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Aggressive interference as a strategy for enhancing resource gain

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The functional response, or rate of resource acquisition for a consumer should decline proportionately in the presence of other consumers vying for the same resources. Aggressive behavior should be adaptive when it serves as a leverage mechanism for enhancing resource gain above what would be obtained under a premise of equal access. Model development expands on the implications of this assertion to make several predictions pertaining to the expression and magnitude of gainful aggressive interference with respect to leverage strength,consumer density, and resource density.

Introduction

Adaptive aggressive behavior

Adaptive explanations of biological traits refer to their functional design. Soever, adaptive behavior entails goal-directed orientation to environmental cues, as perceived through sensory and cognitive capabilities (Dill 1983; Hills 2006); and mediates interactions with the environment to promote Darwinian fitness (Hamilton 1964). Consequently, natural selection favors behavioral traits that enhance individual reproductive success (Klopfer and Hailman 1972). At the population level, heritable genotypic variability modulates the expression of behavioral traits (Benus et al. 1991; Duckworth 2009). Behavioral traits also show phenotypic plasticity in response to the local environment (Chevin and Lande 2015). Likewise, the capacity to learn can improve the efficacy of behavioral traits within a changing environment (Kieffer and Colgan 1992; Fawcett et al. 2013; Jackson et al. 2013; Jackson et al. 2014). Over deeper time scales, selection for secondary traits may reinforce adaptive behavior (Zuk et al. 2014). For example, auxiliary morphological traits like larger size, horns, tusks, etc, may evolve to enhance the efficacy of aggressive behavior and increase fitness. Agonistic behavior encompasses a range of interactions between dominant and subordinate animals, ranging from attack to threat to avoidance and retreat (Scott and Fredericson 1951). When used for gaining priority of access to limited resources, assertive aggressive behaviors include attacking, rushing, displaying, signaling, and other forms of intimidation. Such behaviors collectively fall under the rubric of competitive interference (Peckarsky 1991). Henceforth, the term *aggressive interference* will refer to such behavior.

Aggression pervades the animal kingdom (Holekamp and Strauss 2016). The Darwinian interpretation implies aggressive behaviors fulfill adaptive functions (Lorenz 1967; Kuse and De Fries 1976). As such, aggressive behavior may serve in the defense of self, mates, and offspring. Aggressive behavior also may impose preemptive access to resources (Pellegrini 2008; Holdridge et al. 2016). Preemptive access applies to food, mates, and space, either within an unfixed area of discovery, a fixed territory, or a refuge (Kilgour et al. 2018). Intraspecific aggression prevalently occurs more than interspecific aggression (Lorenz 1967), inferring that the degree of aggression corresponds with potential resource overlap (Moore 1978). The lack of preemptive resource use by a given species indicates the exception that proves the rule. Species that do not vie for access to limited resources occur under ecological conditions unfavorable for such a strategy. Under the proper ecological conditions, some species even cooperate to enhance resource gain (Nilsson et al. 2007; Mazzolini and Celani 2020), although cooperation appears much less often than competition. Moreover, phenotypic plasticity occurs ubiquitously in the expression of aggressive behavior (Sirot 2000; Gibert and DeLong 2015). Aggressive interference behavior clearly provides a flexible strategy for obtaining resources within the context of socially and environmentally variable conditions (Giraldeau and Dubois 2008).

The flexible expression of aggression implies its adaptive value. Resource availability mediates whether aggressive interference behavior can enhance resource gain (Rands et al. 2006; Peiman and Robinson 2010; Fattorini et al. 2018). Consumer density also modulates the efficacy of aggressive interference behavior by directly imposing demands on

resources. Indeed, the competitive relationship can shift from exploitative to interference with increasing consumer density (Holdridge et al. 2016). Aggressive behavior preempts the time available for other gainful behaviors, such as searching, pursuing, and handling resources (Rakocinski et al. 1983). Unlimited resource availability should preclude the expression of aggressive interference behavior in favor of time spent consuming resources (Sirot 2000). Thus, time and energy dedicated to aggressive behavior pose tradeoffs with time spent and energy gained while consuming limited resources. A proper balance between these tradeoffs reflects the efficacy of aggressive interference behavior in enhancing resource gain. Aggressive interference behavior becomes ineffective as a mechanism for enhancing resource gain whenever the realized gain is lower than that potentially obtained in the absence of the behavior.

Aggregated spatial distributions of consumers often occur in nature. Groups form as a predation defense strategy, or in response to local concentrations of food, potential mates, or patchy habitats. Grouping of consumers may also form as an outcome of differential speed of movement with respect to local resource depletion (Richards et al. 2000). Aggregated spatial distributions predispose consumers to vie for limited resources. Thus, contention for limited resources commonly occurs among consumers within groups (Sirot 2000; Giraldeau and Dubois 2008). Aggressive interference can assert access to limited resources within aggregations (Holdridge et al. 2016). Furthermore, the expression of aggressive behavior depends on dispersion patterns of resources with respect to consumers (Scott and Fredericson 1951). Conversely, aggression mediates the spatial dispersion of consumers with respect to shared resources (Gübel et al. 2021). For example, aggressive interactions can generate uniform spacing of consumers with respect to locally shared resources. On the other hand, dominant consumers may prevent access to resources within well-defined territories (Verner 1977; Jensen et al. 2005). Effects of aggression on the spatial dispersion of consumers also extend to the population level (Duckworth and Badyaev 2007; Brownscombe et al. 2012). Uneven demographic effects of agonistic interactions include dominance hierarchies, growth depensation, differential mortality, debilitating effects of stress and injury, mating failure, prey switching, feeding niche expansion, etc. (Winberg and Sneddon 2022). On a suitably large spatial scale, aggressive interactions may facilitate the formation of ideal-free distributions marked by concurrence between the spatial dispersions of consumers and their resources (Farnsworth and Beecham 1997; Meer and Ens 1997; Krivan 2008).

Optimality vs Satisficing

Optimality theory offers a conceptual framework for testing mechanistic hypotheses about how well an adaptive goal-directed behavior conforms to the maximization of an underlying cost/benefit function (Moors et al. 2017). Although animals seldom behave optimally (Fawcett et al. 2013), optimality criteria serve as standards for evaluating adaptive value. Thus, optimality epitomizes the maximum utility of enacting a given behavior. Maximum utility is tractable with respect to a properly defined benefit/cost function. So, a benefit/cost value of one delineates a constraint threshold below which the adaptive behavior should not occur. Known as the satisficing criterion (sensu Simon 1955; Goodrich et al. 2000), this lower limit of profitability is less stringent than the optimality criterion. Although some allege the satisficing criterion to be trivial and unfalsifiable (Nonacs and Dill 1993), both satisficing and optimality criteria involve the same costs, benefits, and trade-offs (Ward 1992). When appropriately framed, the satisficing criterion yields a realistic standard for evaluating the utility of a behavior, including within the context of optimal foraging. Natural selection should prevent the expression of any behavior that does not meet or exceed the satisficing criterion. Framed in this way, hypotheses predicated on a satisficing criterion should be testable. The satisficing principle complements the optimality principle because the larger conceptual space of possible adaptive strategies includes the optimal strategy. Moreover, the use of a satisficing criterion in conjunction with an optimality principle eases comparison and evaluation of behaviors used for alternative strategies. Thus, a threshold satisficing criterion can serve to critically assess the functional value of a behavior. For example, equitable allocation offers a standard satisficing criterion for testing whether aggressive behavior serves as an effective mechanism for garnering resources within a group setting. Moreover, such a premise of equal access provides a baseline for gauging the efficacy of aggressive behavior as a leverage for enhancing resource gain.

Standard Functional Response Models

The Holling functional response model (Holling 1959a) is a cornerstone of evolutionary ecology (DeAngelis et al. 1975) while also fulfilling a vital role within optimal foraging theory (Abrams 1982). Functional response models feature within diverse subfields, including population and community ecology, optimal foraging theory, trophic ecology, allometric scaling, and metabolic ecology (Abrams 1982; Abrams 1990; Weitz and Levin 2006; Basset and DeAngelis

2007; Brose et al. 2008; Brose 2010; Basset et al. 2012; Gibert and DeLong 2015; Holdridge et al. 2016; Abrams 2022). Functional response models specify consumption by one or multiple consumers and pertain to sustained or depleted resource levels (Rosenbaum and Rall 2018). Routinely used to characterize feeding rates, functional response models can describe the 'consumption' of any kind of renewable resource. Although static parameters drive the original Holling disc equations (Skalski and Gilliam 2001), later studies incorporate flexible parameters and ecological covariates, like body size, and consumer-dependent effects such as behavioral interactions of consumers. Despite their wide use, functional response models have not fully addressed how aggressive behavior may serve as leverage for enhancing resource consumption.

The three standard functional response models, Type I, Type II, and Type III forms (Holling 1959a; Holling 1959b), demarcate reference points along a continuum of model forms (Real 1977). Real (1977) derived a general unified functional response model based on enzyme kinetics equations. Depending on the exponent, each of the standard models delineates a benchmark along the continuum. All three standard models specify instantaneous rates of consumption with respect to sustained levels of resource availability, as opposed to consumption integrated over time with respect to depleting concentrations of resource availability. At low levels of resource availability, the rate of encounter, or attack (a), drives the functional response, while the time taken to consume the resource, or handling time (h), constrains the functional response at elevated levels of resource availability (Rosenbaum and Rall 2018). Because search time (Ts), is inversely related to the encounter rate, the functional response approaches its asymptotic value, or saturates, as the search time between items approaches zero. For all three standard models, the functional response ranges from vanishingly low to asymptotically high rates of resource consumption across a wide range in resource availability. Under unlimited resource availability, the functional design of the organism limits the maximum attainable rate of consumption. The Type I functional response describes a linearly increasing approach to the asymptotic saturation level, which applies to consumers that can simultaneously search for and handle resources, like spiders tending a web, or consumers that do not spend time handling resources, such as filter feeders. Because this strategy would seldom apply to animals using aggressive behavior to enhance their rate of resource gain, we will not further consider the Type I functional response.

Consumer-Dependent Effects

Consumer-dependent effects involve behavioral interactions such as interference and facilitation among members of a group (Nilsson et al. 2007). Accounting for consumer dependence helps explain the functional responses of consumers within groups. Even in the absence of direct behavioral interactions, consumer dependence is inevitable with increasing consumer density (Ginzburg 2000). Likewise, consumer dependence should arise as resources concentrate. Based on a meta-analysis, Skalski and Gilliam (2001) found that consumer-dependent effects influenced functional responses in most of the studies they considered (i.e., 18 out of 19). Indeed, Abrams and Ginzberg (2000) documented that most functional response studies conducted in the laboratory involved consumer-dependent effects. Examples of consumer-dependent effects include mutual distraction among consumers, or elevated search time due to the inhibitory effects of consumers on prey behavior (Free et al. 1977). Functional response models typically integrate these "mass-action" effects as interference compounded by the density of interacting consumers (Van Der Meer and Smallegange 2009). Most consumer-dependent models explicitly account for the effect of interference among consumers (sensu Hassell and Varley 1969). Such models also generally assume that time spent consuming resources excludes the time spent on interference (Beddington 1975; DeAngelis et al. 1975). Thus, interference acts as a consumer-dependent inhibitory effect on the collective functional response. Further, interference wanes as the functional response approaches saturation in conjunction with sufficient resource availability (Skalski and Gilliam 2001). However, some models regard interference as nonexclusive of consumptive behaviors (Crowley and Martin 1989). Other consumer-dependent models regard the ratio of consumer to resource density as the main driver of the functional response (Hassell and Varley 1969; Abrams and Ginzburg 2000). Consumer-dependent effects offer increased realism (Skalski and Gilliam 2001), although consumer-dependent models often lack explicit mechanistic explanations.

