Solomon (1949) first proposed the term “functional response” to describe the specific relationship between the number of prey present and the number of prey consumed over a given time interval, per predator. Although early functional response equations could qualitatively describe real predator-prey relationships, they were purely phenomenological (Gause, Smaragdova & Witt 1936; Ivlev 1961; Jassby & Platt 1976). Such phenomenological descriptions eventually gave way to mechanistic models. Mechanistic functional responses incorporate independently measurable components that correspond to specific aspects of the predation process; such as the rate at which predators encounter and successfully attack prey items or the amount of time required to physically manipulate and consume captured prey (Murdoch 1973).

The most commonly used mechanistic functional responses are the Holling type 1, 2, and 3 functional responses (Holling 1959; Holling 1966; Jeschke, Kopp & Tollrian 2002) (Fig. 1.1). The type 1 functional response *f* 1 (*x*) equation produces a curve that is monotonic, linear, and saturating (Fig 1.1). This functional response represents the simplest possible relationship between predators and prey: consumption increases linearly with prey density before sharply leveling off at a maximum consumption rate. In terms of community dynamics, the type 1 functional response is widely seen as the most stabilizing of the Holling type functional responses (Turchin 2003). The equation for the increasing region of the type 1 functional response is presented here:

𝑓1(𝑥)=𝑎 𝑥 (1.1)

where *x* is the density of the prey population. The rate at which predators successfully attack prey, *a*, is assumed to be constant and independent of prey density (Murdoch 1973); additionally, *a* determines the slope of the type 1 functional response. The linear nature of this functional response is due to the assumption that processes such as handling or digesting prey can occur without any reduction in time spent on active foraging (Jeschke, Kopp & Tollrian 2002). Although the belief that predators must have a maximum consumption rate is widely accepted (Morin 2011), many dynamical models that use the type 1 functional response, do not incorporate a maximum consumption rate (Turchin 2003). As shown in Chapter 4, the absence of a maximum consumption rate can have meaningful impacts on model predictions; furthermore, this absence is likely responsible for the view that the type 1 functional response is extremely stabilizing2.

The type 2 functional response *f* 2 (*x*) equation produces a curve that is monotonic, non-sigmoid, and saturating (Fig 1.1). In other words, consumption eventually approaches a maximum but does so at a decelerating rate. The equation for the type 2 functional response is presented here:

𝑓2(𝑥)=𝑎 𝑥 1+𝑎 ℎ 𝑥 (1.2)

where *x* and *a* follow the descriptions given above and *h* is the handling time, which is the amount of time required to physically manipulate and consume captured prey before searching for new prey items. In the type 2 functional response, both *a* and *h* are assumed to be constant and independent of prey density (Murdoch 1973). Because the type 2 functional response incorporates handling time, as the rate of consumption increases, predators must spend more total time handling prey and less total time searching for new prey. Furthermore, predators are assumed to be perpetually hungry, but limited by the rate at which they handle prey and the maximum consumption rate is determined by 1/handling time. Additionally, the type 1 and type 2 functional responses are almost identical at very low prey densities (e.g. when *x=*0, the slope of both curves is equal to *a.* see lower left hand corner of figure 1.1) and/or very low handling times (e.g. when *h*=0, *f* 2 (*x*) simplifies to *f* 1 (*x*)) . However, in terms of community dynamics, the type 2 functional response is seen the least stabilizing of the Holling type functional responses (Rosenzweig 1971; Murdoch, Briggs & Nisbet 2003; Alexander *et al.* 2012).

The type 3 functional response *f* 3 (*x*) equation produces a curve that is monotonic, sigmoid, and saturating (Fig 1.1). In other words, as prey density increases from 0, consumption first increases at an increasing rate, then switches to increasing at a decreasing rate, and finally approaches a maximum. The most commonly used formulation for the type 3 functional response that incorporates handling time is:

