Nonlinear functional responses and ecological pleiotropy alter the strength of disruptive selection in consumers

Kyle E. Coblentz

Integrative Biology, Oregon State University, Corvallis, OR 97331

e-mail: kyle.coblentz@oregonstate.edu.

Keywords: divergent selection; interference competition; handling time; adaptive dynamics; consumer-resource interactions; intraspecific competition

Abstract

Much of the theory on disruptive selection has focused on selection in generalist consumers caused by ecological opportunity through the availability of alternative resources and intraspecific competition for those resources. This theory, however, makes several ecologically unrealistic assumptions. First, this theory assumes that consumers have a linear, resource-dependent functional response, ignoring well-documented effects of resource handling times and consumer dependence. Second, this theory assumes that the trait under selection only influences the per-capita attack rates of the consumer, ignoring other effects of the trait that may influence feeding rates and hence fitness. Here, I develop a one consumer-two resource model to investigate how nonlinear functional responses and ecological pleiotropy (traits that have multiple simultaneous ecological effects) influence the strength of disruptive selection. I find that handling times and interference among consumers are capable of altering disruptive selection by changing feeding rates differentially across consumer phenotypes. In particular, handling times cause a decrease in the strength of disruptive selection while the effects of interference depend on the mechanism through which interference occurs. The effects of handling times and interference, however, are dependent on whether and how ecological pleiotropy causes correlations between handling times or interference rates and attack rates. Overall, my results suggest that features defining the functional responses of consumers and the relationships among those features determine the likelihood and strength of disruptive selection. In particular, disruptive selection should be strongest in generalist populations composed of individual diet specialists who experience lower handling times and interference rates on the resources for which their attack rates are highest.

Introduction

Disruptive selection, a process in which natural selection favors individuals with more extreme phenotypes over individuals with intermediate phenotypes, plays important roles in evolution and ecology. Evolutionarily, disruptive selection causes and maintains genetic and phenotypic variation within populations and can drive speciation and adaptive diversification (Dieckmann and Doebeli, 1999; Doebeli, 2011; Rueffler et al., 2006; Smith, 1962). Ecologically, the intraspecific variation generated by disruptive selection can alter the interactions among species, their coexistence, and their functioning in ecosytems (Bolnick et al., 2011; Gibert and Brassil, 2014; Hart et al., 2016; Hughes et al., 2008; Schreiber et al., 2011).

Central to our understanding of disruptive selection and its consequences are the mechanisms generating disruptive selection in generalist consumers feeding on multiple resources. Generally, disruptive selection in consumers is thought to be the product of two interacting forces: the relative availability of alternative resources and intraspecific competition among individuals for those resources (Abrams et al., 2008; Nosil, 2012; Schluter, 2000). Alternative resources provide a form of ecological opportunity that can lead to disruptive selection when different trait values determine the ability of individuals to use different available resources (Abrams et al., 2008; Nosil, 2012; Schluter, 2000). If the use of different resources requires sufficiently different values of the individual's trait, individuals with trait values near the optimum for a certain resource will have higher fitness than individuals with values of the trait that are intermediate between optima, thus leading to disruptive selection. Intraspecific resource competition, in turn, can modify disruptive selection through ecological opportunity (Martin and Pfennig, 2009; Nosil, 2012; Rozenzweig, 1978). Given that different trait values affect individuals' feeding rates on different resources, the most common phenotypes will reduce the abundance of their associated resources to the greatest extent. The reduced availability of resources then drives higher rates of intraspecific competition in those common phenotypes. Consumers with less common phenotypes reduce their associated resources to a lesser extent and, all else being equal, experience less competition. The resultant

increase in fitness for less common phenotypes leads to negative frequency-dependent disruptive selection because the relative fitness of phenotypes is dependent on their relative abundance in the population (Dieckmann and Doebeli, 1999; Smith, 1962). Given the apparent generality of these mechanisms, theory has suggested that disruptive selection and its resultant effects should be widespread in generalist consumers (Dieckmann and Doebeli, 1999; Doebeli, 2011; Schluter, 2000).

Despite this seeming theoretical generality, empirical evidence has been mixed. Several studies have indeed shown clear evidence for disruptive selection and increased intraspecific variation in consumers related to ecological opportunity and intraspecific competition (Bolnick, 2001, 2004; Cucherousset et al., 2011; Hendry et al., 2009; Martin and Pfennig, 2009). However, several other studies, particularly those examining the relationship between intraspecific competition and intraspecific variation, have found results contrary to theory (Jones and Post, 2013; Mateus et al., 2016; Parent et al., 2014; Rundle et al., 2003; Schindler et al., 1997). One explanation for this variation in results is that the strength of disruptive selection due to intraspecific competition and ecological opportunity is dependent on features of the underlying consumer-resource interactions, particularly their strength (Abrams et al., 2008; Jones and Post, 2013, 2016). For example, disruptive selection through intraspecific competition requires that consumers deplete resources to an extent that it alters fitness across phenotypes; but, if the consumer-resource interactions are weak, prey depletion will be minimal and the resulting strength of disruptive selection will be weak (Abrams et al., 2008; Jones and Post, 2013, 2016). Alternatively, if species interactions are strong, consumers can deplete resources to local extinction causing a decrease in ecological opportunity, again, altering the strength of disruptive selection (Abrams et al., 2008; Jones and Post, 2013, 2016). These results suggest a need to evaluate the assumptions of previous theory, particularly in regards to the factors that influence the strength of consumer-resource interactions, and how altering these assumptions influences the strength of disruptive selection.

The majority of theory on disruptive selection is based on a consumer-resource model derived by MacArthur (1972). This model assumes that the consumer feeds across a continuous spectrum

of resources. The consumer has a linear functional response on each of the resources with the attack rate of the functional response given by a resource utilization function that is typically assumed to be Gaussian. Generally, the center of the resource utilization function is assumed to be determined by some trait of the consumer. A relationship between competition and resource-use overlap among either phenotypes or species can then be derived and this relationship has been used to investigate disruptive selection, limiting similarity among competitors, and character displacement (Case, 1981; Dieckmann and Doebeli, 1999; Roughgarden, 1976). Although this model has provided several insights, many of the assumptions the model makes regarding the underlying consumer-resource interactions are unrealistic and may be partially responsible for the mismatch between data and theory on disruptive selection in generalist consumers.

One of the assumptions made by the MacArthur model is that the consumer has a linear, resource-dependent functional response. As the functional response defines the relationship between the density of resources and the feeding rates of consumers, it is directly related to the strength of the consumer-resource interactions, and therefore likely to influence the strength of disruptive selection. Linear functional responses are known to be rare (Jeschke et al., 2004). Nonlinearities in functional responses are the product of nearly ubiquitous properties of consumer-resource interactions including consumer satiation through the time required to handle resources and mutual predator effects among consumer individuals, including interference and facilitation (Abrams and Ginzburg, 2000; DeLong and Vasseur, 2011; Holling, 1959; Novak et al., 2017).