Incorporating behavioral effects into consumer-dependent functional response models should improve their explanatory ability. Interference models can demonstrably fit functional responses better than exclusively resource-dependent models (Skalski and Gilliam 2001). However mutual interference lowers the functional response symmetrically by reducing the time available for engaging with resources equally for all interacting consumers. Asymmetric

dominant-subordinate interactions are lacking within a functional response context. Such asymmetric types of consumer-dependent interaction often exemplify aggressive interference between consumers (Abrams and Ginzburg 2000). Furthermore, consumers facultatively display aggressive interference to increase net resource gain in the face of ecological trade-offs (Stillman et al. 1997; Goss-Custard et al. 1998, as cited in Sirot 2000).

The hawk-dove game theory model confirms the evolutionary stability of an aggressive interference strategy for gaining priority of access to resources (Cowden 2012). This modeling approach considers the probability of assuming alternative hawk or dove strategies within the context of pairwise interactions depending on costs and benefits in terms of energy and time (sensu Smith and Price 1973). An adaptation of the model predicts that aggressive interference varies inversely with respect to resource availability and increases concomitantly with consumer density (Sirot 2000). Furthermore, the amount of time spent during an aggressive interaction modulates whether a consumer assumes the hawk strategy despite a net benefit for employing the strategy (Křivan and Cressman 2017).

The Leverage Effect of Aggressive Interference

Aggressive interference potentially elevates the realized rate of resource gain (Goss-Custard et al. 1998). Thus, consumer-dependent functional response models should include costs and benefits of directed aggressive interference to enhance resource gain (Meer and Ens 1997). As such, the effect of aggressive interference would serve as leverage for elevating resource gain by suppressing competing consumers within the 'area of discovery' (sensu Hassell and Varley 1969; Sirot 2000) of the aggressive agent. A premise of equal access would serve as the satisficing criterion for comparison with the realized gain/cost value associated with using leverage. Furthermore, the optimality principle dictates the maximization of the realized energy/time (E/T) ratio (Schoener 1971) with respect to the equal access criterion.

In the ensuing models, the leverage coefficient (λ) specifies the degree to which aggressive interference boosts the rate of resource encounter within the 'area of discovery' (sensu Hassell and Varley 1969; Sirot 2000), herein referred to as the ambit of the aggressive consumer. Haskell and Varley (1969) formerly defined the 'area of discovery' as, "the area it (i.e., an animal) visits per unit of searching time". The area of discovery provides a means to normalize resource abundance for obtaining resource density within the ensuing models. Herein, the ambit refers to the effective area or volume of discovery within which the focal consumer can enhance its rate of encounter with a resource through aggressive interference. The magnitude of λ reflects its efficacy for enhancing gain/cost with respect to competitors. Thus, the effect of leverage drives resource encounter compared to a baseline value of 1.0, standing for the equal access rate of encounter within a group of P consumers (i.e., a/P). Additionally, λ scales continuously with the rate of resource encounter. Importantly, the enhanced functional response value cannot exceed the asymptotic rate of resource gain denoted by T/h, as set by inherent constraints on consumer design.

In standard functional response models, total time (T) includes the time spent obtaining resources, and handling time (h) denotes time spent consuming one unit of resource (e.g., one prey item). With increasing resource availability, standard functional responses approach the asymptotic value defined by T/h, while search time (Ts) approaches zero. For standard models, time spent searching for resources occurs exclusively of time spent consuming resources (Free et al. 1977). Likewise, time spent on aggressive interference occurs exclusively of time spent on consuming resources, made up by searching, pursuing, attacking, and handling behaviors. So, time spent on aggressive interference connotes a tradeoff (Sirot 2000), potentially compensated by an enhanced rate of consumption in fulfillment of an energy maximization strategy (E/T) (Schoener 1971). The leverage coefficient thus parameterizes the effect of aggressive interference in enhancing the rate of consumption.

Results – Model Description

Type II functional response – leverage within a group under sustained resource availability

The standard Type II functional response describes a decelerating asymptotic curve with increasing resource density (N). It reflects the capacity to process the resource which hinges on the encounter rate and handling time relative to resource density (N). The difference equation defined for a single consumer recursively describes the Type II functional response over a fixed period:

$$Ni_{II} = a\,N\,(T - h\,Ni_{II}) \qquad \textbf{(1.0)}$$

where,

Ni_{II} = number of resource units consumed;

a = rate of encounter per unit of resource per unit time (e.g., mates, food items, etc.);

N = abundance or density of resources;

T = total number of time units while obtaining resources (e.g., hrs);
h = handing time per unit of resource consumed.

When solved, equation **1.0** yields the standard Type II functional response in the form of the disc equation for a single consumer:

$$Ni_{II} = \frac{a\,N\,T}{1+(a\,h\,N)} \qquad \textbf{(1.1)}$$

The disc form of the Type II equation describes a decelerating rectangular hyperbola with respect to increasing sustained resource density (N). The functional response approaches the asymptotic saturated level corresponding with the maximum of T/h as resource availability increases. The consumer has reached its full physical capacity at T/h because all available time is committed to handling resources. The model assumes a constant encounter rate, a, with respect to resource abundance. The individual consumes Ni_{II} resource units during the period, T, dedicated to obtaining resources at a sustained level of resource availability, N (i.e., N not depleted). This implies that resources renew by some process at the same rate that they are consumed. At low levels of N, the encounter rate governs the functional response, (i.e., the reciprocal of search time per unit of resource), and at elevated levels of N, handling time governs the rate of consumption. Thus, total search time, $T_s = [T - (h \times Ni_{II})]$, and search time per resource unit consumed, $T_s/Ni_{II} = [T - (h \times Ni_{II})]/\ Ni_{II}$.

When multiple consumers co-occur within an *unrestricted* resource availability scenario, the foregoing Type II functional response for an individual will scale up directly with the abundance (or density) of non-overlapping consumers (P). The difference equation for multiple consumers facing *unrestricted* resources recursively describes the Type II functional response over a fixed period:

$$Ne_{IIP} = P\,a\,N\,(T - h\,Ne_{II}) \qquad \textbf{(1.2)}$$

When solved, equation **1.2** yields the standard Type II functional response in the form of the disc equation for multiple consumers:

$$Ne_{IIP} = \frac{P\,a\,N\,T}{1+(P\,a\,h\,N)} \qquad \textbf{(1.3)}$$

where,
$Ne_{IIP} = Ne_{II} \times P$;
Thus, Ne_{IIP} stands for consumption by P consumers within an *unrestricted* resource availability scenario.

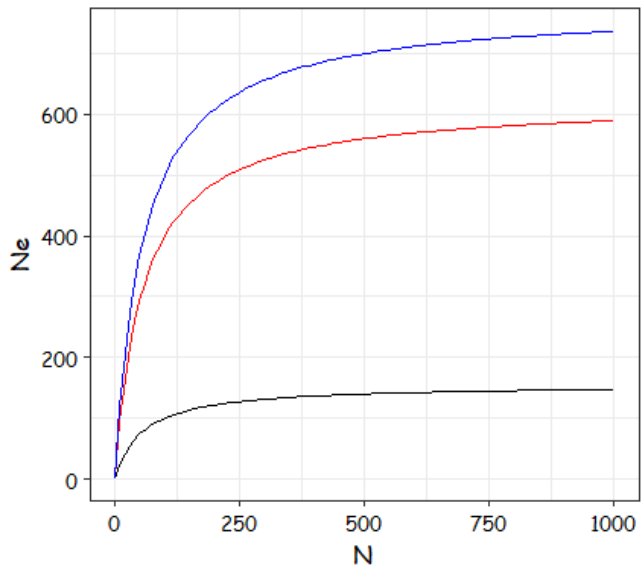

Figure 1: Type II functional responses for multiple consumers co-occurring within an *unrestricted* resource availability scenario. The functional response scales up additively with the abundance of non-overlapping consumers (P). Black curve – P = 1, asymptotic Ne = 150; Red curve – P = 4, asymptotic Ne = 600; Blue curve – P = 5, asymptotic Ne = 750 (i.e., sum of black and red curves. Encounter rate (a) = 0.2, h = 0.09, T = 14.

This multiple consumer-extended form of the Type II functional response implies each consumer reaches the same average rate of resource consumption defined by equation **1.1** in an additive manner (Fig. 1). Per capita consumption is independent of the presence of other consumers and resource availability stays at the level supporting consumption by P consumers collectively. Therefore, the encounter rate, a, also stays undiminished within the ambit of each consumer. For example, a consumer-extended functional response might reflect consumption by multiple consumers across an expansive prey field. Under such an *unrestricted* resource availability scenario, aggressive interference would not effectively increase resource encounter rates.

When multiple consumers co-occur within a *restricted* resource availability scenario, the per capita encounter rate reflects overlap in resource use. Thus, the model focuses on a group of P consumers sharing the ambit area/volume for a single consumer under an *unrestricted* resource availability scenario. Consequently, multiple consumers partition the rate of resource consumption. Partitioning reduces the per capita encounter rate for an individual consumer, while a resource replacement process sustains the *restricted* Type II functional response. The difference equation for a single consumer recursively describes the Type II functional response based on a premise of equal access:

$$Ni_{IIP} = \frac{a}{P}\, N\,(T - h\, Ni_{IIP}) \qquad \textbf{(1.4)}$$

where,
a/P denotes the per capita encounter rate; and
Ni_{IIP} = per capita resource units consumed.

As a reflection of the average overlap, P may be an integer or a fractional number.

