledge they invariably consider population-level differences rather than the effect of a single keystone individual (Modlmeier et al. 2014). In short, keystone individuals can affect population-level mortality rates, with potentially important consequences for subsequent population dynamics.

Keystone individuals affected not only gross mortality rates but also determine the composition of the consumer community. Bird attacks tripled in populations containing keystone individuals, but parasitoid attack was unchanged (fig. 1*B*). Increased bird attack was likely caused by the conspicuousness of galls high on stems, with highly placed galls experiencing greater attack by birds in previous stud-
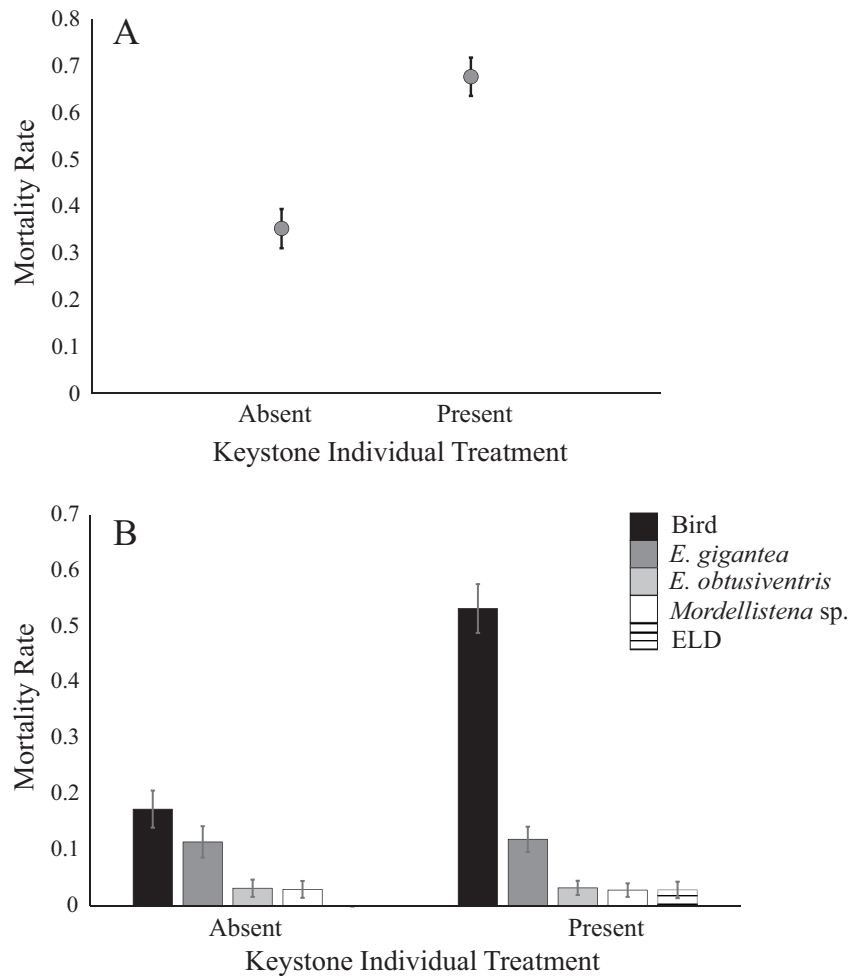
**Figure 1:** Presence of a keystone individual altered mortality rates and consumer community composition. Mortality was doubled in the presence of a keystone individual (*A*). These differences in mortality rate are analogous to differences in relative fitness between treatments. Bird attack rates tripled in populations with keystone individuals, but attack by other enemies and mortality caused by early larval death (ELD) were unchanged (*B*). Presence and absence of keystone individuals refer to high and low focal galls, respectively. Error bars represent 95% confidence intervals.