Incorporating nonlinear functional responses into models of disruptive selection also provides an opportunity to address another assumption of the MacArthur model: the traits of individuals only influence their per capita attack rates on resources. It is more likely that traits influencing an individual's attack rates influence other parameters of the functional response (i.e. handling and interference) causing parameters to be correlated across individuals. The presence of such correlated ecological trait effects has been termed 'ecological pleiotropy' (hereafter, just pleiotropy; DeLong, 2017; DeLong and Gibert, 2016; Strauss and Irwin, 2004). Pleiotropic trait effects are likely to be common in functional responses. For example, a study of protists has shown attack

rates, handling times, and interference rates to all covary with one another (DeLong, 2017). In another study, body size has been shown to have allometric relationships with both attack rates and handling times of consumers (Vucic-Pestic et al., 2009). Although pleiotropic trait effects in functional responses have been shown to alter population dynamics (DeLong, 2017), the means by which they constrain or promote selection on underlying traits remains an open question.

Here, I use a one consumer-two resource model to investigate how the parameters of nonlinear functional responses – attack rates, handling times, and interference rates – and potential correlations among them arising from a pleiotropic trait, influence the strength of disruptive selection. My analyses indicate that nonlinear functional responses alter the strength of disruptive selection in ways that are dependent on the correlations between attack rates and handling times or attack rates and interference rates. This suggests that nonlinear functional responses and the presence of pleiotropy can determine the strength of disruptive selection generated by intraspecific competition and ecological opportunity, offering a potential explanation for some of the variation seen among empirical studies.

Methods

Below, I first introduce the general one consumer-two resource model used to investigate the relationships between nonlinear functional responses, pleiotropy, and the strength of disruptive selection. I then explain the methods used to analyze the model. Lastly, I introduce the particular nonlinear functional responses investigated and explain how I modeled pleiotropy among functional response parameters.

The General Model

To investigate the effects of nonlinear functional responses and pleiotropy on the strength of disruptive selection, I extended a one consumer-two resource model developed by Schreiber et al. (2011) to include nonlinear functional responses. The model begins with the assumption

that the consumer population has a quantitative trait, x, that is normally distributed with mean, $\bar{x}$, and variance, σ^2, such that the distribution of x in the population, $p(x, \bar{x})$, is described by,

$$p(x, \bar{x}) = \frac{1}{\sqrt{2\pi\sigma^2}} \mathbf{exp}[-\frac{(x-\bar{x})^2}{2\sigma^2}]. \tag{1}$$

The value of an individual's trait, x, determine its attack rates, $\alpha_i(x)$, on the two resources, R_i ($i = 1, 2$), respectively. The maximum attack rate of an individual on the ith resource, $\alpha_{i,max}$, occurs at a trait value of $x = \theta_i$. The attack rate then decreases as the trait value moves away from θ_i in a Gaussian manner,

$$\alpha_i(x) = \alpha_{i,max} \mathbf{exp}[-\frac{(x-\theta_i)^2}{2\tau_i^2}], \tag{2}$$

with the rate of decrease determined by τ_i^2. Assuming logistic growth in the resources, linear conversion efficiencies of resources into consumers, and a constant density independent mortality rate for the consumer, I described the dynamics of the consumer and resource populations as,

$$\frac{dR_i}{dt} = r_i R_i \left(1 - \frac{R_i}{K_i}\right) - C \int_{-\infty}^{\infty} f_i(R_1, R_2, C, x) p(x, \bar{x}) dx, \tag{3}$$

$$\frac{dC}{dt} = C(\int_{-\infty}^{\infty} \sum_{i=1}^{2} [e_i f_i(R_1, R_2, C, x)] p(x, \bar{x}) dx - m), \tag{4}$$

where r_i is the intrinsic growth rate of resource i, K_i is its carrying capacity, e_i is the conversion efficiency of resource i into consumers, and m is the per capita mortality rate of the consumer. Note that $f_i(R_1, R_2, C, x)$ is the functional response of the consumer on resource i which is dependent on both resources, the trait, x, and possibly consumer density in models including consumer interference.

Measuring Disruptive Selection and Methods of Analysis

I determined the strength of disruptive selection on the consumer's mean trait value, $\bar{x}$, using an adaptive dynamics approach. This approach models the evolutionary dynamics of traits involved in the ecological dynamics of a population (Dieckmann, 1997; Geritz et al., 1998). It does so by assuming that there is a resident phenotype that reaches an ecological equilibrium given the value

of its trait and the 'environment' determined by the values of other parameters in the model. The evolutionary dynamics are then determined by assuming a constant supply of mutations with small effects on the resident's trait. Mutants that are able to invade the ecological equilibrium set by the resident's trait value are assumed to then become the new resident. This process is assumed to continue until the trait value reaches an evolutionary equilibrium.

In the present model, if all of the resource specific parameters are equal (e.g. $r_1 = r_2$, $K_1 = K_2$) except the θ_i's, and the θ_i's are symmetric about zero (i.e. $\theta_2 = -\theta_1$), parameter values can be chosen such that the ecological and evolutionary dynamics of the system have a convergent stable equilibrium at $\bar{x} = 0$. Depending on the relative values of the model parameters, the evolutionary equilibrium at $\bar{x} = 0$ is either a fitness maximum or a fitness minimum. If the equilibrium is a fitness maximum, then there is stabilizing selection and the equilibrium is is an Evolutionarily Steady Strategy (ESS) (Geritz et al., 1998). In contrast, if the equilibrium is a fitness minimum, then there is frequency-dependent disruptive selection and the equilibrium is an evolutionary branching point (Geritz et al., 1998). At the evolutionary branching point, the per capita fitness of the resident population is zero by definition of being at an ecological equilibrium. Under this scenario, any mutant with a slightly shifted value of $\bar{x}$ will have positive fitness. Following Abrams et al. (2008), I use the magnitude of this fitness increase as my measure of the strength of disruptive selection.

To evaluate how changes in the parameter values of nonlinear functional responses alter the strength of disruptive selection, I used numerical analyses of the above model in Mathematica (v.11.0.1.0, code for the analyses can be found in the Online Supplementary Material). I restricted my analyses to combinations of parameter values that led to disruptive selection in the consumer and for which the consumer-resource interactions reached a fixed point equilibrium (i.e. did not exhibit cycles). After determining that disruptive selection occurred and the consumer-resource dynamics were at a fixed point using linear stability analysis, I varied the parameters of interest and calculated how the strength of disruptive selection changed by measuring the change in fitness of a mutant exhibiting a shift of $\bar{x} = 0.01$ in the consumer's mean trait value. Although

analytical results for the model were not possible, the results presented below were qualitatively similar across all of the different parameter values investigated that met the above criteria.

Nonlinear Functional Response Due to Handling Times

To determine how handling times influence the strength of disruptive selection, I substituted a multispecies Holling Type-II functional response (Holling, 1959),

$$f_i(R_1, R_2, C, x) = \frac{\alpha_i(x) R_i}{1 + \sum_{i=1}^{2} \alpha_i(x) \eta_i R_i}, \tag{5}$$

into equations 3–4, where η_i is the handling time of the consumer on resource i. I first investigated how handling times in general influenced the strength of disruptive selection by assuming that the handling times for both resources were equal (i.e. $\eta_1 = \eta_2$). I then altered the magnitude of the handling times and examined the resulting effects on the strength of disruptive selection.