When solved, equation **1.4** yields the Type II functional response for an individual in the context of P consumers under *restricted* resource availability (Fig. 2):

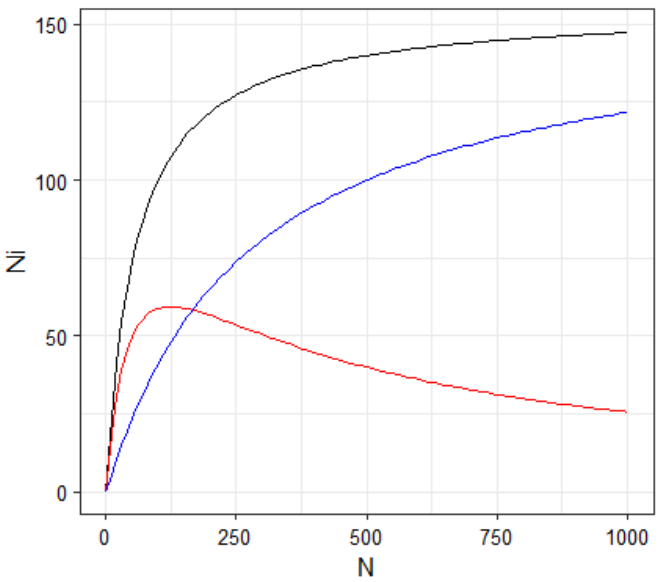

Figure 2: Type II functional responses for consumers within a *restricted* resource availability scenario. The difference in functional responses for a consumer with exclusive access to a resource (i.e., encounter rate, a = 0.2, h = 0.09, T = 14, black curve) and that for a consumer with equal access to the resource within a group (i.e., encounter rate = a/P; blue curve), hypothetically impels the degree to which aggression serves as leverage for potential gain (i.e., red curve). Blue curve, P = 5, (i.e., a/P = 0.2/5 = 0.04), h = 0.09, T = 14. Difference curve asymptotically converges to zero at N_{iIIP} = T/h for blue curve (i.e., 155.6). The peak value of the difference curve (i.e., maximum aggression) occurs at N = sqr(P)/a h, (i.e., 124.23).

$$Ni_{IIP} = \frac{a\,N\,T}{P + (a\,h\,N)} \qquad \textbf{(1.5)}$$

When multiple consumers co-occur within a *restricted* resource availability scenario, the previous Type II functional response for an individual will scale up with the abundance (or density) of overlapping consumers (P). The difference equation for multiple consumers facing *restricted* resources recursively describes the Type II functional response over a fixed period:

$$Ne_{IIP} = P\,\frac{a}{P}\, N\,(T - h\, Ni_{IIP}) \qquad \textbf{(1.6)}$$

When solved, equation **1.6** yields the Type II functional response for multiple consumers under *restricted* resource availability:

$$Ne_{IIP} = \frac{a\,N\,T}{1 + (a\,h\,N)} \qquad \textbf{(1.7)}$$

Here, Ne_{IIP} stands for consumption by P consumers within a *restricted* resource availability scenario. The functional response equation for P consumers under *restricted* resource availability is identical to the standard per capita functional response equation described by equation **1.1**.

Under *restricted* resource availability, a consumer may use aggressive interference to elevate its rate of encounter above a/P, but less than a. Construed as aggressive interference behavior by a dominant consumer to enhance resource gain, the parameter λ signifies *leverage*. As such, λ raises resource gain above the level inferred by a premise of equal access within a group of P consumers. Consumption cannot exceed the effect of P consumers ($\lambda/P = 1$), because $\lambda/P = 1$ connotes the per capita rate of consumption under *unrestricted* resource availability.

The following conditions apply to the realization of λ:

(1) λ must exceed 1 for aggressive interference to be gainful,
(2) λ cannot exceed P (i.e., $\lambda \leq P$),
(3) λ can vary continuously.

The time spent on aggressive interference (i.e., T_λ) as opposed to obtaining resources denotes a key tradeoff (c.f., Sirot 2000) within the functional response of a consumer. The model assumes that time spent for aggressive interference is independent of time spent searching, pursuing, or apprehending/handling resources. Thus, the total time spent obtaining resources (i.e., T) includes the time spent searching for and consuming resources (i.e., $T_f = T_s + T_h$) in addition to the time dedicated to aggressive interference (i.e., T_λ). So, T_f constitutes search time (i.e., T_s) and handling time (i.e., T_h). And $T - T_\lambda$ leaves T_f, or the time dedicated to obtaining resources at the leverage-enhanced rate of encounter for an aggressive consumer.

The following difference equation recursively defines the Type II functional response for an aggressive consumer within a group of multiple consumers with equal access to resources:

$$Ni_{II\lambda} = \lambda \frac{a}{P} N\,(T - h\,Ni_{II\lambda} - T_{\lambda}) \qquad \textbf{(1.8)}$$

When solved, equation **1.8** yields the Type II functional response as a disc equation for a consumer using aggressive interference as leverage:

$$Ni_{II\lambda} = \frac{\lambda\, a\, N\,(T - T_{\lambda})}{P + (\lambda\, a\, h\, N)} \qquad \textbf{(1.9)}$$

$Ni_{II\lambda}$ in equation **1.9** specifies the Type II functional response for an aggressive consumer overlapping with a group of P consumers at any sustained level of resource availability, N. How much the functional response specified by equation **1.9** exceeds that for equation **1.5** for any level of resource availability (N), reflects the efficacy of aggressive interference behavior for elevating resource gain.

The difference between Ni_{II} (equation **1.1)** and Ni_{IIP} (equation **1.5**) defines how aggressive interference should perforce apply with respect to N. This follows from the premise that the scope for elevating resource gain drives the degree of aggressive interference in terms of T_{λ}. Thus, T_{λ} should mirror the normalized difference between Ni_{II} and Ni_{IIP}:

$$Ni_{II} - Ni_{IIP} = \frac{a\, N\,(P-1)\, T}{(a\, h\, N+1)\,(a\, h\, N+P)} \qquad \textbf{(2.0)}$$

This difference describes a right-skewed hump-shaped curve with respect to N (Fig. 2). The proportional difference between Ni_{II} and Ni_{IIP} ranges from 0 at both extreme levels of resource to 1 at some intermediate level of N, for which the difference is greatest. The greatest difference occurs at Ni_{IImax}, where the partial derivative of the difference curve with respect to N = 0:

$$\frac{\partial(Ni_{II} - Ni_{IIP})}{\partial N} = \frac{(P-1)\, T\,(a\, P - a^3\, h^2\, N^2)}{(a\, h\, N+1)^2\,(a\, h\, N+P)^2} = 0 \qquad \textbf{(2.1)}$$

Alternatively, assuming all parameters are positive:

$$\frac{\partial(Ni_{II} - Ni_{IIP})}{\partial N} = (P-1)(P - a^2 h^2 N^2) = 0 \qquad \textbf{(2.2)}$$

Equation **2.2** solution:

$$\frac{\partial(Ni_{II} - Ni_{IIP})}{\partial N} = 0 \;\; at\; N = \frac{\sqrt{P}}{a\, h} \qquad \textbf{(2.3)}$$

So: $N_{IImax} = \frac{\sqrt{P}}{a\, h}$, such that:

$$Ni_{IImax} = Ni_{II} - Ni_{IIP} \;\; at\; N_{IImax} = \frac{\sqrt{P}}{a\, h} \qquad \textbf{(2.4)}$$

After substitution and rearrangement:

$$\frac{Ni_{II} - Ni_{IIP}}{Ni_{IImax}} = \frac{a\, h\, N\,(\sqrt{P}+1)^2}{(a\, h\, N+1)\,(a\, h\, N+P)};\; ranges\; from\; 0\; to\; 1\; at\; N_{IImax} = \frac{\sqrt{P}}{a\, h} \qquad \textbf{(2.5)}$$

Type II functional response – Threshold for aggressive interference

Based on the foregoing, one can deduce the threshold resource density and corresponding functional response value at which aggressive interference should cease owing to the functional response for an aggressive consumer falling below that for a consumer with equal access to the resource. Thus, the threshold resource density for the expression of aggressive interference should concur with the intersection of the respective functional responses (Fig. 3). Also, the intersection of Ni_{IIP} and $Ni_{II\lambda}$ coincides with the threshold resource density, N_{IIt}:

$$N_{IIt} = \frac{a\, N_{IIt}\, T}{P + (a\, h\, N_{IIt})} - \frac{\lambda\, a\, N_{IIt}\,(T - T_{\lambda crit})}{P + (\lambda_{crit}\, a\, h\, N_{IIt})} = 0 \qquad \textbf{(2.6)}$$

Solving equation **2.6** for N_{IIt}:

$$N_{IIt} = \frac{(P\,(\lambda_{crit}\,(T - T_{\lambda crit}) - T)}{(\lambda_{crit}\, a\, h\, T_{\lambda})} \qquad \textbf{(2.7)}$$

In equation **2.7**, the threshold time dedicated to aggressive interference (i.e., $T_{\lambda crit}$) and critical leverage (i.e., λ_{crit}) are explicit. Solving equation **2.6** for these critical parameters yields the threshold time dedicated to aggressive interference ($T_{\lambda crit}$) and the required threshold leverage (λ_{crit}):

$$T_{\lambda crit} = \frac{(\lambda crit - 1)\, P\, T}{\lambda crit\,(a\, h\, N_{IIcrit} + P)} \qquad \textbf{(2.8)}$$

$$\lambda_{crit} = \frac{P\, T}{P\, T - a\, h\, T_{\lambda crit}\, N_{IIcrit} - P\, T_{\lambda crit}} \qquad \textbf{(2.9)}$$

More generally, the product of $T_{\lambda max}$ and the normalized difference between functional responses for an aggressive consumer and for a consumer within a group of P consumers with equal access specifies T_{λ}. Accordingly, for the Type II functional response:

$$T_{\lambda} = \frac{Ni_{II} - Ni_{IIP}}{Ni_{IImax}}\, T_{\lambda max} \qquad \textbf{(3.0)}$$

And based on rearrangement of equations **1.9** and **2.5**:

$$Ni_{II\lambda} = \frac{\lambda\, a\, N\left(T - T_{\lambda max}\,\frac{(a\, h\, N(\sqrt{P}+1)^2)}{(a\, h\, N+1)(a\, h\, N+P)}\right)}{P + (\lambda\, a\, h\, N)} \qquad \textbf{(3.1)}$$

The threshold functional response value (Ni_{IIcrit}) corresponding to the threshold resource density (i.e., N_{IIt}) for aggressive interference for a Type II functional response concurs where there is no difference between equations **3.1** and **1.5**:

$$Ni_{IIcrit} = \frac{\lambda\, a\, N\left(T - T_{\lambda max}\frac{(a\, h\, N(\sqrt{P}+1)^2)}{(a\, h\, N+1)(a\, h\, N+P)}\right)}{P+(\lambda\, a\, h\, N)} - \frac{a\, N\, T}{P+(a\, h\, N)} = 0 \qquad \textbf{(3.2)}$$

Solving expression **3.2** for Ni_{IIcrit}:

$$Ni_{IIcrit} = \frac{(\lambda-1)\, P\, T}{a\, h\,(\lambda\, T_{\lambda max} + \lambda\, T_{\lambda max}\, P + 2\lambda\, T_{\lambda max}\sqrt{P} - \lambda\, P\, T + P\, T)} \qquad \textbf{(3.3)}$$

where Ni_{IIcrit} stands for the threshold functional response value for which no difference exists between aggressive interference and equal access strategies. Equation **3.3** obviates resource density. Thus, Ni_{IIcrit} denotes the point where aggressive interference and equal access functional responses intersect with respect to the critical resource density, N_{IIt} (Fig. 3). Implicitly, profitability for the equal access strategy exceeds that for the aggressive interference strategy at resource densities greater than N_{IIt}.

