Ontogenesis

Eco-evolutionary perspective on life history complexity

Hin, V.

Creative Commons License (see https://creativecommons.org/use-remix/cc-licenses):
Other

Citation for published version (APA):
Chapter 4

Cannibalism and Intraguild Predation
Community Dynamics: Coexistence, Competitive Exclusion and the Loss of Alternative Stable States

Benjamin J. Toscano
Vincent Hin
Volker H. W. Rudolf

Accepted for publication by The American Naturalist on 09 June 2017
http://www.journals.uchicago.edu/toc/an/current
ABSTRACT

Predators often exert strong top-down regulation of prey, but in many systems, juvenile predators must compete with their future prey for a shared resource. In such life-history intraguild predation (LHIGP) systems, prey can therefore also regulate the recruitment and thus population dynamics of their predator via competition. Theory predicts that such stage-structured systems exhibit a wide range of dynamics including alternative stable states. Here we show that cannibalism is an exceedingly common interaction within natural LHIGP systems that determines what coexistence states are possible. Using a modeling approach that simulates a range of ontogenetic niche shift scenarios along a productivity gradient, we demonstrate that only if the predator is competitively dominant can cannibalism promote coexistence by allowing prey to persist. If the prey is competitively dominant, cannibalism instead results in competitive exclusion of the predator and the loss of potential alternative stable states. Further, predator exclusion occurs at low cannibalistic preference relative to empirical estimates and is consistent across LHIGP systems in which the predator undergoes a complete diet shift or diet broadening over ontogeny. Given that prey is frequently competitively dominant in natural systems, our results demonstrate that even weak cannibalism can inhibit predator persistence, prompting exploration of mechanisms that reconcile theory with the common occurrence of such interactions in nature.
Conspecific individuals that vary in size or stage often differ in their ecological (i.e., functional) roles (Werner and Gilliam, 1984). For example, in many predatory species, individuals either switch resources or add resources to their diet as they develop (Rudolf and Lafferty, 2011; Rudolf et al., 2014; Werner and Gilliam, 1984). Predator populations can thus be simultaneously regulated by stage-specific interactions with different species. Furthermore, these shifts in interspecific interactions among stages are generally associated with concurrent shifts in intraspecific interactions (Miller and Rudolf, 2011). Accordingly, structured systems exhibit a wider range of dynamics relative to unstructured systems, including alternative stable states (De Roos and Persson, 2013; Miller and Rudolf, 2011). In particular, which state or dynamics occur depends on the relative strength of different stage-specific interactions. Thus any process, biogenic or anthropogenic, that shifts population size or stage distribution will also alter the relative strength of these interactions, and therefore the capacity of predator-prey systems to transition between alternative stable states. Accordingly, the processes that govern predator-prey coexistence may fundamentally differ for structured versus unstructured predator-prey systems.