Consumer-dependent Functional Responses

Although there are several 'standard' functional responses models that include interference, all were developed for a specialist consumer consuming a single resource (Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975; Hassel and Varley, 1969). To examine the effects of interference on the strength of disruptive selection in the one consumer-two resource model considered here, I extended two of the more mechanistic functional response models including interference – the Beddington-DeAngelis and Crowley-Martin functional responses – to more than one resource (Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975).

The Beddington-DeAngelis and Crowley-Martin functional responses make different assumptions about how interference effects consumer feeding rates, and therefore could lead to differences in how they predict interference to alter the strength of disruptive selection (Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975). The Beddington-DeAngelis functional response model assumes that consumers interfere with one another at a rate, γ, and that interference decreases the time available for searching for resources. These assumptions lead to the

following functional response for two resources,

$$f_i(R_1, R_2, C, x) = \frac{\alpha_i(x) R_i}{1 + \sum_{i=1}^{2} \alpha_i(x) \eta_i R_i + \gamma C}. \tag{6}$$

The Crowley-Martin functional response model extends the Beddington-DeAngelis functional response model by assuming that consumers also interfere while handling resources (Crowley and Martin, 1989). Under these assumptions, with a interference rate, λ, the Crowley-Martin functional response extended to two resources is,

$$f_i(R_1, R_2, C, x) = \frac{\alpha_i(x) R_i}{1 + \sum_{i=1}^{2} \alpha_i(x) \eta_i R_i + \sum_{i=1}^{2} \alpha_i(x) \eta_i \lambda R_i C + \lambda C}. \tag{7}$$

Given these two functional responses, I examined how interference in general changed the strength of disruptive selection by altering the magnitude of interference and examining the resultant effects on the strength of disruptive selection.

Ecological Pleiotropy

To determine how a pleiotropic trait controlling both attack rates and handling times or attack rates and interference rates may influence the strength of disruptive selection, I assumed that pleiotropy causes attack rates and handling times or interference rates to covary.

For pleiotropy affecting both attack rates and handling times, I modeled the effects of plieotropy by making the handling times of each resource a linear function of the trait-dependent attack rates,

$$\eta_i(\alpha_i(x)) = \eta_{i,min/max} + \eta_{i,slope} \times \alpha_i(x), \tag{8}$$

where $\eta_i(\alpha_i(x))$ is the handling time of an individual on resource i with attack rate $\alpha_i(x)$, $\eta_{i,min/max}$ is the handling time of an individual on resource i when the individual has an attack rate of zero on resource i, and $\eta_{i,slope}$ is the slope of the relationship exhibited across individuals with different trait values between the attack rates and handling times on resource i.

To model the effects of pleiotropy affecting both attack rates and interference rates, I made the interference rate a linear function of the total attack rate of an individual on resources combined.

Letting y represent either type of interference examined (i.e. γ for the Beddington-DeAngelis functional response or λ for the Crowley-Martin functional response), I modeled the correlation between interference and attack rates as,

$$y(\alpha_1(x), \alpha_2(x)) = y_{min,max} + y_{slope} \times (\alpha_1(x) + \alpha_2(x)) \tag{9}$$

where $y(\alpha_1(x), \alpha_2(x))$ is the interference rate of an individual with attack rates $\alpha_1(x)$ and $\alpha_2(x)$, $y_{min,max}$ is the interference rate that would be experienced if both attack rates were zero, and y_{slope} is the slope of the relationship between the total attack rate interference rates across individuals having different trait values.

I considered both positive and negative correlations between attack rates and handling times and attack rates and interference rates. For positive correlations, $\eta_{i,min/max}$ and $y_{min/max}$ are minimums and $\eta_{i,slope}$ and y_{slope} are positive. For negative correlations, $\eta_{i,min/max}$ and $y_{min/max}$ are maximums and $\eta_{i,slope}$ and y_{slope} are negative. To examine the effects of the correlations between attack rates and handling times or attack rates and interference rates, I altered the strength of the relationship by increasing the magnitude of the slope parameters with a constant maximum or minimum and examined the resulting changes in the strength of disruptive selection.

Results

Handling Times

When there is no correlation between attack rates and handling times, analysis of the model with a multispecies Holling Type-II functional response shows that increasing handling times reduce the strength of disruptive selection (Figure 1A). This decrease is due to relative changes in feeding rates across the consumer's phenotypes (Figure 1B,C). In particular, as handling times increase, individuals with the highest attack rates show a decrease in feeding rates while individuals with lower attack rates show an increase in feeding rates (Figure 1B,C). This reduces the increase in per capita fitness of an invader and leads to a reduction in the strength of disruptive

selection. The relative changes in feeding rates among individuals with different phenotypes are the product of the interaction between attack rates and the saturating effect of handling times and the consequent changes in the equilibrium densities of resources (Figure 1B-E). As handling times increase, individuals with the highest attack rates saturate at increasingly lower resource densities (Figure 1D). This reduces the feeding rates of individuals with the highest attack rates which simultaneously increases equilibrium resource densities (Figure 1D). Individuals with low attack rates do not experience saturation from handling times and thus show an increase in feeding rates due to the increase in equilibrium densities of the resources (Figure 1E).

The effects of handling time on the strength of disruptive selection depend on whether pleiotropy causes a positive or negative correlation between attack rates and handling times. If handling times and attack rates are positively correlated, then the strength of disruptive selection decreases the stronger the relationship between attack rates and handling times becomes (Figure 2A). In contrast, if handling times and attack rates are negatively correlated, the strength of disruptive selection increases the stronger the negative relationship between attack rates and handling times becomes (Figure 2C). These effects occur because correlations between attack rates and handling times either exacerbate or alleviate the saturating effects of handling times on individuals with high attack rates. When correlations between attack rates and handling times are positive, individuals with high attack rates experience greater saturation with an increase in the strength of the correlation causing a decrease in their feeding rates and subsequent increases in the feeding rates of consumers with low attack rates due to increases in equilibrium resource densities (Figure 2B). When correlations are negative, individuals with high attack rates experience less saturation with an increase in the strength of the correlation leading to higher feeding and with subsequent decreases in the feeding rates of individuals with low attack rates due to decreases in equilibrium resource densities (Figure 2D).

Interference Rates

When there is no correlation between attack rates and interference rates, the effects of interference on the strength of disruptive selection depend on the functional response considered. If interference is modeled using the Beddington-DeAngelis functional response, interference has no effect on the strength of disruptive selection (Figure 3A). As interference rates increase, the feeding rates across phenotypes remain constant because equilibrium resource and consumer densities change in a manner that compensates for the increased interference (Figure 3B). In contrast, if interference is modeled using the Crowley-Martin functional response, increasing interference decreases the strength of disruptive selection (Figure 3C). This occurs because feeding rates change differentially across the phenotypes (Figure 3D).

The reason for the contrasting effects of the two functional responses is that they encapsulate different ways by which interference interacts with the consumer trait through attack rates. In the Beddington-DeAngelis functional response interference reduces the time available for foraging by consumers and influences all consumer's equally, regardless of their phenotype. In the Crowley-Martin functional response, because interference can occur while consumers are handling resources, interference does interact with the attack rates of the consumer and leads to differences in feeding rates across the consumer phenotype.