ies (Confer and Paicos 1985). Conversely, parasitoid attack rates were unchanged, perhaps because they use other cues to locate hosts (Weis et al. 1985). Regardless of the underlying mechanism, the presence of an individual with an extreme phenotype altered consumer community composition. Notably, this effect is distinct from other work investigating the role of intraspecific variation in community ecology (Bolnick et al. 2011; Sih et al. 2012; Violle et al. 2012). Specifically, the keystone individual concept as applied here differs in that it explicitly investigates the effects of a single phenotypically extreme individual (on the tail of a trait distribution) rather than the differences in the mean or variance of a trait within or among populations (Bolnick et al. 2011; Sih et al. 2012; Violle et al. 2012). Overall, these results suggest that phenotypically extreme

individuals can serve as keystone individuals, radically altering community composition.

The effects of keystone individuals on mortality rates and the composition of consumer communities ultimately caused differences in selection. In populations lacking keystone individuals, attack by *Eurytoma* selected for larger galls (fig. 2). When keystone individuals were present, increased bird attack of large galls weakened directional selection (fig. 2*B*, 2*C*). I contend that these types of changes in selection are likely to be general, with selection differing among populations whenever keystone individuals affect consumption rates, and consumption is biased toward particular resource phenotypes (McPeek 1997). However, in this study the strength of stabilizing selection was unaffected by keystone individuals. This lack of change may
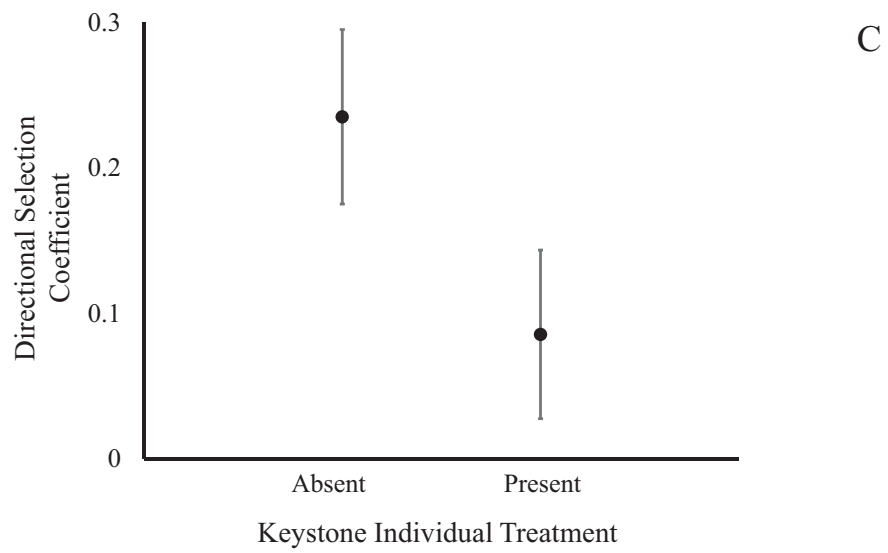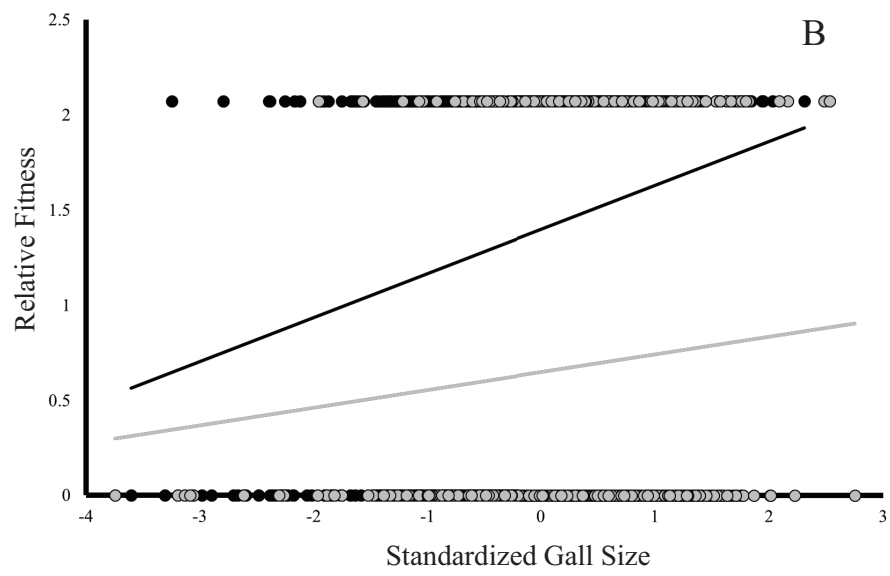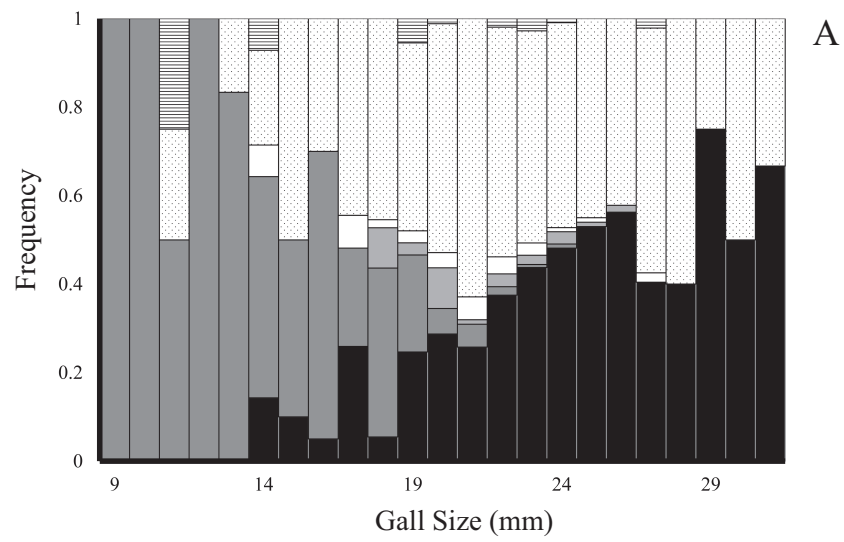
have occurred because the increase in bird predation was not large enough to overcome strong directional selection (Lande and Arnold 1983; Weis and Abrahamson 1985). In sum, keystone individuals can alter ecological dynamics, with consequences for some but not all components of selection.