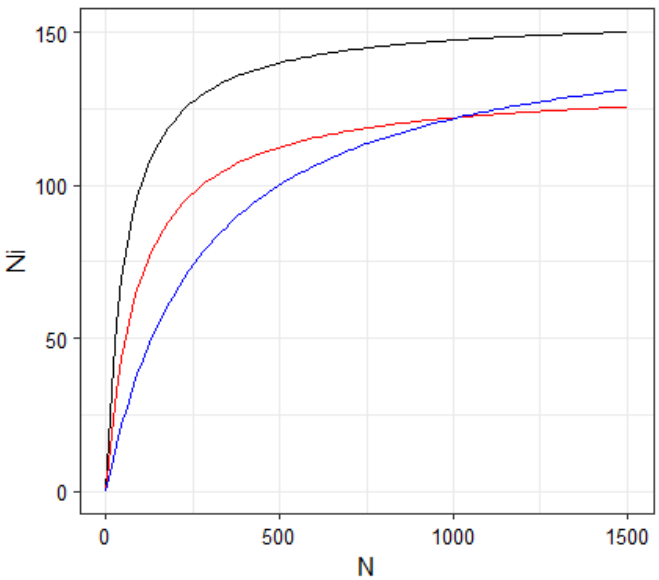

Figure 3: Type II functional responses for consumers within a *restricted* resource availability scenario, including that for an aggressive consumer exerting leverage on resource gain. Parameters in common: a = 0.2, h = 0.09, T = 14. The black curve describes the functional response of a consumer with exclusive access to a resource, while the blue curve describes the functional response for one of five consumers (i.e., P = 5) with equal access to the resource (i.e., encounter rate = a/P). The red curve describes the functional response for an aggressive consumer applying leverage (i.e., $\lambda = 3$, $T_\lambda = 2$). Here, aggressive interference is expected to occur between resource levels N = 0 and 1,018.52, where the curves intersect at $Ni_{IIcrit} = 122.22$.

Type III functional response – leverage within a group under sustained resource availability

Like the Type II, the Type III functional response describes an asymptotic curve with respect to increasing resource density (N) (Holling 1959). However, the Type III functional response forms a sigmoid curve which accelerates up to an inflection point, after which it decelerates and levels off with increasing resource density. Systematic increases in the rate of encounter with resources as an effect of learning or experience drive the sigmoid-shaped nature of the Type III curve.

The difference equation defined for a single consumer recursively describes the Type III functional response over a fixed period:

$$Ni_{III} = a\, N\,(T - h\, Ni_{III});\ where\ a = bN \qquad \textbf{(3.4)}$$

and thus, $Ni_{III} = b\, N^2\,(T - h\, Ni_{III})$ **(3.5)**

where,
Ni_{III} = number of resource units consumed;
b = the resource-density dependent rate of encounter (i.e., the attack rate, a = bN);
N = abundance or density of resources;
T = total time while obtaining resources (e.g., hrs);
h = handing time per unit of resource consumed.

When solved equation **3.5** yields the standard Type III functional response for a single consumer in the form of the disc equation:

$$Ni_{III} = \frac{b\, N^2\, T}{1+(b\, N^2\, h)} \qquad \textbf{(3.6)}$$

When multiple consumers co-occur within an *unrestricted* resource availability scenario, the foregoing Type III functional response for an individual will scale up directly with the abundance (or density) of non-overlapping consumers (P). The difference equation for multiple consumers facing *unrestricted* resources recursively describes the Type III functional response over a fixed period:

$$Ne_{IIIP} = P\, b\, N^2\,(T - h\, Ne_{III}) \qquad \textbf{(3.7)}$$

When solved, equation **3.7** yields the standard Type III functional response in the form of the disc equation for multiple consumers:

$$Ne_{IIIP} = \frac{P\, b\, N^2\, T}{1+(P\, b\, h\, N^2)} \qquad \textbf{(3.8)}$$

where, $Ne_{III} = Ni_{III} \times P$;
Thus, Ne_{III} stands for consumption by P consumers within an *unrestricted* resource availability scenario.

This multiple consumer-extended form of the Type III functional response implies each consumer reaches the same average rate of resource consumption defined by equation **3.6** in an additive manner (Fig. 4). Per capita consumption is independent of the presence of other consumers and resource availability stays at the level supporting consumption by P consumers collectively. Therefore, the encounter rate, b, stays undiminished within the ambit of each consumer. In nature, such a consumer-extended functional response might reflect consumption by multiple consumers across an expansive prey field. Under such an *unrestricted* resource availability scenario, aggressive interference would not effectively increase resource encounter rates.

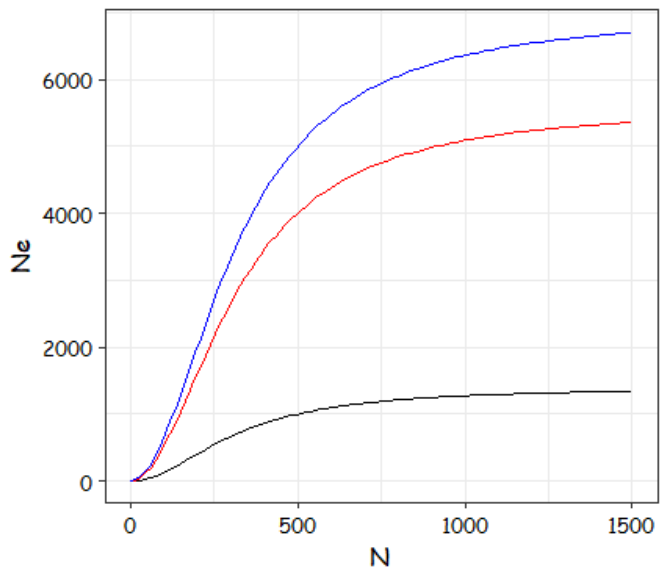

Figure 4: Type III functional responses for multiple consumers co-occurring within an *unrestricted* resource availability scenario. The functional response additively scales up with the abundance of non-overlapping consumers (P). Black curve – P = 1, asymptotic Ne = 1400; Red curve – P = 4, asymptotic Ne = 5600; Blue curve – P = 5, asymptotic Ne = 7000 (i.e., sum of black and red curves. Encounter rate (b) = 0.001, h = 0.01, T = 14.

When multiple consumers co-occur within a *restricted* resource availability scenario, the per capita encounter rate reflects overlap in resource use. Thus, the model focuses on a group of P consumers sharing the ambit area/volume for a single consumer when under an *unrestricted* resource availability scenario. Consequently, multiple consumers partition the rate of resource consumption. Partitioning reduces the per capita encounter rate for an individual consumer, while a resource replacement process sustains the *restricted* Type III functional response.

The difference equation for a single consumer recursively describes the Type III functional response based on a premise of equal access:

$$Ni_{IIIP} = \frac{bN}{P}\, N\,(T - h\, Ni_{IIIP}) \qquad \textbf{(3.9)}$$

where,

$\frac{bN}{P}$ denotes the per capita encounter rate; and

Ni_{IIIP} = per capita resource units consumed.

As a reflection of the average overlap, P may be an integer or a fractional number.

When solved, equation **3.9** yields the Type III functional response for an individual in the context of P consumers under *restricted* resource availability (Fig. 5):

$$Ni_{IIIP} = \frac{b\ N^2\ T}{P + (b\, h\, N^2)} \qquad \textbf{(4.0)}$$

When multiple consumers co-occur within a *restricted* resource availability scenario, the previous Type III functional response for an individual will scale up with the abundance (or density) of overlapping consumers (P). The difference equation for multiple consumers facing *restricted* resources recursively describes the Type III functional response over a fixed period:

$$Ne_{IIIP} = P\, \frac{bN}{P}\, N\,(T - h\, Ni_{IIIP}) \qquad \textbf{(4.1)}$$

Where Ne_{IIIP} represents resource units consumed by the group of P consumers. When solved, equation **4.1** yields the disc equation form of the Type III functional response for multiple overlapping consumers:

$$Ne_{IIIP} = \frac{b\ N^2\ T}{1 + (b\, N^2\, h)} \qquad \textbf{(4.2)}$$

Where Ne_{IIIP} stands for consumption by P consumers. Depending on the degree of overlap within the ambit (area/volume of discovery), P may be an integer or a fractional number. The functional response equation for P consumers under *restricted* resource availability is identical to the standard per capita functional response equation described by equation **3.6**.

The following difference equation recursively defines the Type III functional response for an aggressive consumer within a group of multiple consumers with equal access to

resources:

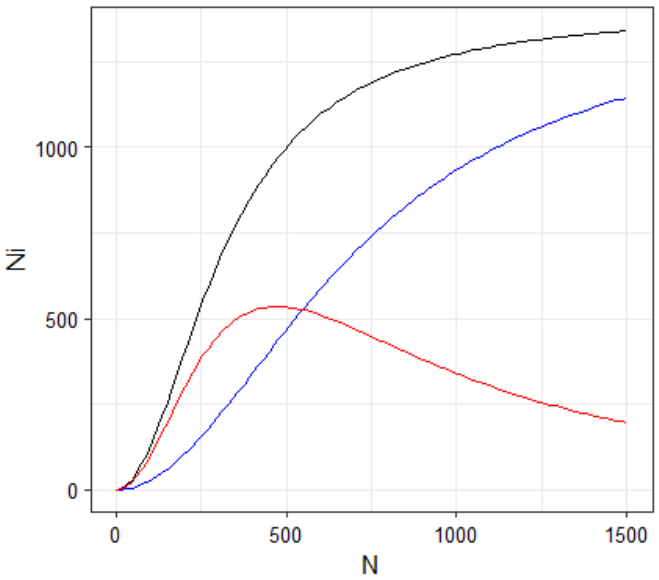

Figure 5: Type III functional responses for consumers within a *restricted* resource availability scenario. The difference in functional responses for a consumer with exclusive access to a resource (i.e., encounter rate, b = 0.001, h = 0.01, T = 14, black curve) and that for a consumer with equal access to the resource within a group (i.e., encounter rate = (bN/P); blue curve), hypothetically impels the degree to which aggression serves as leverage for potential gain (i.e., red curve). Blue curve, P = 5, bN/P = (0.001 N)/5; h = 0.01, T = 14. Difference curve asymptotically converges to zero at N_{IIIP} = T/h for blue curve (i.e., 1400). The peak value of the difference curve (i.e., maximum aggression) occurs at N = (frth(P)/sqr(b) sqr(h)), (i.e., 472.87).

$$Ni_{III\lambda} = \left(\lambda \frac{bN}{P}\right) N\,(T - h\,Ni_{III\lambda} - T_{\lambda}) \qquad \textbf{(4.3)}$$

When solved, equation **4.3** yields the Type III functional response as a disc equation for a consumer using aggressive interference as leverage:

$$Ni_{III\lambda} = \frac{\lambda\, b\, N^2\,(T - T_{\lambda})}{P + (\lambda\, b\, h\, N^2)} \qquad \textbf{(4.4)}$$

$Ni_{III\lambda}$ in equation **4.4** specifies the Type III functional response for an aggressive consumer overlapping wit a group of P consumers at a sustained level of resource availability (N). How much the functional response specified by equation **4.4** exceeds that for equation **4.0** for any level of resource availability (N), reflects the efficacy of aggressive interference behavior for elevating resource gain.