As for handling times, the effects of interference on the strength of disruptive selection are dependent on whether pleiotropy causes correlations between attack rates and interference rates. Regardless of the functional response considered, a positive relationship between attack rate and interference leads to a decrease in the strength of disruptive selection as the positive relationship strengthens (Figures 4A,5A). A negative relationship between attack rates and interference leads to an increase in the strength of disruptive selection as the strength of the relationships increases (4C,5C). These effects occur because the correlation causes the saturating effect of interference to affect consumers differently across phenotypes. For positive relationships between attack rates and interference, phenotypes with the highest attack rates experience the most saturation and experience reduced feeding rates, while this increases feeding rates for individuals with low attack

rates because of increased equilibrium resource densities (Figures 4B,5B). For negative relationships between attack rates and interference, consumers with high attack rates experience less interference and have increased feeding rates, while consumers with low attack rates experience higher interference and lower equilibrium resource densities causing a decrease in feeding rates (Figures 4D,5D).

Discussion

At the core of theory on disruptive selection is its generation through the mechanisms of ecological opportunity and intraspecific resource competition in generalist consumers. As these mechanisms ought to be common, theory has supposed that disruptive selection in generalist consumers should also be common. However, empirical results have been mixed and call into question the assumptions of previous models. Here, using a one consumer-two resource model, I show that two widespread factors – nonlinear functional responses and ecological pleiotropy – are capable of altering the strength of disruptive selection. Because the strength of disruptive selection is mediated by features of the underlying consumer-resource interactions, differences in these features across generalist consumers may explain some variation in the results of empirical studies. My results also inform predictions for the situations in which disruptive selection is most likely to occur.

The consumer-resource models presented here predict that disruptive selection in generalist consumers should be most common in populations in which handling times and interference are low or negatively correlated with attack rates. Confirmation of this with existing data is difficult, but some of the best known examples of disruptive selection in consumers do exhibit some of these features. For example, disruptive selection in beak size of the medium ground finch (*Geospiza fortis*) of the Galapagos Islands has been shown to be related to the ability of finches with different beak sizes to handle different sized seeds (Hendry et al., 2009; Schluter and Grant, 1984). Thus, attack rates and handling times should be negatively correlated with large-beaked

individuals preferring and having lower handling times on large seeds and small-beaked individuals preferring and having lower handling times on small seeds. Interference during foraging also likely has little effect (A. Hendry; Pers. Comm.). Another canonical example of disruptive selection is disruptive selection in several traits related to the use of benthic v. limnetic resources in three spine stickleback (Schluter, 1993). Morphological differences among individuals in resource-use traits have been shown to correlate with the feeding efficiency and growth rates of stickleback in benthic versus limnetic habitats (Schluter, 1993, 1995). How interference operates in this system is unclear, but the use of separate habitats may reduce interference by reducing the potential number of competitors or increase interference by concentrating individuals within habitats. Future empirical work should aim to more explicitly examine the relationship between consumer functional responses and natural selection. One possibility for doing so is to use comparative studies across populations or species measuring both functional responses and disruptive selection. Another possibility is to estimate the functional responses of individuals and correlate these functional responses to individual fitness proxies. Recent advances in estimating functional responses from observational data in the field (Novak et al., 2017) and the long history of estimating natural selection (Kingsolver et al., 2001; Lande and Arnold, 1983) should facilitate this effort.

The effects of handling time and interference on the strength of disruptive selection were largely dependent on whether the underlying trait was assumed to have pleiotropic effects that caused correlations between these parameters and the attack rates. The parameters describing nonlinear functional responses are likely to be correlated due to their determination by the same traits, however, the sign and strength of correlations among parameters are likely to be system specific. Some generalizations nevertheless might be possible. Optimal foraging theory, for example, suggests that individuals feeding on energetically equivalent resources should prefer the resources on which they have the lowest handling times (Stephens and Krebs, 1986). This will cause a negative correlation between attack rates and handling times among individuals (e.g. Tinker et al., 2007) which should increase the strength of disruptive selection. Positive

correlations seem less likely. One possible source of this pattern could be changes in preferred resource size with consumer body size. For example, relative to mid-sized individuals, large bodied consumers may have higher attack rates on larger prey which require longer handling times, while small bodied consumers may have higher attack rates on smaller bodied resources but have higher handling times due to inefficiencies in handling resources given their size (Hassel et al., 1976).

Interference rates could have both positive or negative correlations with attack rates. For example, positive correlations have been observed in at least one protist system where both parameters were positively related to the swimming speed of the consumer (DeLong and Vasseur, 2013). However, the case could also be made that interference and attack rates should be negatively correlated. For example, attack rates commonly scale with body size (Berlow et al., 2009; Brose, 2010), a trait that often confers an advantage in bouts of interference which could reduce the effects of interference on individuals with high attack rates (Rowland, 1989; Schoener, 1983). Individuals with high attack rates may also use resources more efficiently which may reduce their exposure to interference. Furthermore, individuals with high attack rates on particular resources may inhabit different habitats. Examples of this occur in several lake fish species, such as three spine stickleback (*Gasterosteus aculeatus*) which have polymorphisms associated with using either benthic v. limnetic habitats (Lavin and McPhail, 1985; Schluter, 1995). As mentioned above, the use of different habitats may constrain the number of individuals that interfere with one another, thereby leading to an overall reduction in interference relative to the case in which all individuals use the same habitat. Conversely, individuals with high attack rates on the same resource may be concentrated within the same habitat, increasing interference. Unfortunately, data on the correlations among parameters in nonlinear functional responses are sparse, although traits that simultaneously influence multiple functional response parameters should be common.

To model the effects of mutual interference competition on consumer functional responses, I used two of the more 'mechanistic' functional response models including interference – the Beddington-DeAngelis and Crowley-Martin functional responses (Beddington, 1975; Crowley

and Martin, 1989; DeAngelis et al., 1975). Which functional response was considered influenced the effects of interference on the strength of disruptive selection. The two functional responses differ primarily in whether or not interference occurs while consumers are handling resources. The most appropriate model for interference therefore is likely dependent on the biology of the particular system. For example, in systems with kleptoparasitism, fighting amongst consumers over already captured resources, or increased handling times in the presence of other consumers, the Crowley-Martin functional response may more appropriate (e.g. Ens and Goss-Custard, 1984; Norris and Johnstone, 1998; Smallegange et al., 2006; Zimmermann et al., 2015). In contrast, in systems where interference occurs largely separate from the handling of resources, or where time spent foraging is distinct from time spent interfering, the Beddington-DeAngelis functional response is likely to be more appropriate (e.g. Getty, 1981; Kratina et al., 2009; Pyke, 1979). Although the Crowley-Martin and Beddington-DeAngelis functional responses are sometimes unable to be distinguished statistically (Lang et al., 2012; Skalski and Gilliam, 2001; Stier and White, 2014; Zimmermann et al., 2015), the models here suggest that distinguishing among them mechanistically may be important to understand the evolutionary consequences of interference. Lastly, the functional responses used here assumed that interference rates, or their relationships with attack rates, were equal for both resources. Recent evidence has suggested that this may not be the case and that interference rates and facilitation effects may be prey-specific in nature (Novak et al., 2017). These results suggest that theory incorporating prey-specific interference rates may be needed to understand the ecological and evolutionary consequences of interference with more than one resource.