𝑓3(𝑥)=𝑎(𝑥) 𝑥 1+𝑎(𝑥) ℎ 𝑥 ,where 𝑎(𝑥)=α 𝑥 (1.3)

and where *x* and *h* follow the descriptions given for Equation 1.2 and the attack rate *a*(*x*) increases linearly with prey density according to α *x.* Attack rate may be positively correlated with prey density because as prey density increases, a decreasing proportion of prey are able to utilize refuges; thus, a higher proportion of prey are vulnerable to predation. Additionally, optimal foraging theory suggests that predators may refrain from actively pursuing prey, when those prey are present at low density (MacArthur & Pianka 1966). This is often attributed to narrow-minded predators that are actively pursuing a separate, more abundant, prey species (Heidarian, Fathipour & Kamali 2012); however, it is also possible that predators reduce search effort in an attempt to balance energy expenditure and energy intake (Abrams 1982). Although the type 3 incorporates an increasing attack rate, it also incorporates handling time; therefore, as prey density increases, predators must spend more total time handling prey and less total time searching for new prey. Furthermore, as seen in the type 2 functional response, handling time limitation in the type 3 functional response results in a maximum consumption rate that is equal to 1/handling time. In terms of community dynamics, the type 3 is often seen as stabilizing and may even help prevent the overexploitation and eventual extinction of some species (Alexander *et al.* 2012).

While the type 1, 2, and 3 functional responses appear to have very different functional forms, all three can be described by a single equation:

𝑓(𝑥)=𝑎 𝑥𝑝1+𝑎 ℎ 𝑥𝑝 (1.4)

where *x, a*, and *h* follow the descriptions given for Equation 1.2 and *p* is a variable that allows for scaling between the type 2 and 3 functional responses (i.e. when 0<*p*≤1, Equation 1.3.4 simplifies to the type 2 functional response; when *p*>1, Equation 1.4 becomes the type 3 functional response). Additionally, when *p*=1 and *h*=0, Equation 1.4 simplifies to the type 1 functional response. Although Equation 1.4 can be transformed into any of the three original Holling type functional responses, it does not address the concerns of many ecologists, who question the biological realism and relevance of the type 1 and 3 functional responses (Abrams & Allison 1982).

Although a large body of empirical work supports the existence of the type 1 functional response (Jeschke 2004), this evidence is often discounted for two reasons. First, many predator prey interactions that are best described by the type 1 functional response, may actually be ‘truly’ type 2 functional responses; this argument is based on the fact that at low prey densities, the type 1 and 2 functional responses are almost indistinguishable. In fact, one can easily find examples of experiments that produce linearly increasing consumption rates but not saturation (Mohr & Adrian 2000; Kushner & Hovel 2006; Parajulee *et al.* 2006; Long & Whitefleet-Smith 2013). While this is only circumstantial and inconclusive evidence against the type 1 (e.g. the majority of type 2 functional response datasets also fail to test prey densities that cause saturating consumption (Kovach-Orr *et al. unpublished manuscript*), it does cast doubt on type 1 functional responses. Second, only one class of predators, filter feeders, has been shown to exhibit type 1 functional responses (Jeschke 2004). However, less than half of filter feeder species actually exhibit type 1 functional responses (Jeschke 2004). Thus, it seems highly likely that the prevalence and therefore, relevance, of the type 1 functional response has been historically overestimated.

Like the type 1, the type 3 functional response has received support from [an albeit smaller body of] empirical studies (Jeschke 2004). It is widely accepted that sigmoid functional responses (e.g., the type 3) play important roles in complex systems (e.g., multiple prey species, spatial heterogeneity, etc.). However, the type 3 functional response has been criticized as being unrealistic in more simple systems (i.e. bitrophic food chains in a homogenous environment) (Abrams & Allison 1982). Instead, the type 2 functional response is favored as the most reasonable description of consumption in these systems (Murdoch, Briggs & Nisbet 2003; Turchin 2003). This represents the dominant view that the components of the functional response (i.e. handling time and attack rate) are rigid, unchanging, constants (Murdoch, Briggs & Nisbet 2003; Turchin 2003). Nevertheless, there is growing sentiment that these rigid components are being used for historical reasons or out of convenience, which has lead researchers to question if these components actually are constants (Jeschke 2004; Fussmann, Weithoff & Yoshida 2005; Jeschke 2006; Okuyama 2010; Braza 2012). It is particularly important to address such concerns because terms that can serve equally well as descriptors of species interactions frequently lead to drastically different outcomes in a dynamical context (Fussmann & Blasius 2005). In this thesis, I first investigate the consequences of allowing evolutionary and plastic change to prey traits that control the components of the type 2 functional response. I then combine theoretical analyses with a systematic review of empirical data to determine the prevalence and dynamical consequences of inducible offenses that result in prey density-dependent attack rates and/or handling times.

**Appendix 4.D – Data set references**

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