The dramatic ecological effects of stage-specific interactions are apparent in a widespread interaction module known as life-history intraguild predation (LHIGP) (Abrams, 2011; Hin et al., 2011; Pimm and Rice, 1987; Rudolf, 2007; Toscano et al., 2016; Walters and Kitchell, 2001). LHIGP occurs when juvenile predators compete with their future prey (i.e., an intermediate consumer, hereafter ‘consumer’) for a shared resource (figure 4.1A). Thus, LHIGP allows for competitive dynamics in addition to predation. Within LHIGP systems, juvenile and adult predators may feed on separate resources (i.e., a complete diet shift: figure 4.1A; Hin et al., 2011; Toscano et al., 2016) or adults may continue to feed on the juvenile resource, thereby broadening their diet over ontogeny (figure 4.1B; Rudolf, 2007; Van de Wolfshaar et al., 2006). Due to the opposing forces of competition and predation on different life-history stages, LHIGP systems are predicted to exhibit alternative stable states: when consumers are competitively dominant, strong competition between consumers and juvenile predators can eliminate predator recruitment to the adult stage (i.e., juvenile competitive bottleneck), driving predator exclusion (a consumer-resource equilibrium: Hin et al., 2011; Walters and Kitchell, 2001). Alternatively, adult predators can regulate consumers, facilitating their own recruitment and persistence (a predator-present equilibrium: Hin et al., 2011; Van de Wolfshaar et al., 2006). Consequently, the long-term trajectory of LHIGP systems is potentially sensitive to predator stage structure: a preponderance of juveniles in LHIGP should free consumers from top-down control leading to predator exclusion, while a preponderance of adults and resulting top-down control should promote predator persistence.
Cannibalism (i.e. intraspecific predation) occurs in most animal taxa (Fox 1975; Polis 1981; Polis and Myers 1985) with major ramifications for both population dynamics and size/stage structure (Claessen et al. 2000, 2004; Ohlberger et al. 2012a; Persson et al. 2003; Rudolf 2007, 2008). Within LHIGP systems, juvenile predators and consumers must co-occur in order to compete for a common resource, and thus adult predators frequently encounter both conspecific and heterospecific prey (Byström et al. 2013; Rudolf 2007). Furthermore, empirical studies indicate that during such encounters, LHIGP predators often preferentially consume conspecific versus heterospecific prey (figure 4.2). Specifically, in a literature review of 65 experiments in which invertebrate and vertebrate predators were simultaneously offered both conspecific and heterospecific prey (figure 4.2 see caption for details), only 4 experiments failed to measure some degree of cannibalism (i.e. Manly’s $\alpha = 0$), while 31 experiments demonstrated cannibalistic preference (i.e. Manly’s $\alpha > 0.5$). These preference estimates come from a diversity of predator taxa (crustaceans, arachnids, insects, fish, amphibians, reptiles), all of which exhibit ontogenetic diet shifts (Werner and Gilliam 1984) and thus presumably engage in LHIGP interactions in nature. The ubiquity of cannibalism and commonness of cannibalistic preference within stage-structured predator-prey systems suggests that cannibalism must be incorporated into current

**Figure 4.1** — Life-history intraguild predation (LHIGP) with cannibalism: complete ontogenetic diet shift (panel A) and ontogenetic diet broadening (panel B) scenarios. Solid arrows depict feeding relationships while dotted lines depict demographic transitions between predator stages (maturation and reproduction). Adult predators ($P_a$) feed solely on consumers ($C$) (complete diet shift: panel A), or feed equally on consumers and the resource ($R$) (diet broadening: panel B). In both scenarios, juvenile predators ($P_j$) compete with consumers for the resource and adult predators cannibalize juveniles.
Figure 4.2 – Cannibalistic preference estimates ($n = 65$; measured as Manly’s $\alpha$, see Chesson (1978) for calculation) from empirical studies ($n = 19$; references listed in appendix 4.B). Manly’s $\alpha$ is a measure of the probability that a conspecific or heterospecific prey item is selected when both prey types are offered simultaneously. Manly’s $\alpha$ scales from 0 to 1 with $\alpha = 0.5$ indicating no preference (marked with vertical dashed line), and $\alpha < 0.5$ and $\alpha > 0.5$ indicating cannibalistic aversion or preference, respectively. Prey depletion was accounted for in calculating Manly’s $\alpha$ according to Chesson (1978) in studies in which depletion occurred (as opposed to prey replacement). When Manly’s $\alpha$ or data necessary to calculate Manly’s $\alpha$ were not reported directly, a plot digitizer (Web Plot Digitizer 3.8) was used to extract relevant data from graphs. Empirical studies were found with a literature search conducted on March 2017 using Google Scholar. Search terms were: “cannibalistic” or “cannibalism” combined with “preference”, “choice”, “heterospecific”, “interspecific”, “Manly’s” and “Chesson”.