In the models presented here, adaptive dynamics would predict that disruptive selection leads to evolutionary branching (Geritz et al., 1998). In reality, evolutionary branching and speciation is only one of many possible outcomes of disruptive selection, and the particular outcome may be a function of the strength of disruptive selection (Rueffler et al., 2006). For example, although ecological opportunity and intraspecific resource competition may cause disruptive selection on a trait, opposing directional or stabilizing selection on that trait from other sources, or gene flow,

might overwhelm weak disruptive selection (Lande and Arnold, 1983; Nosil, 2012). The strength of disruptive selection could also determine whether divergence in phenotype occurs or whether the evolution of increased variation or plasticity in the trait results instead (Rueffler et al., 2006). Future theory explicitly examining how the strength of selection is likely to lead to different evolutionary outcomes will help to further understand how changes to the strength of disruptive selection through ecological factors are likely to manifest in nature.

Overall, my results support the assertions of Abrams et al. (2008) and Jones and Post (2013, 2016) that the strength of disruptive selection is dependent on the strength of the underlying consumer-resource interactions. In the model presented here, the effects of nonlinear functional responses and pleiotropy are largely due to how the handling or interference produces saturation in the feeding rates of the consumers with the highest attack rates. If saturation is increased, the consumer-resource interactions weaken resulting in weakened disruptive selection and vice versa. Abrams et al. (2008) and Jones and Post (2013, 2016), however, have predicted a unimodal relationship between the strength of consumer-resource interactions and the strength of disruptive selection. Their reasoning is that when consumer-resource interactions are very weak there is little depletion of resources, intraspecific resource competition is weak, and thus disruptive selection is weak. In contrast, when consumer-resource interactions are very strong resources associated with the most common consumer phenotypes will go locally extinct, ecological opportunity will decrease, and disruptive selection will weaken. Examining the effects of resource extinction in the model here was not possible, although I expect results would be similar. Allowing for this effect would require extending the theory here to models with a continuous distribution of resources such as the MacArthur model (MacArthur, 1972). Caution should be taken in doing so. The MacArthur model with linear functional responses has been shown to have a stable global equilibrium (Chesson, 1990). Nonlinear functional responses, however, can lead to cycling in population dynamics which may alter evolutionary dynamics (Svanbäck et al., 2009). Nevertheless, the incorporation of nonlinear functional responses and pleiotropy into these models would be worthwhile and can provide insight into additional topics beyond disruptive

selection such as the coevolution of competitors and character displacement.

Acknowledgments

I am grateful to Mark Novak, the NovakLab, and the OSU IB Journal Club for critical feedback of both the ideas and writing herein. This project was funded by a National Science Foundation Graduate Research Fellowship DGE-1314109.

Literature Cited

Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent, or neither? Trends in Ecology and Evolution 15:337–341.

Abrams, P. A., C. Rueffler, and G. Kim. 2008. Determinants of the strength of disruptive and/or divergent selection arising from resource competition. Evolution 62:1571–1586.

Beddington, J. R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. Journal of Animal Ecology 51:331–340.

Berlow, E. L., J. A. Dunne, N. D. Martinez, P. B. Stark, R. J. Williams, and U. Brose. 2009. Simple prediction of interaction strengths in complex food webs. Proceedings of the National Academy of Sciences 106:187–191.

Bolnick, D. I. 2001. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. Nature 410:463–466.

———. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. Evolution 58:608–618.

Bolnick, D. I., P. Amarasakare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. Rudolf, S. J. Schreiber, M. C. Urban, and D. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26:183–192.

Brose, U. 2010. Body-mass constraints on foraging behavior determine population and food-web dynamics. Functional Ecology 24:28–34.

Case, T. J. 1981. Niche packing and coevolution in competition communities. Proceedings of the National Academy of Sciences USA 78:5021–5025.

Chesson, P. 1990. Macarthur's consumer-resource model. Theoretical Population Biology 37:26–38.

Crowley, P. H., and E. K. Martin. 1989. Functional responses and interference within and between year classes of a dragonfly population. Journal of the North American Benthological Society 8:211–221.

Cucherousset, J., A. Acou, S. Blanchet, J. R. Britton, W. R. C. Beaumont, and R. E. Gozlan. 2011. Fitness consequences of individual specialisation in resource use and trophic morphology in european eels. Oecologia 167:75–84.

DeAngelis, D. L., R. A. Goldstein, and R. V. O'Neill. 1975. A model for trophic interaction. Ecology 56:881–892.

DeLong, J. P. 2017. Ecological pleiotropy suppresses the dynamic feedback generated by a rapidly changing trait. The American Naturalist 189:592–597.

DeLong, J. P., and J. P. Gibert. 2016. Gillespie eco-evolutionary models (GEMs) reveal the role of heritable trait variation in eco-evolutionary dynamics. Ecology and Evolution 6:935–945.

DeLong, J. P., and D. A. Vasseur. 2011. Mutual interference is common and mostly intermediate in magnitude. BMC Ecology 11:1.

———. 2013. Linked exploitation and interference competition drives the variable behavior of a classic predator-prey system. Oikos 122:1393–1400.

Dieckmann, U. 1997. Can adaptive dynamics invade? Trends in Ecology and Evolution 12:121–131.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. Nature 400:354–357.

Doebeli, M. 2011. Adaptive Diversification. Princeton University Press, New Jersey.

Ens, B. J., and J. D. Goss-Custard. 1984. Interference among oystercatchers *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the exe estuary. Journal of Animal Ecology 53:217–231.

Geritz, S. A. H., E. Kisde, Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology 12:35–57.

Getty, T. 1981. Territorial behavior of eastern chipmunks (*Tamias striatus*): Encounter avoidance and spatial time-sharing. Ecology 62:915–921.

Gibert, J. P., and C. E. Brassil. 2014. Individual phenotypic variation reduces interaction strengths in a consumer-resource system. Ecology and Evolution 4:3703–3713.

Hart, S. P., S. J. Schreiber, and J. M. Levine. 2016. How variation between individuals affect species coexistence. Ecology Letters 19:825–838.

Hassel, M. P., J. H. Lawton, and J. R. Beddington. 1976. The components of arthropod predation: I. The prey death-rate. Journal of Animal Ecology 45:135–164.

Hassel, M. P., and G. C. Varley. 1969. New inductive population model for insect parasites and its bearing on biological control. Nature 223:1133–1137.

Hendry, A. P., S. K. Huber, L. F. De León, A. Herrel, and J. Podos. 2009. Disruptive selection in a bimodal population of darwin's finches. Proceedings of the Royal Society B 276:753–759.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the european pine sawfly. The Canadian Entomologist 91:293–320.

Hughes, R. A., B. D. Inouye, M. T. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. Ecology Letters 11:609–623.

Jeschke, J. M., M. Kopp, and R. Tollrian. 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biological Reviews 79:337–349.

Jones, A. J., and D. M. Post. 2013. Consumer interaction strength may limit the diversifying effect of intraspecific competition: a test in alewife (*Alosa pseudoharengus*). The American Naturalist 181:815–826.