The difference between Ni_{III} (equation **3.6**) and Ni_{IIIP} (equation **4.0**) defines how aggressive interference should perforce apply with respect to N. This follows from the premise that the scope for elevating resource gain drives the degree of aggressive interference in terms of T_{λ}. Thus, T_{λ} should mirror the normalized difference between Ni_{III} and Ni_{IIIP}:

$$Ni_{III} - Ni_{IIIP} = \frac{b\, N^2 (P-1)\, T}{(b\, h\, N^2 + 1)\,(b\, h\, N^2 + P)} \qquad \textbf{(4.5)}$$

Like for the Type II model, the difference describes a hump-shaped curve with respect to N (Fig. 5). The proportional difference between Ni_{III} and Ni_{IIIP} ranges from 0 at both extreme levels of resource to 1 at some intermediate level of N, for which the difference is greatest. The greatest difference occurs at Ni_{IIImax}, where the partial derivative of the difference curve with respect to N = 0:

$$\frac{\partial(Ni_{III} - Ni_{IIIP})}{\partial N} = \frac{2\, b(P-1)\, TN\,(P - b^2 h^2 N^4)}{(bhN^2+1)^2\,(bh\,N^2 P)^2} = 0 \qquad \textbf{(4.6)}$$

Given:

$$\frac{\partial(Ni_{III} - Ni_{IIIP})}{\partial N} = 0 \;\; at\; N = \frac{\sqrt[4]{P}}{\sqrt{b}\sqrt{h}} \qquad \textbf{(4.7)}$$

So:

$$Ni_{IIImax} = Ni_{III} - Ni_{IIIP} \;\; at\; N = \frac{\sqrt[4]{P}}{\sqrt{b}\sqrt{h}} \qquad \textbf{(4.8)}$$

After substitution and rearrangement:

$$\frac{Ni_{III} - Ni_{IIIP}}{Ni_{IIImax}} = \frac{b\, h\, N^2 \left(\sqrt{P} + 1\right)^2}{(b\, h\, N^2 + 1)(b\, h\, N^2 + P)};$$
$$ranges\; from\; 0\; to\; 1\; at\; Ni_{IIImax} = \frac{\sqrt[4]{P}}{\sqrt{b}\sqrt{h}} \qquad \textbf{(4.9)}$$

Real's General Functional Response Model

The general functional response model based on enzyme catalysis as proposed by Real (1977; 1979) to unify can also unify the standard functional response models can also incorporate the aggressive interference models. Real's general model subsumes all three standard functional response models along a continuum. Instead of the squared exponent as in the Type III equation, the general model uses the global exponent (1 + q) to customize any functional response (i.e., q = 0 for Type II; q = 1 for Type III) (Rosenbaum and Rall 2018). Thus, the *general* functional response for a dominant consumer using aggressive interference as leverage ($Ni_{G\lambda}$) expressed in the form of a disc equation:

$$Ni_{G\lambda} = \frac{\lambda\, b\, N^{\,q+1}\,(T - T_{\lambda})}{P + (\lambda\, b\, h\, N^{\,q+1})} \qquad \textbf{(5.0)}$$

Type III functional response – Threshold for aggressive interference

As for the Type II functional response, one can deduce the threshold resource density and corresponding functional response value at which aggressive interference should cease for the Type III functional response. Because an effective functional response for an aggressive consumer must exceed

the corresponding per capita functional response for a consumer with equal access to the resource, the threshold resource density for the expression of aggressive interference should correspond with the intersection of the respective functional responses. Therefore, the intersection of Ni_{IIIP} and $Ni_{III\lambda}$ coincides with the threshold resource density, N_{IIIt}:

$$N_{IIIt} = \frac{b\,N^2_{IIIcrit}\,T}{P+(b\,h\,N^2_{IIIcrit})} - \frac{\lambda_{crit}\,b\,N^2_{IIIcrit}\,(T-T_{\lambda crit})}{P+(\lambda_{crit}\,b\,h\,N^2_{IIIcrit})} = 0 \qquad \textbf{(5.1)}$$

Solving equation **5.1** for N_{IIIt}, (assuming all parameters are positive):

$$N_{IIIt} = \pm\sqrt{\frac{P\,(\lambda_{crit}\,(T-T_{\lambda crit})-T)}{b\,h\,\lambda_{crit}\;T_{\lambda crit}}} \qquad \textbf{(5.2)}$$

In equation **5.2**, the threshold time dedicated to aggressive interference (i.e., $T_{\lambda crit}$) and critical leverage (i.e., λ_{crit}) are explicit. Solving equation **5.1** for these critical parameters yields the threshold time dedicated to aggressive interference ($T_{\lambda crit}$) and the required threshold leverage (λ_{crit}):

$$T_{\lambda crit} = \frac{(\lambda crit-1)\,P\,T}{\lambda crit\,(b\,h\,N^2_{IIIcrit}+P)} \qquad \textbf{(5.3)}$$

$$\lambda_{crit} = \frac{P\,T}{P\,T - b\,h\,T_{\lambda crit}\,N^2_{IIIcrit} - P\,T_{\lambda crit}} \qquad \textbf{(5.4)}$$

More generally, as the maximum time dedicated to aggressive behavior (i.e., $T_{\lambda max}$) occurs at N_{max}, equation **3.0** applies to any type of standard functional response:

$$T_{\lambda} = \frac{Ni-Ni_P}{Ni_{Tmax}}\;T_{\lambda max}$$

And based on rearrangement of equations **4.4** and **4.9**:

$$Ni_{III\lambda} = \frac{\lambda\,b\,N^2\left(T-T_{\lambda max}\frac{b\,h\,N^2(\sqrt{P}+1)^2}{(b\,h\,N^2+1)(b\,h\,N^2+P)}\right)}{P+(\lambda\,b\,h\,N^2)} \qquad \textbf{(5.5)}$$

The threshold functional response value ($N_{IIIcrit}$) corresponding to the threshold resource density (i.e., N_{IIIt}) for aggressive interference for a Type III functional response concurs where there is no difference between equations **5.5** and **4.0**:

$$Ni_{IIIcrit} = \frac{\lambda\,b\,N^2\left(T-T_{\lambda max}\frac{b\,h\,N^2(\sqrt{P}+1)^2}{(b\,h\,N^2+1)(b\,h\,N^2+P)}\right)}{P+(\lambda\,b\,h\,N^2)} - \frac{b\;N^2\,T}{P+(b\,h\,N^2)} = 0 \qquad \textbf{(5.6)}$$

Solving expression **5.6** for $Ni_{IIIcrit}$:

$$Ni_{IIIcrit} = \sqrt{\frac{(\lambda-1)\,P\,T}{b\,h\left(\lambda\,T_{\lambda max}\left(\sqrt{P}+1\right)^2-(\lambda-1)\,P\,T\right)}} \qquad \textbf{(5.7)}$$

where Ni_{giri} stands for the threshold functional response value for which no difference exists between aggressive interference and equal access strategies. Equation **5.7** obviates resource density. Thus, $Ni_{IIIcrit}$ denotes the point where aggressive interference and equal access functional responses intersect with respect to the critical resource density, N_{IIIt}. Implicitly, profitability for the equal access strategy exceeds that for the aggressive interference strategy at resource densities greater than N_{IIIt}.

Time spent on aggressive interference - Implications

Expressing time spent on aggressive interference (T_{λ}) in terms of other model parameters lends further insights into this cost.

Starting with the following premises:

(1) The time spent on aggressive interference or submissive interference behaviors precludes time for obtaining resources (e.g., Ts, Th, etc.).

(2) The difference between functional responses for individuals within *unrestricted* and *restricted* resource availability scenarios standardized by the maximum difference, $\frac{Ni-Ni_P}{Ni_{max}}$, ranges as a proportion from 0 to 1:

   a. The difference = 0 at N = 0 and at N → ∞ (i.e., lim Δ = 0 at N → ∞ at Ni = T/h);

   b. The maximum difference between *Ni* and Ni_P defines Ni_{max};

   c. The peak value of 1 for the difference corresponds with the resource density, N_{max}, for which time spent on aggressive interference is greatest ($i.e., T_{\lambda max}$).

Thus, the maximum proportion of time dedicated to aggressive interference occurs at resource density, N_{max}:

$$\frac{T_{\lambda max}}{T} \qquad \textbf{(5.8)}$$

So, at any level of resource availability the product of three terms specifies time dedicated to aggression, T_{λ} . The form of the T_{λ} curve which peaks at $T_{\lambda max}$ should mirror the forgoing normalized difference between individuals within *unrestricted* and *restricted* resource availability scenarios with respect to resource availability:

$$T_{\lambda} = \frac{Ni-Ni_P}{Ni_{Tmax}}\;T\left(\frac{T_{\lambda max}}{T}\right) \qquad \textbf{(5.9)}$$

Cancelling the terms for total time in equation **5.9** yields the same relationship inferred in equation **3.0** for specifying time spent on aggressive interference:

$$T_\lambda = \frac{Ni - Ni_P}{Ni_{Tmax}} \; T_{\lambda max}$$

Specifically, at any level of resource density (i.e., N), the time spent on aggressive interference equals $T_{\lambda max}$ scaled by the normalized difference between per capita functional response values for *unrestricted* exclusive access and *restricted* equal access consumers.

The time spent on aggressive interference should vary with certain key parameters that modulate the functional response of an aggressive consumer. Both consumer density (P) and leverage (λ) should help explain the time required for aggressive interference:

- Higher P ≈ higher $T_{\lambda max}$
- Higher λ ≈ lower $T_{\lambda max}$

The proportion of time spent on aggressive interference ($T_{\lambda max}$/T) can be exemplified by a function, $f(A)$, incorporating effects of P and λ:

1) $f(A) * [T * (\frac{Ni - Ni_P}{Ni_{max}})] = T_\lambda$, which varies dependently with N.
2) $f(A)$ equates to the maximum proportion of time spent on aggressive interference, or $f(A) = \frac{T_{\lambda max}}{T}$.
3) As the product of two proportional values, $\{f(A) * (\frac{Ni - Ni_P}{Ni_{max}})\}$ can also vary between 0 and 1:
    a. So, $f(A)$ is a function that expresses the proportion of time spent on aggressive interference in terms of related functional response parameters;
        i. $f(A)$ does not vary with resource availability, N;
        ii. $f(A)$ does vary with λ and P;
    b. $\frac{Ni - Ni_P}{Ni_{max}}$ varies between 0 and 1 with resource availability, N;
        i. The forgoing expression for T_λ applies to any type of functional response:
            1. assuming Ts, Th, and T_λ do not coincide.

The leverage function (f(A))

The proposed function $f(A)$ relates the counteracting effects of leverage (λ) and consumer density (i.e., P-1) on the functional response of a consumer exhibiting aggressive interference as leverage. Because λ reflects the efficacy of aggressive interference, it should vary inversely with time dedicated to such behavior. On the other hand, time dedicated to aggressive interference must increase with the density of contenders (i.e., P-1) within the ambit of the aggressive consumer.

The reciprocal exponential function (i.e., *exp*, raised to a negative power) fulfills the stipulation that the function, $f(A)$, varies between the limits 0 and 1:

$$\lim_{A \to \infty} e^{-A} = \lim_{A \to \infty} 1/e^A = 0$$
$$\lim_{A \to 0} e^{-A} = \lim_{A \to 0} 1/e^A = 1$$

The parameters λ and P affect $f(A)$ in the following manner:

(1) the leverage effect on $f(A)$ ranges from 1 when λ is ineffectual to 0 when λ is completely effective (i.e., T_λ = T at λ = 0; $T_\lambda = 0$ at λ = ∞); and
(2) the effect of P on $f(A)$ ranges from 0 at (P-1) = 0 (i.e., solitary consumer) to 1 at (P-1) = ∞ (i.e., T_λ = 0 at (P-1) = 0; T_λ = T at (P-1) = ∞);
(3) because $f(A) = (1 - e^{-A})$, $f(A) = 0$ at $e^{-A} = 1$, and $f(A) = 1$ at $e^{-A} = 0$.