Differences in selection can in some cases cause local adaptation, creating the potential for eco-evolutionary feedbacks (Craig et al. 2007; Start and Gilbert 2016). In this study, over time we may expect keystone individuals to cause individuals in a population to evolve smaller gall sizes (or less large; fig. 2). However, local adaptation is unlikely for at least two reasons. Because of their position high on the stem, keystone individuals are extremely likely to be attacked by birds (Confer and Paicos 1985), meaning that should the high-stem phenotype be a heritable trait, keystone individuals would be quickly removed from the population. Indeed, barring disruptive selection, extreme phenotypes are likely to be selected against. Conversely, while unlikely in this system, rarity advantages may cause negative frequency-dependent selection when keystone individuals disadvantage other individuals to their own benefit, ultimately maintaining keystone genotypes at some equilibrium frequency (Koskella and Lively 2009). More generally, keystone individuals may be maintained in a system when their extreme phenotype is sometimes favored (i.e., temporally variable directional selection) or when environmental effects consistently create extreme phenotypes. The second reason that local adaptation may be unlikely is that extreme phenotypes may not be highly heritable but instead result from plastic environmental differences (Soule and Cuzin-Roudy 1982). For example, in this system, while genetic variation in phenology and hence gall height exists (Horner et al. 1999), the tallest individual likely results from a combination of late-emerging genotypes, cool microclimatic conditions, and oviposition on particularly tall plants (plant height being itself a genotype by environment interaction; Horner et al. 1999). An open question is then, in general, to what degree is the presence of a keystone individual consistent through time? If populations are consistently affected by keystone individuals, then local adaptation may mitigate the effects of increased mortality (Start and Gilbert 2016), but if the presence of a keystone individual is sporadic, then its effect will be to increase temporal variation in ecological and evolutionary dynamics (Lande 1993; Modlmeier et al. 2014). Put simply, the likelihood of local adaptation will depend on the consistency with which a keystone individual is present in a population and the degree to which they influence ecological and evolutionary dynamics.