———. 2016. Does intraspecific competition promote variation? a test via synthesis. Ecology and Evolution 6:1646–1655.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vigniere, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. The American Naturalist 157:245–261.

Kratina, P., M. Vos, A. Bateman, and B. R. Anholt. 2009. Functional responses modified by predator density. Oecologia 159:425–433.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Lang, B., B. C. Rall, and U. Brose. 2012. Warming effects of consumption and intraspecific interference competition depend on predator metabolism. Journal of Animal Ecology 81:516–523.

Lavin, P. A., and J. D. McPhail. 1985. The evolution of freshwater diversity in the threespine stickleback (*Gasterosteus aculeatus*): Site-specific differentiation of trophic morphology. Canadian Journal of Zoology 63:2632–2638.

MacArthur, R. H. 1972. Geographical Ecology. Princeton University Press, New Jersey.

Martin, R. A., and D. W. Pfennig. 2009. Disruptive selection in natural populations: The roles of ecological specialization and resource competition. The American Naturalist 147:268–281.

Mateus, L., J. Ortega, A. Mendes, and J. Penha. 2016. Nonlinear effect of density on trophic niche width and between-individual variation in diet in a neotropical cichlid. Austral Ecology 41:492–500.

Norris, K., and I. Johnstone. 1998. Interference competition and the functional response of oystercatchers searching for cockles by touch. Animal Behaviour 56:639–650.

Nosil, P. 2012. Ecological Speciation. Oxford University Press, New York.

Novak, M., C. Wolf, K. E. Coblentz, and I. D. Shepard. 2017. Quantifying predator dependence in the functional response of generalist predators. Ecology Letters 20:761–769.

Parent, C. E., D. Agashe, and D. I. Bolnick. 2014. Intraspecific competition reduces niche width in experimental populations. Ecology and Evolution 20:3978–3990.

Pyke, G. H. 1979. The economics of territory size and time budget in the golden-winged sunbird. The American Naturalist 114:131–145.

Roughgarden, J. 1976. Resource partitioning among competing species: coevolutionary approach. Theoretical Population Biology 9:388–424.

Rowland, W. J. 1989. The effects of body size, aggression and nuptial coloration on competition for territories in male threespine sticklebacks, *Gasterosteus aculeatus*. Animal Behaviour 37:282–289.

Rozenzweig, M. L. 1978. Competitive speciation. Biological Journal of the Linnean Society 10:275–289.

Rueffler, C., T. J. M. Van Dooren, O. Leimar, and P. A. Abrams. 2006. Disruptive selection and then what? Trends in Ecology and Evolution 238-245:238–345.

Rundle, H. D., S. M. Vamosi, and D. Schluter. 2003. Experimental test of predation's effect on divergent selection during character displacement in sticklebacks. Proceedings of the National Academy of Sciences USA 100:14943–14948.

Schindler, D. E., J. R. Hodgson, and J. F. Kitchell. 1997. Density-dendent changes in individual foraging specialization of largemouth bass. Oecologia 110:192–600.

Schluter, D. 1993. Adaptive radiation in sticklebacks: Size, shape, and habitat use efficiency. Ecology 74:699–709.

———. 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. Ecology 76:82–90.

———. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford.

Schluter, D., and P. R. Grant. 1984. Ecological correlates of morphological evolution in a Darwin's finch *Geospiza difficilis*. Evolution 38:856–869.

Schoener, T. W. 1983. Field experiments on interspecific competition. The American Naturalist 122:240–285.

Schreiber, S. J., R. Bürger, and D. I. Bolnick. 2011. The community effects of phenotypic and genetic variation within a predator population. Ecology 92:1582–1593.

Skalski, G. T., and J. F. Gilliam. 2001. Functional responses with predator interference: Viable alternatives to the holling type II model. Ecology 82:3083–3092.

Smallegange, I. M., J. van der Meer, R. H. J. M. Kurvers, and L. Persson. 2006. Disentangling interference competition for exploitative competition in a crab-bivalve system using a novel experimental approach. Oikos 113:157–167.

Smith, J. M. 1962. Disruptive selection, polymorphism and sympatric speciation. Nature 195:60–62.

Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. Princeton University Press, New Jersey.

Stier, A. C., and J. W. White. 2014. Predator density and the functional responses of coral reef fish. Coral Reefs 33:235–240.

Strauss, S. Y., and R. E. Irwin. 2004. Ecological and evolutionary consequences of multispecies plant-animal interactions. Annual Review of Ecology, Evolution, and Systematics 35:435–466.

Svanbäck, R., M. Pineda-Krch, and M. Doebeli. 2009. Fluctuating population dynamics promotes the evolution of phenotypic plasticity. The American Naturalist 174:176–189.

Tinker, M. T., G. Bentall, and J. A. Estes. 2007. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proceedings of the National Academy of Sciences 105:560–565.

Vucic-Pestic, O., B. C. Rall, G. Kalinkat, and U. Brose. 2009. Allometric functional response model: body masses constrain interaction strengths. Journal of Animal Ecology 79:249–256.

Zimmermann, B., H. Sand, P. Wabakken, O. Liberg, and H. P. Anreassen. 2015. Predator-dependent functional response in wolves: from food limitation to surplus killing. Journal of Animal Ecology 84:102–112.