So:

$$f(A) = \left(1 - e^{-\frac{(P-1)}{(c\lambda)}}\right) \qquad \textbf{(6.0)}$$

Where $A = \frac{(P-1)}{(c\,\lambda)}$. The scaling factor, c, transforms the joint effects of λ and P into a suitable form for reflecting $T_{\lambda max}$/T.

Furthermore, because:

$$f(A) = (1 - e^{-\frac{(P-1)}{(c\lambda)}}) = \frac{T_{\lambda max}}{T} \qquad \textbf{(6.1)}$$

then:

$$c = \frac{(1-P)}{\lambda \ln\left(1 - \frac{T_{\lambda max}}{T}\right)} \qquad \textbf{(6.2)}$$

$$\lambda = \frac{(1-P)}{c \ln\left(1 - \frac{T_{\lambda max}}{T}\right)} \qquad \textbf{(6.3)}$$

Note: Because both (1- P) and ln (1 - $T_{\lambda max}$/T) define negative values, both c and λ define positive values. And given both c and λ vary inversely with $T_{\lambda max}$ (i.e., a lower $T_{\lambda max}$ yields a higher (1- $T_{\lambda max}$/T) as well as a higher (i.e., not as negative) ln (1 - $T_{\lambda max}$/T) value), the maximum proportion of time dedicated to aggressive interference deceases with both c and λ.

Joint consumption within a group for a Type II functional response under sustained resource availability

Characterizing joint consumption by an aggressive agent within a group of consumers for a Type II functional response entails the synthesis of scenarios for the aggressive consumer and for the P-1 non-aggressive consumers. Firstly, the encounter rate is partitioned proportionately within the group, so that it comprises terms representing the aggressive agent as well as the P-1 other consumers within a *restricted* scenario.

Thus,

$$a = \left(\lambda \frac{a}{P}\right) + \left(a - \left(\lambda \frac{a}{P}\right)\right) \qquad \textbf{(6.4)}$$

For an aggressive consumer within a group setting, the encounter rate:

$$a_{\lambda} = \left(\lambda \frac{a}{P}\right) \qquad \textbf{(6.5)}$$

Rearrangement of the second term in **6.4** followed by division by P-1 yields the per capita encounter rate for an individual non-aggressive consumer:

$$a_{(P-1)} = \left(\frac{a\,(P-\lambda)}{(P-1)\,P}\right) \qquad \textbf{(6.6)}$$

So, the compound difference equation for the joint Type II functional response under a sustained *restricted* resource availability scenario:

$$Ne_{II(\lambda,P)} = \left(\left(\lambda \frac{a}{P}\right) N\left(T - \left(h\, Ni_{II\lambda} + T_{\lambda}\right)\right)\right) + \left(\left(\frac{a(P-\lambda)}{(P-1)P}\right) N\left((P-1)\,T - \left(h\left(Ne_{II(\lambda,P)} - Ni_{II,\lambda}\right) + T_{\lambda}\right)\right)\right) \qquad \textbf{(6.7)}$$

Where $Ni_{II\lambda}$ represents consumption by the aggressive consumer, T_{λ} denotes time dedicated to interference behavior, and $Ne_{II(\lambda,P)}$ represents total consumption by the group, including the aggressive consumer. Furthermore, T_{λ} is spread equally among the P-1 non-aggressive consumers to account for the deficit in time available for consumption. The left-hand term in equation **6.7** does not differ from the isolated difference equation for the aggressive agent in equation **1.8**; whereas differences between the right-hand term of equation **6.7** and equation **1.6** for the P-1 other consumers include effects of aggressive interference on encounter rates, reduced time available for consumption, and the specification of P-1 rather than P consumers (i.e., excluding the aggressive consumer).

Solving equation **6.7** for $Ne_{II(\lambda,P)}$ yields the following definitive equation:

$$Ne_{II(\lambda,P)} = \frac{a\,N(T_{\lambda}\,(-2\,\lambda+\lambda\,P+P)+P\,(h\,(\lambda-1)\,Ni_{II\lambda}-P\,T+T))}{-a\;\lambda\,h\,N+P\,(a\,h\,N-1)+P^2} \qquad \textbf{(6.8)}$$

Conversely solving equation **6.7** for $Ni_{II\lambda}$ yields the following definitive equation for obtaining $Ni_{II\lambda}$:

$$Ni_{II\lambda} = \frac{a\,N(T_{\lambda}\,(-2\,\lambda+\lambda\,P+P)+h\,P\,Ne_{II(\lambda,P)}-h\,\lambda\,Ne_{II(\lambda,P)}+P^2(-T)+P\,T)+(P-1)\,P\,Ne_{II(\lambda,P)}}{a\,h\,(\lambda-1)\,N\,P} \qquad \textbf{(6.9)}$$

For any sustained level of resource availability (N) and set of model parameters, expected consumption by the aggressive consumer as well as by the non-aggressive consumers can be obtained and compared to actual values as a test of the model. Estimation of expected values for unknown model parameters based on experiments can further test equation **6.7**.

Joint consumption within a group for a Type III functional response under sustained resource availability

As with the Type II functional response, characterizing joint consumption by an aggressive agent within a group of consumers for a Type III functional response entails the synthesis of scenarios for the aggressive consumer and for the P-1 non-aggressive consumers. For this composite scenario involving sustained resource availability, the dynamic encounter rate, a=bN, would need to be partitioned proportionately within the group. Thus, the dynamic encounter rate (bN) comprises terms for the aggressive agent as well as for the P-1 other consumers within a *restricted* scenario.

Thus, $$a = bN = \left(\lambda \frac{bN}{P}\right) + \left(bN - \left(\lambda \frac{bN}{P}\right)\right) \qquad \textbf{(7.0)}$$

For an aggressive consumer within a group setting, the encounter rate:

$$b_{\lambda}N = \left(\lambda \frac{bN}{P}\right) \qquad \textbf{(7.1)}$$

When parameters b, λ, N, and P are positive:

$$b = \left(\lambda \frac{b}{P}\right) + \left(\frac{b\,(P-\lambda)}{P}\right) \qquad \textbf{(7.2)}$$

Rearrangement of the second term in **7.0** followed by division by P-1 yields the per capita encounter rate for an individual non-aggressive consumer:

$$b_{(P-1)}N = \left(\frac{bN\,(P-\lambda)}{(P-1)\,P}\right) \qquad \textbf{(7.3)}$$

So, the compound difference equation for the joint Type III functional response under a sustained *restricted* resource availability scenario:

$$Ne_{III(\lambda,P)} = \left(\left(\lambda\ \frac{bN}{P}\right) N\left(T - (h\,Ni_{III\lambda} + T_\lambda)\right)\right) + \left(\left(\frac{b\,N\,(P-\lambda)}{(P-1)\,P}\right) N\left((P-1)\,T - \left(h\left(Ne_{III\,(\lambda,P)} - Ni_{III\lambda}\right) + T_\lambda\right)\right)\right) \qquad \textbf{(7.4)}$$

Where $Ni_{III\lambda}$ represents consumption by the aggressive consumer, T_λ denotes time dedicated to interference behavior, and $Ne_{III(\lambda,\,P)}$ represents total consumption by the group, including the aggressive consumer. Furthermore, T_λ is spread equally among the P-1 non-aggressive consumers to account for the deficit in time available for consumption. The left-hand term in equation **7.4** does not differ from the isolated difference equation for the aggressive agent in equation **4.3**; whereas differences between the right-hand term of equation **7.4** and equation **3.9** for the P-1 other consumers include effects of aggressive interference on encounter rates, reduced time available for consumption, and the specification of P-1 rather than P consumers (i.e., excluding the aggressive consumer).

Solving equation **7.4** for $Ne_{III(\lambda,P)}$ yields the following definitive equation:

$$Ne_{III(\lambda,P)} = \frac{b\,N^2(-\,T_\lambda\,\lambda\,(P-2) + T_\lambda\,(P-1)\,P + h\,\lambda\,P\,Ni_{III\lambda} - (P-1)\,P\,(h\,Ni_{III\lambda} + T) + \lambda\,(P-2)\,T)}{b\,h\,N^2\,(P-1)(\lambda-P) - P} \qquad \textbf{(7.5)}$$

For any sustained level of resource availability (N) and set of model parameters, expected consumption by the aggressive consumer as well as by the non-aggressive consumers can be obtained and compared to actual values as a test of the model. Estimation of expected values for unknown model parameters based on experiments can further test equation **7.4**.

Joint consumption within a group for a Type II functional response under depleted resource availability

Consumption by an aggressive agent within a group often proceeds during diminishing resource availability, formally known as resource depletion (Rosenbaum and Rall 2018). While often observed under experimental conditions, resource depletion should also frequently occur under natural conditions. Because the rate of consumption depends on resource availability, under resource depletion consumption decreases nonlinearly and continuously with time and resource density (Rogers 1972). Ordinary differential equation (ODE) methods can resolve the ensuing dynamic functional response under resource depletion (Rosenbaum and Rall 2018). Instead of a static expected rate of consumption under a sustained resource availability scenario, the resource depletion scenario integrates consumption over a specific period marked by known starting and ending resource densities.

An analytical solution to ODE known as the Rogers' Random Predator Equation (RRPE) describes the Type II Functional Response under a depleted resource availability scenario (Royama 1971; Rogers 1972):

$$Ne = N_0\left(1 - exp\left(a\,(Ne\,h - TP)\right)\right) \qquad \textbf{(7.6)}$$

where Ne signifies the cumulative consumption realized at the end of an observation period, and N_0 denotes the starting resource density. A practical method for explicitly solving the RRPE employs the Lambert W function, also referred to as the product logarithm function (henceforth the product log function) (Rosenbaum and Rall 2018). The generalized product log function, $f(w) = we^w$, specifies the product of any complex number, w, and the exponential function, e^w, raised to the power of the same complex number. In terms of z and w, $we^w = z$. The product log function has been used to describe various dynamic biological processes, including population growth (Corless et al. 1996), epidemiology (Lehtonen 2015), functional responses of predators and parasitoids (Arditi 1983), and microhabitat-related variability in the functional responses of crabs (Lipcius and Hines 1986). Similarly, the functional response involving an aggressive consumer within a group under resource depletion be amenable to the product log function.