Another open question is, how common are these types of keystone individual dynamics and in what systems might we expect them to occur? I suggest that the specific mechanism of enemy attraction presented here may be surprisingly common among the thousands of gall-making species (Price et al. 1998), although perhaps more so when considering other nonpredator systems. For example, while predators rarely leave their prey intact and capable of continuing to attract other predators, herbivores and parasites do, suggesting that the enemy attraction mechanism may be common in these systems. More generally, keystone individuals may occur in such systems via other mechanisms. Because they do not necessarily kill their host, herbivores and parasites can multiply and spread, perhaps more so when attacking individuals with extreme phenotypes. An interesting example is a super spreader, an individual that contributes disproportionately to the spread of a disease and often exhibits extreme phenotypes (e.g., showing no symptoms; Paull et al. 2012). Similarly, in free-living systems, plant genetics can underlie the composition of herbivore communities (Crutsinger et al. 2009), and plants often share herbivores with their neighbors (Potvin and Dutilleul 2009), suggesting that keystone individuals may arise if both processes co-occur and some plant genotypes are particularly prone to herbivory. Consistent with this example, we may expect keystone individuals to arise in the same types of systems where keystone species occur, such as communities dominated by either a top predator or a single basal resource species (Modlmeier et al. 2014; Yamaguchi and Kishida 2016; Start and Gilbert 2017). In sum, regardless of the mechanism underlying their effect, I contend that keystone individuals may be common, particularly in trophic systems dominated by a single species.

By incorporating concepts from behavioral ecology with trophic processes and evolutionary dynamics, this study has begun to elucidate the intricacies and applications of the keystone individual concept in evolutionary ecology. I have demonstrated that, consistent with the keystone individual concept from behavioral ecology (Modlmeier et al. 2014), extreme phenotypes represent important components of ecological and evolutionary dynamics. Keystone

**Figure 2:** Keystone individuals combined with the preference of enemies for particular gall sizes weakened directional selection on gall size. *A*, Birds (black bars) and *Eurytoma gigantea* (dark gray bars) preferred large and small galls, respectively, causing survival to be high at intermediate gall sizes (dotted bars). Conversely, attack by *Eurytoma obtusiventris* (light gray bars) and *Mordellistena* sp. (white bars) and early larval death (striped) did not vary across gall size. *B*, Between treatments, selection was weaker when keystone individuals were present (gray circles) than absent (black circles). *C*, Among plots, directional selection coefficients were three times greater when keystone individuals were absent. Presence and absence of keystone individuals refer to high and low focal galls, respectively. Best fit lines show predicted values from the appropriate linear models. Error bars represent 95% confidence intervals.