Figures

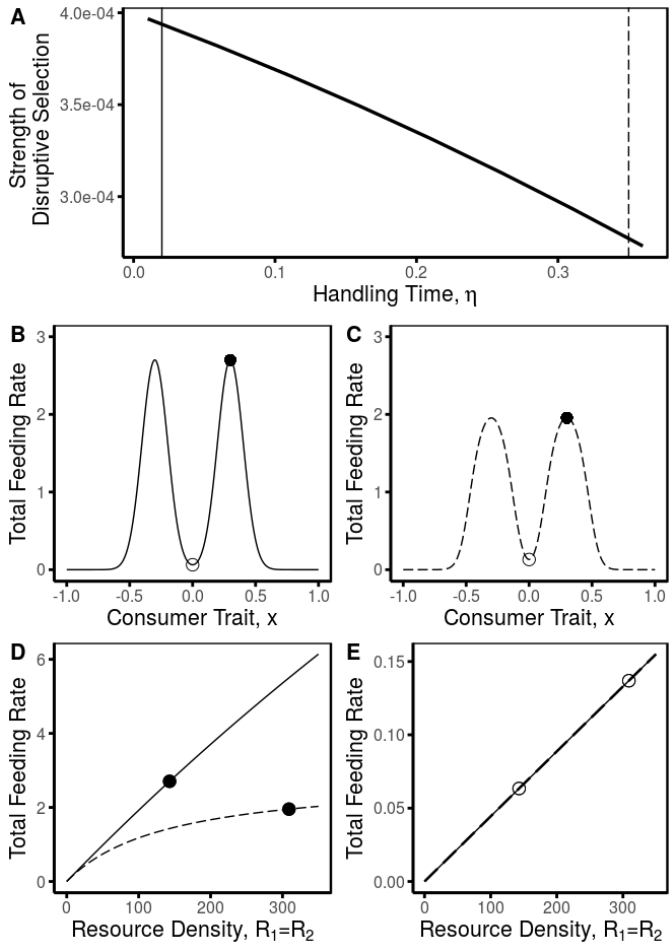

Figure 1: Larger handling times are associated with weaker disruptive selection (**A**). This occurs because handling times differentially affect feeding rates across the consumer's phenotype (compare feeding rates with low handling times in **B** (solid line in A-E, $\eta_1 = \eta_2 = 0.01$) and feeding rates with high handling times in **C** (dashed line in **A-E**, $\eta_1 = \eta_2 = 0.4$)). For individuals with high attack rates (solid dots in **B-D**), feeding rates decrease with higher handling times, despite an increase in equilibrium resource densities due to saturation caused by higher handling times (**D**). Individuals with low attack rates (open dots in **B,C, E**) do not approach saturation with an increase in handling times and their feeding rates increase because of the increase in equilibrium resource densities (**E**). Parameters used in the figure are: $\bar{x} = 0, \sigma^2 = 0.04, \alpha_{1,max} = \alpha_{2,max} = 0.02, \theta_1 = -\theta_2 = 0.3, \tau_1^2 = \tau_2^2 = 0.01, r_1 = r_2 = 0.2, K_1 = K_2 = 500, e = 0.5, m = 0.5$.

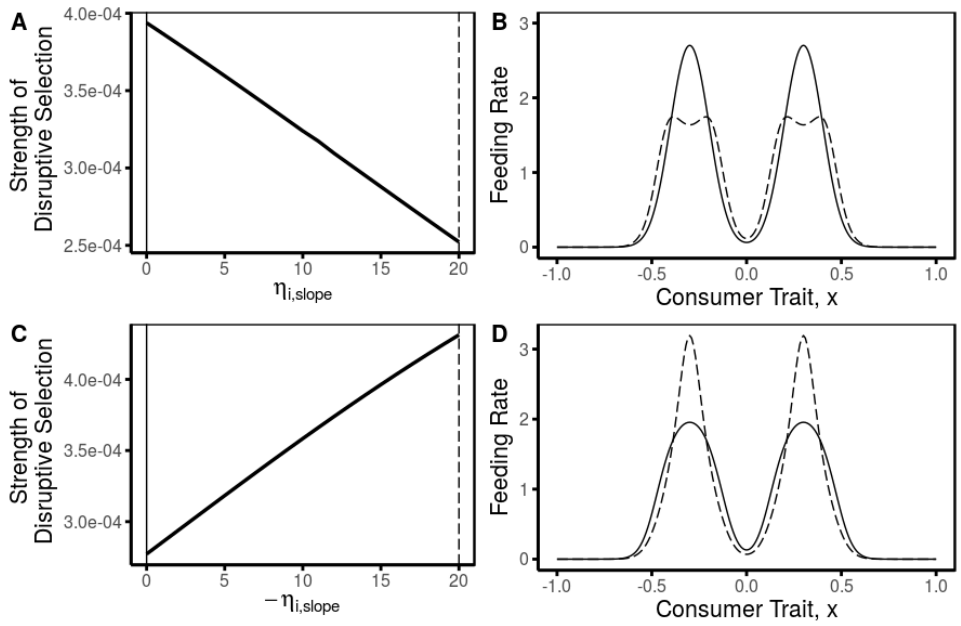

Figure 2: Ecological pleiotropy leading to a positive correlation between attack rates and handling times leads to a decrease in the strength of disruptive selection as the slope of the relationship increases (**A**). This happens because the correlation changes feeding rates across phenotypes such that the feeding rates of individuals with high attack rates decrease and feeding rates of individuals with low attack rates increase as the slope of the relationship goes from low (solid line in **A,B**) to high (dashed line in **A,B**). Pleiotropy leading to a negative correlation between attack rates and handling times leads to an increase in the strength of disruptive selection as the magnitude of the slope of the relationship increases (**C**). This occurs because the correlation changes feeding rates across phenotypes leading to an increase in feeding rates for individuals with high attack rates and decreases in feeding rates for individuals with low attack rates as the magnitude of the slope of the relationship goes from low (solid line in **C,D**) to high (dashed line in **C,D**). Parameter values used in the figure are: $\bar{x} = 0, \sigma^2 = 0.04, \alpha_{1,max} = \alpha_{2,max} = 0.02, \theta_1 = -\theta_2 = 0.3, \tau_1^2 = \tau_2^2 = 0.01, r_1 = r_2 = 0.2, K_1 = K_2 = 500, e = 0.5, m = 0.5$, and $\eta_{1,min} = \eta_{2,min} = 0.01$ in **A** and **B**, and $\eta_{1,max} = \eta_{2,max} = 0.4$ in **C** and **D**.

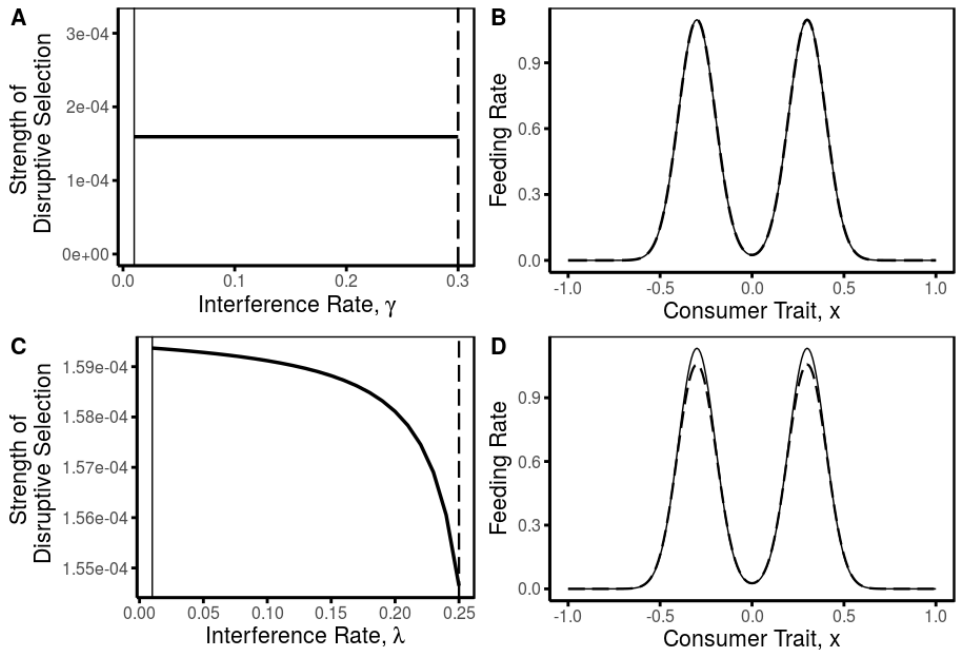

Figure 3: The effects of interference on the strength of disruptive selection are dependent on which functional response is considered (**A** – Beddington-DeAngelis functional response,**C** – Crowley-Martin functional response). The interference rate of the Beddington-DeAngelis functional response, (γ), has no effect on the strength of disruptive selection (**A**). This is because the interference rate alters the equilibrium densities of the consumer and resources, but has no effect on the feeding rates of the consumers across their phenotypes (**B**, solid line is low interference, dashed line is high interference). The interference rate of the Crowley-Martin functional response (λ) weakens the strength of disruptive selection (**C**). This is because the interference rate differentially effects the feeding rates of consumers across the consumers phenotype (**D**, solid line is low interference, dashed line is high interference). Parameter values used in the figure are: $\bar{x} = 0, \sigma^2 = 0.04, \alpha_{1,max} = \alpha_{2,max} = 0.3, \theta_1 = -\theta_2 = 0.3, \tau_1^2 = \tau_2^2 = 0.01, r_1 = r_2 = 0.2, K_1 = K_2 = 500, e = 0.5, m = 0.2, \eta_1 = \eta_2 = 0.01$.