Equation **7.7** specifies the Type II functional response expressed in RRPE form for P consumers assuming *unrestricted* encounter under a resource depletion scenario:

$$Ne_{II(P)d} = N\left(1 - exp\left(a\,(Ne_{II(P)d}\,h - P\,T)\right)\right) \qquad \textbf{(7.7)}$$

The following product log function estimates the solution for equation **7.7**:

$$Ne_{II(P)d} \approx \frac{a\,h\,N - W(a\,e^{a\,h\,N - a\,P\,T})\,h\,N}{a\,h} \qquad \textbf{(7.8)}$$

In contrast, equation **7.9** specifies the RRPE when expressed as per capita consumption within a group of P consumers assuming *restricted* encounter under a resource depletion scenario:

$$Ni_{II(P)d} = N\left(1 - exp\left(\frac{a}{P}\left(Ni_{II(P)d}\,h - P\,T\right)\right)\right) \qquad \textbf{(7.9)}$$

An alternative form of equation **7.9**:

$$Ni_{II(P)d} = N\left(1 - exp\left(a\left(Ni_{II(P)d}\,h - P\,T\right)\right)/P\right) \qquad \textbf{(8.0)}$$

The estimated product log function solution for equations **7.9** and **8.0**:

$$Ni_{II(P)d} \approx \frac{a\,h\,N - P\,W\left(\frac{a\,e^{(a\,h\,N)/P - a\,T}\,h\,N}{P}\right)}{a\,h} \qquad \textbf{(8.1)}$$

Equation **8.1** provides a reference condition for per capita consumption within a group of P consumers assuming *restricted* encounter under a resource depletion scenario.

Recalling, the joint functional response assuming *restricted* encounter under a sustained resource availability scenario combines terms for the aggressive agent and for P-1 other consumers (i.e., equation **6.7**). Accordingly, equation **8.2** gives the RRPE equation for an aggressive agent and P-1 other consumers assuming *restricted* encounter under a resource depletion scenario:

$$Ne_{II(\lambda,P)d} = N\left(1 - exp\left(\left(\lambda\frac{a}{P}\right)\left(h\,Ni_{II(\lambda)d} - (T - T_\lambda)\right) + \left(\left(\frac{a(P-\lambda)}{(P-1)P}\right)\left(h\left(Ne_{II(\lambda,P)d} - Ni_{II(\lambda)d}\right) - (P-1)\,T + T_\lambda\right)\right)\right)\right) \qquad \textbf{(8.2)}$$

Given the initial resource density, N, and a set of parameter values, solutions of equation **8.2** yield expected consumption by the aggressive agent ($Ni_{II(\lambda)d}$) as well as total consumption ($Ne_{II(P)d}$) (Fig. 6). Solving equation **8.2** given $Ne_{II(P)d}$ provides a solution for the aggressive agent:

$$Ni_{II(\lambda)d} = \left(\frac{-2\,a\,T_\lambda\,\lambda + a\,T_\lambda\,\lambda\,P + a\,T_\lambda\,P + a\,h\,P\,Ne_{II(\lambda,P)d} - a\,h\,\lambda\,Ne_{II(\lambda,P)d} - a\,P^2\,T + a\,P\,T - P^2\log\left(-\frac{Ne_{II(\lambda,P)d} - N}{N}\right) + P\log\left(-\frac{Ne_{II(\lambda,P)d} - N}{N}\right)}{(a(-h\,\lambda + h\,P + \lambda - \lambda P))}\right) \qquad \textbf{(8.3)}$$

Solving equation **8.2** given $Ni_{II(\lambda)d}$ also yields the product log equation specifying total consumption by the aggressive agent and the P-1 other consumers under resource depletion:

$$Ne_{II(\lambda,P)d} = \frac{1}{a\,h\,(P-\lambda)}\left(P^2\left(-W_n\left(\frac{a\,e^{\left(\frac{a(T\,P^2 - T_\lambda\,P - h\,N\,P - T\,P + h\,Ni_{II(\lambda)d}\,P - T_\lambda\,\lambda\,P - Ni_{II(\lambda)d}\,\lambda\,P + 2\,T_\lambda\,\lambda + h\,N\,\lambda - h\,Ni_{II(\lambda)d}\,\lambda + Ni_{II(\lambda)d}\,\lambda)}{(P-1)P}\right)h\,N\,(P-\lambda)}}{(P-1)P}\right)\right) + P\,W_n\left(\frac{a\,e^{\left(\frac{a(T\,P^2 - T_\lambda\,P - h\,N\,P - T\,P + h\,Ni_{II(\lambda)d}\,P - T_\lambda\,\lambda\,P - Ni_{II(\lambda)d}\,\lambda\,P + 2\,T_\lambda\,\lambda + h\,N\,\lambda - h\,Ni_{II(\lambda)d}\,\lambda + Ni_{II(\lambda)d}\,\lambda)}{(P-1)P}\right)h\,N\,(P-\lambda)}}{(P-1)P}\right) - a\,\lambda\,h\,N - a\,h\,N\,P\right) \qquad \textbf{(8.4)}$$

Consumption by the P-1 other consumers can then be obtained by subtraction (i.e., $Ne_{II(\lambda,P)d}$ - $Ni_{II(\lambda)d}$), followed by division by P-1 to obtain the per capita cumulative consumption for non-aggressive consumers at time T under resource depletion. Equation **8.2** can also provide solutions for unknown parameters, such as the leverage coefficient, λ.

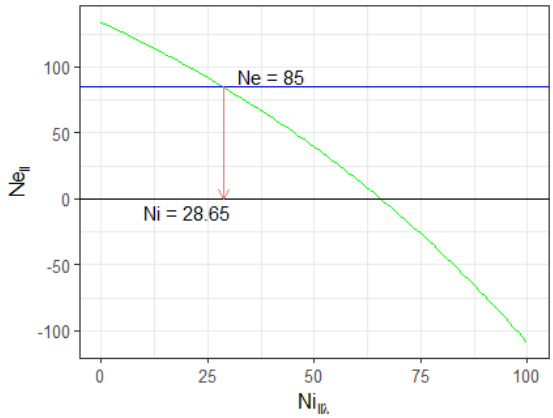

Figure 6: Joint consumption within a group for a Type II functional response under depleted resource availability. Graphic solution of the product log function for expected consumption while resource abundance is progressively depleted, where the total consumption by the entire group ($Ne_{II(P)}$) is 85 and consumption by the aggressive agent ($Ni_{II(\lambda)}$) is 28.65. For this depletion curve, a = 0.2, h = 0.09, P = 5, T = 4, λ = 3, and T_λ ,= 0.4. Per capita consumption by the P-1 other consumers, $Ni_{II(P)}$ = ($Ne_{II(P)}$ - $Ni_{II(\lambda)}$)/P-1, or (85-28.65)/4 = 14.09.

Joint consumption within a group for a Type III functional response under depleted resource availability

Because the Type III functional response involves a continuously changing resource-dependent encounter rate, Rosenbaum and Rall (2018) presented a corrected product log function for estimating the Type III functional response under resource depletion, based on a simplified form of the version by Okuyama and Ruyle (2011). Consequently, the RRPE equation yielding the correct log product function for the Type III functional response under a resource depletion scenario is analogous to and consistent with the RRPE equation for the Type II functional response:

$$Ne_{III(P)d} = N\left(1 - exp\left(bN\left(Ne_{III(P)d}\,h - P\,T\right)\right)\right) \qquad \textbf{(8.5)}$$

The product log function solution of the Type III functional response for P consumers assuming *unrestricted* encounter under a resource depletion scenario:

$$Ne_{III(P)d} \approx \frac{b\,h\,N^2 - W\left(b\,h\,N^2\,e^{b\,N(h\,N - P\,T)}\right)}{b\,h\,N} \qquad \textbf{(8.6)}$$

Equation **8.6** compares favorably with the product log function given in Rosenbaum and Rall (2018) for the Type III functional response as expressed for P consumers.

In contrast, equation **8.7** gives the per capita RRPE equation for a group of P consumers assuming *restricted* encounter under a resource depletion scenario:

$$Ni_{III(P)d} = N\left(1 - exp\left(\frac{b\,N}{P}\left(Ni_{III(P)d}\,h - P\,T\right)\right)\right) \qquad \textbf{(8.7)}$$

An alternative form of equation **8.6** expressed for a group of P consumers assuming *restricted* encounter under a resource depletion scenario:

$$Ni_{III(P)d} = N\left(1 - exp\left(\frac{b\,N}{P}\left(Ni_{III(P)d}\,h - P\,T\right)\right)/P\right) \qquad \textbf{(8.8)}$$

The product log function solution for equations **8.7** and **8.8**:

$$Ni_{III(P)d} \approx N - \frac{P\,W\left(\frac{b\,e^{(b\,N(h\,N - P\,T)/P}\,h\,N^2}{P}\right)}{b\,N\,h} \qquad \textbf{(8.9)}$$

Equation **8.9** provides a reference condition for per capita consumption within a group of P consumers assuming *restricted* encounter under a resource depletion scenario.

Recalling, the joint functional response assuming *restricted* encounter under a sustained resource availability scenario combines terms for the aggressive agent and for P-1 other consumers (i.e., equation **7.4**). Accordingly, equation **9.0** gives the RRPE equation for an aggressive agent and P-1 other consumers assuming *restricted* encounter under a resource depletion scenario:

$$Ne_{III(\lambda,P)d} = N\left(1 - exp\left(\left(\lambda\frac{b\,N}{P}\right)\left(h\,Ni_{III(\lambda)d} - (T - T_\lambda)\right) + \left(\left(\frac{b\,N(P-\lambda)}{(P-1)P}\right)\left(h\left(Ne_{III(\lambda,P)d} - Ni_{III(\lambda)d}\right) - (P-1)\,T + T_\lambda\right)\right)\right)\right) \qquad \textbf{(9.0)}$$

Given the initial resource density, N, and a set of parameter values, solutions of equation **9.0** yield expected consumption by the aggressive agent ($Ni_{III(\lambda)d}$) as well as total consumption ($Ne_{III(P)d}$). Solving equation **9.0** given $Ne_{III(P)d}$ provides a solution for the aggressive agent:

$$Ni_{II(\lambda,P)d} = \qquad \textbf{(9.1)}$$

$$\left(\frac{-b\,T_\lambda\,\lambda - b\,T_\lambda\,\lambda N + b\,T_\lambda\,\lambda\,N\,P + b\,T_\lambda\,P + b\,h\,P\,Ne_{III(\lambda,P)d} - b\,h\,\lambda N\,Ne_{III(\lambda,P)d} - b\,\lambda N\,P\,T + b\,\lambda N\,T - b\,P^2\,T + b\,\lambda\,P\,T + b\,P\,T - b\,\lambda\,T - P^2\log\left(-\frac{N_{III(\lambda,P)d} - N}{N}\right) + P\log\left(-\frac{N_{III(\lambda,P)d} - N}{N}\right)}{(b(-h\,\lambda + h\,P + \lambda N - \lambda N\,P))}\right)$$

When given $Ni_{III(\lambda)d}$, equation **9.0** also yields the product log equation specifying the total cumulative consumption under resource depletion. Consumption by the P-1 other consumers can be obtained by subtraction (i.e., $Ne_{III(\lambda,\,P)d}$ - $Ni_{III(\lambda)d}$), followed by division by P-1 to obtain the per capita consumption for non-aggressive consumers at time T under resource depletion. Finally, equation **9.0** can provide solutions for unknown parameters, such as the leverage coefficient, λ.