individuals altered not only population dynamics (mortality; fig. 1*A*) but also species interactions and consumer community composition (attack rates; fig. 1*B*). These ecological differences caused keystone individuals to affect patterns of selection (fig. 2), potentially allowing for eco-evolutionary feedbacks. I suggest that keystone individuals may be common in nature and particularly in trophic systems, with potentially large consequences for ecology and evolution.
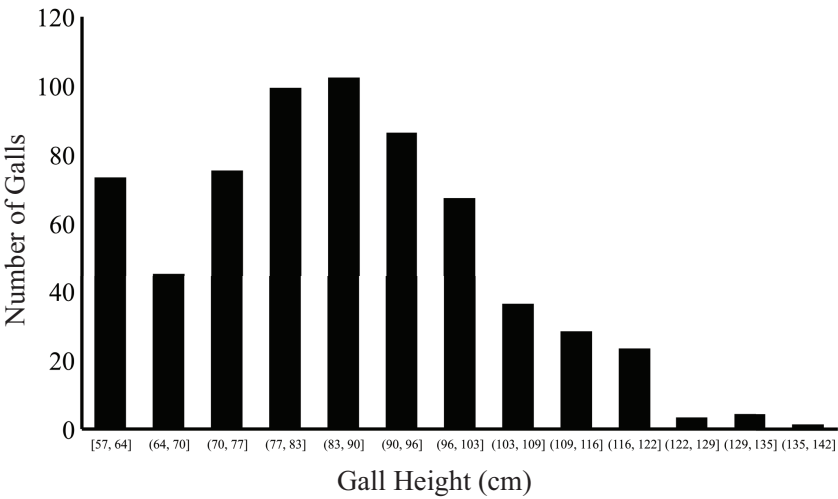
# APPENDIX

## Supplementary Figures



**Figure A1:** Histogram of gall height in the trait survey. Only 1% of galls were 130 cm or higher (putatively keystone individuals), with the average galls being 85 cm high (control galls). I used these trait values to inform the focal individual experiment.
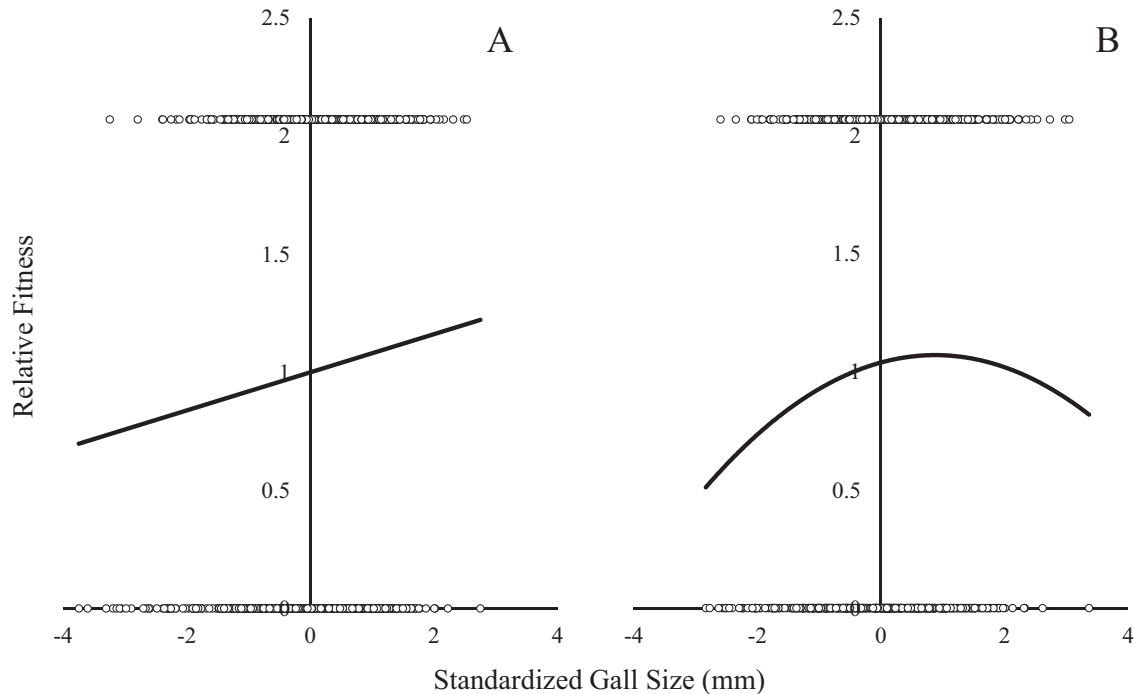
**Figure A2:** Selection coefficients across all individuals in the focal individual experiment. Directional selection favored larger galls (*A*) but had a stabilizing component (*B*). Best fit lines show predicted values from corresponding linear models.

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