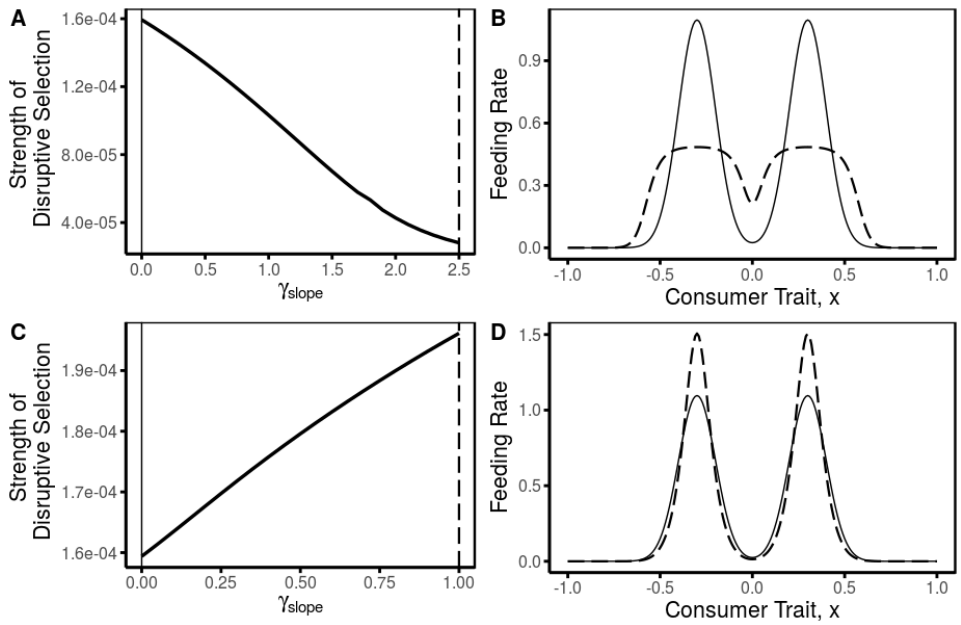

Figure 4: Ecological pleiotropy leading to a positive correlation between attack rates and interference rates in the Beddington-DeAngelis functional response leads to a decrease in the strength of disruptive selection as the slope of the relationship increases (**A**). This is due to changes in feeding rates across phenotypes such that the feeding rates of individuals with high attack rates decrease and feeding rates of individuals with low attack rates increase as the slope of the relationship goes from low (solid line in **A,B**) to high (dashed line in **A,B**). Pleiotropy leading to a negative correlation between attack rates and interference rates in the Beddington-DeAngelis functional response leads to an increase in the strength of disruptive selection as the magnitude of the slope of the relationship increases (**C**). This is because feeding rates change in an opposite manner to that seen when the correlation is positive (**C,D**). Parameter values used in the figure are: $\bar{x} = 0, \sigma^2 = 0.04, \alpha_{1,max} = \alpha_{2,max} = 0.3, \theta_1 = -\theta_2 = 0.3, \tau_1^2 = \tau_2^2 = 0.01, r_1 = r_2 = 0.2, K_1 = K_2 = 500, e = 0.5, m = 0.2, \eta_1 = \eta_2 = 0.01$, and in **A** and **B** $\gamma_{1,min} = \gamma_{2,min} = 0.01$ and in **C** and **D** $\gamma 1, max = \gamma_{2,max} = 0.3$.

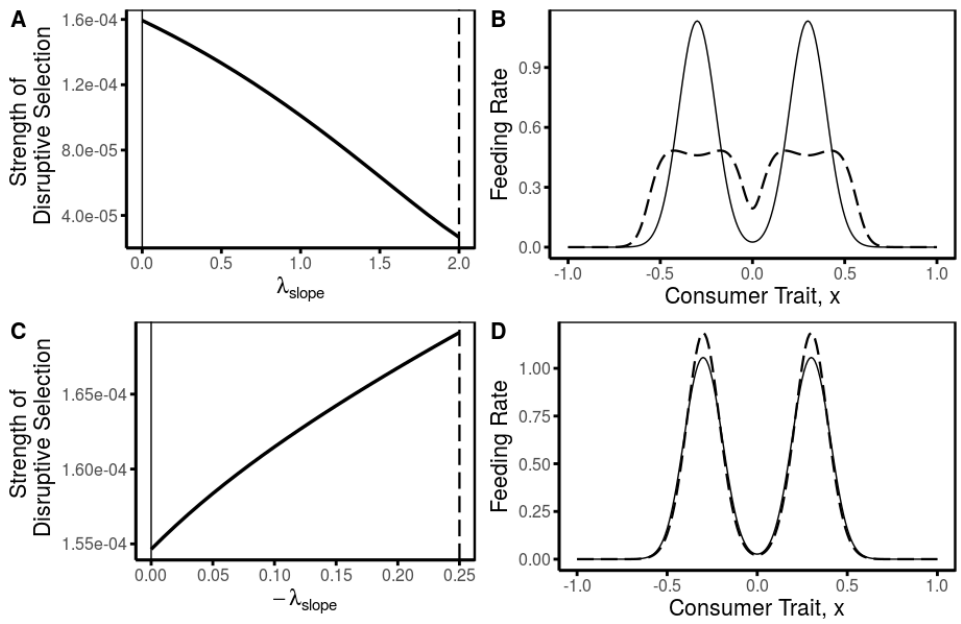

Figure 5: Pleiotropy leading to a positive correlation between attack rates and interference rates in the Crowley-Martin functional response leads to a decrease in the strength of disruptive selection as the slope of the relationship increases (**A**). This is due to changes in feeding rates across phenotypes such that the feeding rates of individuals with high attack rates decrease and feeding rates of individuals with low attack rates increase as the slope of the relationship goes from low (solid line in **A,B**) to high (dashed line in **A,B**). Pleiotropy leading to a negative correlation between attack rates and interference rates in the Crowley-Martin functional response leads to an increase in the strength of disruptive selection as the magnitude of the slope of the relationship increases (**C**). This is because feeding rates change in an opposite manner to that seen when the correlation is positive (**C,D**). Parameter values used in the figure are: $\bar{x} = 0, \sigma^2 = 0.04, \alpha_{1,max} = \alpha_{2,max} = 0.3, \theta_1 = -\theta_2 = 0.3, \tau_1^2 = \tau_2^2 = 0.01, r_1 = r_2 = 0.2, K_1 = K_2 = 500, e = 0.5, m = 0.2, \eta_1 = \eta_2 = 0.01$, and in **A** and **B** $\lambda_{1,min} = \lambda_{2,min} = 0.01$ and in **C** and **D** $\lambda_{1,max} = \lambda_{2,max} = 0.25$.