Discussion

The proposed functional response models explicitly integrate hypothetical costs and benefits of aggressive interference within the E/T paradigm of OFT. These models differ from other functional response models, including those integrating mutual interference (Novak and Stouffer 2021) and interspecific competition (Abrams 1980). They also contrast with functional response models employing the predator/prey ratio as a means of accounting for consumer-dependent effects on predator population dynamics (Abrams and Ginzburg 2000). In the proposed models, aggressive interference behavior directed at other consumers within a group act as leverage to increase the rate of resource consumption above the level conferred by a premise of equal access, as a standard of comparison. Consequently, asymmetric effects of leverage increase the rate of gain for aggressive agents while suppressing the realized rate of gain for subordinate consumers. Within most functional response models involving interference, the behavioral interaction applies mutually and increases with consumer density as a mass action effect (Novak and Stouffer 2021). Earlier asymmetric aggressive interference models for which dominant consumers prevail over subordinates do not fall within the functional response rubric. Instead, such aggressive interference models typically employ game theory (SirotClick or tap here to enter text. 2000; Dubois and Giraldeau 2005). Another kind of asymmetric aggressive interference model uses an individual based procedure within which optimal decision rules mediate behavioral interactions involving kleptoparasitism (Stillman et al. 1997). Earlier models also make specific predictions under prescribed conditions. For example, they variously predict an inverse relationship between aggression and resource availability (Sirot 2000), a hump-shaped frequency of aggression with increasing group size (Dubois and

Giraldeau 2005), and the threshold consumer density for which the net benefit of aggression should be zero (Stillman et al. 1996).

Importantly, the proposed functional response models yield explicit falsifiable predictions, including the expected resource density at which aggressive interference should be maximal, and the threshold resource density and functional response value above which aggressive interference should cease to be effective. In addition, the proposed models specify expected differences in consumption between aggressive and nonaggressive consumers for both sustained and depleted resource scenarios. Whereas resource gain within the game theory-derived aggressive interference model accrues as the outcome of multiple probabilistic one-to-one conflicts involving costs in time and energy (Sirot 2000), the effect of leverage within the proposed functional response models concurrently deters multiple contenders while distracting the aggressor from searching, pursuing, or consuming resources. Consequently, the intensity of aggression peaks at some intermediate level of resource availability within the proposed functional response models. In contrast, aggressive behavior varies inversely with resource availability within game-theory models of aggressive interference (Sirot 2000), in agreement with classic competition theory (Fattorini et al. 2018). The clear distinction in the expression of aggression with respect to resource availability provides a means to discern which model applies for a specific situation.

The efficacy of leverage within the proposed aggressive interference models should vary in conjunction with risk associated with specific traits evolved for intimidation. Similarly, the conceptual basis of the "ecology of fear" subfield envisages how the threat of predation affects prey behavior (Brown et al. 1999). Such indirect effects of predation extensively influence the trophic dynamics within trophic cascades. For example, predation risk induced by a top predator produces non-consumptive effects (NCE) on a basal prey via suppression of feeding by intermediate predators (Peacor et al. 2020; Schweiss and Rakocinski 2020). Analogously, the effect of aggression could alleviate predation pressure by detracting from the time available for resource consumption by both aggressive and subordinate consumers.

The demands of other consumers constrain the rate of consumption an aggressive consumer can reach within the proposed aggressive interference functional response models. When unconstrained, the rate of consumption reaches that afforded an individual by the level of sustained resource availability, notwithstanding other consumers. The volume/area potentially under control of the aggressive consumer and from which it may garner resources defines its ambit, or 'area of discovery.' For a fixed ambit, space becomes the de facto resource when control by the aggressor extends to territorial defense. However, the ambit typically moves about with the aggressive consumer as it searches for resources within the group setting. Although other consumers within the ambit may vary from moment to moment, the mean number of overlapping consumers will stabilize within a suitable period. Consequently, leverage can simultaneously suppress multiple other consumers within the ambit. Conversely, an implicit trade-off with multiple contenders means some consumers may benefit while the aggressor actively suppresses others. These qualifying features of the proposed functional response models contrast with the game-theory based model involving consecutive one-to-one contests (Sirot 2000). Which model applies depends upon the circumstances.

Various heuristic assumptions can limit the applicability of the proposed aggressive interference functional response models. Just like other functional response models, time spent on dispensing or evading aggression is exclusive from time spent for consumption. Also, the models assume fixed leverage with respect to P and resource availability. Encounter rate or handling time parameters prove unrealistic under certain conditions requiring flexible parameters (Abrams 1990; Abrams 2010; Okuyama 2010; Okuyama 2012; Gibert and DeLong 2015). Indeed, the standard Type III functional response model involves a dynamic encounter rate to account for learning or other skills with respect to resource availability (Holling 1966). Likewise, handling time may decrease with respect to resource availability (Abrams 1990) or vary among individual consumers (Hartley et al. 2019). Where tests of the proposed simpler models reveal faulty assumptions, modified aggressive interference functional response models can integrate dynamic parameters in the interest of realism. For example, leverage could vary with respect to resource availability or contender density. Learning might improve leverage by decreasing the time dedicated to aggressive interference while increasing avoidance by subordinate consumers (Stillman et al. 1997).

The proposed aggressive interference functional response models yield several specific predictions amenable to falsification. Definitive tests could entail replicated experiments involving quantification of consumption and aggression by a focal dominant subject together with two or three subordinate consumers within the same size class. Experiments could test either general or more specific predictions. Indeed, an earlier experiment employing a dominance hierarchy of bluegill sunfish (*Lepomis macrochirus*) supported the general expectation that the frequency of aggressive interference followed a hump-shaped curvilinear distribution with respect to depleting food availability (Rakocinski et al. 1983). Recorded observations of per capita consumption using video would potentially test more specific predictions. Uncertainty estimates for parameters would involve replicated observations made at various sustained levels of resource availability. Key variables to consider include the rate of consumption by the aggressive consumer, as well as rates of consumption for the P-1 subordinate consumers. In addition, estimates of handling time (h) encounter rate (a) and T_λ would facilitate estimation of Tf, Ts and T. Comparing the functional response of the aggressive consumer with the per capita equal access functional response for unaggressive consumers would facilitate the estimation of lambda (λ). Effects of satiation or other extraneous variables might affect the parameters via variable motivation levels of the subjects.

Outcomes from aggressive interference experiments can vet various aspects of the proposed models. Replication would enable evaluation of parameter estimates according to associated margins of statistical error. For example, replicated observations at various sustained resource densities could help find whether $T_{\lambda max}$ occurs at the resource density for which the difference is greatest between the functional responses of the aggressive consumer and the per capita consumer with equal access. Similarly, one could resolve whether aggression ceases at the expected level of resource availability where the functional response of the aggressive consumer is equivalent with that of the per capita consumer. Using depleting resource availability could help test whether cumulative consumption by aggressive consumers agrees with expectations based on the proposed depletion models. Experiments can also test whether alternative hypotheses like mutual interference or aggressive interference models better describe functional response data.

Although models can help explain phenomena by ruling out alternative explanations (Ylikoski and Aydinonat 2014), simplified mathematical relationships cannot idealize complex natural phenomena. For example, while the proposed deterministic models specify the cumulative time dedicated to aggression integrated over the period spent consuming resources, they do not characterize the dispersion of aggressive and consumptive behaviors in real time. Presumably, the aggressor would perform tactically with respect to the dispersion of resources and consumers. Also, how effectively coupled stimuli induce aggressive interference behavior for accruing resources depends on how appropriately the stimuli elicit the behavioral response (Bindra 1978, Zaman et al. 2024). Natural selection should favor the strategic expression of aggressive behavior to enhance resource gain due to a direct connection with fitness (Georgiev et al. 2013). However, natural selection also favors other risk factors that could reinforce the expression of aggressive interference. Consumers at lower positions within a dominance hierarchy face greater risk of mortality from compounded effects of aggressive interference, due to combined effects of slower growth, greater injury, and higher predation. Such auxiliary effects would reinforce selection for effectively wielding leverage through aggressive interference to maximize resource gain. Ensuing density-dependent effects of aggressive interference also include spacing of consumers, mediating reproductive outputs, and regulating population structures.

The proposed models of aggressive interference define functional responses for which one dominant consumer elevates its intake of resources by aggressively interfering with P-1 unaggressive consumers via equilaterally distributed leverage with equal access to resources. These simplified scenarios exemplify plausible straightforward dominance-subordinate configurations. Groups within natural settings involve complex hierarchies of consumers displaying aggression within the context of variable resource availability. One can imagine more realistic models describing complex hierarchical configurations using the same precepts as those in this paper. Fully developed dominance hierarchies form cascading networks of behavioral interactions (Cumming 2016; Fattorini et al. 2018). The overarching trait of body size often confers position-related polarity within a dominance hierarchy; thus, leverage within a group should vary in conjunction with body size. However, aggressive interference may

also decrease with increasing disparity in body size (Woodward et al. 2005), due to corresponding non-overlap in resource requirements. Furthermore, greater foraging skill as reflected by lower handling time can favor higher position within dominance hierarchies, despite body-size disparities (Hartley et al. 2019).

Although one could formulate more complex aggressive interference models using the same approach as in this paper, added complexity would prove computationally challenging. Instead, a general systematic approach for specifying diverse pairwise interactions might employ matrix calculus along with optimization methods such as linear and nonlinear programming. Such an approach would also be conducive to extended models based on relaxed parameter assumptions. For example, such models could incorporate flexible leverage coefficients between different pairs of consumers within a dominance hierarchy. Matrix-based methods could also aid in the formulation of stochastic aggressive interference functional response models by accommodating variance/covariance structures for parameters, etc. Earlier stochastic forms of classical functional response models show some approaches (Gilioli et al. 2008; Van Der Meer and Smallegange 2009; Palamara et al. 2021). In addition to consumption, more realistic models could regard resource availability and aggressive interference as stochastic processes. For example, an exemplary study used maximum likelihood for parameter estimation within the Beddington functional response model of mutual interference among a small finite number of predators (Van Der Meer and Smallegange 2009).

Conclusions

The proposed aggressive interference functional response models reveal some testable predictions:

1) If the difference between the functional responses for a solitary consumer with exclusive access and an average consumer within a group with equal access to a restricted resource drives the intensity of aggressive interference, the maximum intensity of aggressive behavior should occur at an intermediate resource density equal to $\frac{\sqrt{P}}{a\,h}$ for a Type II, or $\frac{\sqrt[4]{P}}{\sqrt{b}\sqrt{h}}$ for a Type III functional response.

2) The resource density below which aggressive interference should not gainfully serve as leverage occurs at explicitly defined thresholds for Type II and Type III functional responses.

3) The functional response value below which aggressive interference should not gainfully provide leverage occurs at explicitly defined thresholds for Type II and Type III functional responses.

4) The maximum proportion of time dedicated to aggressive interference (i.e., $(\frac{T_{\lambda max}}{T})$) can be redefined in terms of leverage and consumer density and tested for a more mechanistic interpretation.

5) Using appropriately normalized encounter rates, equations for joint consumption by an aggressive agent and P-1 other consumers under sustained resource availability can be constructed for Type II and Type II functional responses.

6) Using appropriately normalized encounter rates, RRPE equations for joint consumption by an aggressive agent and P-1 other consumers under depleted resource availability can be constructed for Type II and Type II functional responses. The RRPE equations yield product log solutions for expected consumption by the aggressive agent and for the entire group under resource depletion.

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