LHIGP theory to better understand and predict natural LHIGP dynamics. For example, a recent study using freshwater zooplankton (Toscano et al. 2016) demonstrates a juvenile competitive bottleneck and the alleviation of this bottleneck by adult predators: the precise interactions predicted to drive alternative stable states within LHIGP systems (Toscano et al. 2016). This study further shows that cannibalism modifies
the strength and qualitative outcomes of these interactions (Toscano et al. 2016). For this empirical LHIGP system (Toscano et al. 2016) and many others (figure 4.2), we currently lack theory to predict how the alteration of these short-term interactions by cannibalism might scale up to influence long-term LHIGP dynamics.

Cannibalism could have strong effects on long-term LHIGP dynamics. Within LHIGP systems, predators often feed in a size-dependent manner (Pimm and Rice 1987), becoming cannibalistic at the transition from resource- to prey (i.e. consumer)-feeding (Byström et al. 2013; Rudolf 2007). Adult predators thus gain an additional food resource with cannibalism, while juvenile predators experience an additional source of mortality. Such stage-specific effects can have dramatic consequences for the distribution of biomass across stages (De Roos and Persson 2013; De Roos et al. 2007; Reichstein et al. 2015). Cannibalism is therefore an important but currently understudied factor that could determine the dynamics of LHIGP systems and possible coexistence states.

Here, we examine the effects of cannibalism on LHIGP dynamics using models that account for the food-dependence of development and reproduction (De Roos and Persson 2013; De Roos et al. 2007). We explore the effects of cannibalism on LHIGP when adult predators exhibit either: (1) a complete diet shift (juveniles and adults feed on separate food resources: figure 4.1A); or (2) diet broadening over ontogeny (adults continue to feed on the resource of juveniles: figure 4.1B). Both patterns of ontogenetic diet change are common in nature (Rudolf and Lafferty 2011; Werner 1988; Werner and Gilliam 1984), allowing us to assess the generality of potential effects.

We model cannibalism as a single parameter that represents the preference for conspecific versus heterospecific prey. Cannibalistic preference has been estimated empirically for a diversity of predator species (figure 4.2), allowing us to make general predictions for how these cannibalistic predators might influence the long-term dynamics of the LHIGP systems in which they occur. We found that even weak cannibalism can inhibit predator persistence in both LHIGP system variants due a reduction in the total biomass of adult predators and thus the top-down control of competitively-dominant consumers. We further discuss mechanisms that may facilitate predator persistence in LHIGP systems with cannibalism, thus reconciling our findings with the apparently common occurrence of such interactions in nature.

4.2 — Model

Model formulation

We examine the effects of cannibalism on LHIGP dynamics using a stage-structured, bioenergetics modeling approach (De Roos et al. 2007; see also Yodzis and Innes 1992). Using this approach, Hin et al. (2011) analyze a model of LHIGP in which the predator
undergoes a complete ontogenetic diet shift. We build upon this model to explore the effects of cannibalism on both complete diet shift and diet broadening LHIGP scenarios. Two ordinary differential equations (ODEs) keep track of juvenile ($P_j$) and adult predator ($P_a$) total biomass densities (mass per unit volume; table 4.1). Despite a simple two-stage population structure, this formulation, under equilibrium conditions, yields predictions identical to that of a physiologically structured population model that explicitly accounts for a continuous population size distribution and mass-specific individual-level physiological rates (De Roos et al. 2007b).

Total biomass densities of unstructured consumer and resource populations, denoted $C$ and $R$, respectively, are modeled with separate ODEs (table 4.1). In the absence of the consumer and predator, the resource exhibits semi-chemostat growth $\delta (R_{max} - R)$ with $\delta$ and $R_{max}$ as turnover rate and maximum resource biomass, respectively (table 4.1). Resource productivity, $\delta R_{max}$, increases linearly with $R_{max}$, and so we use $R_{max}$ as a proxy for productivity throughout the model analysis (see ‘Model parameterization and analysis’). Consumers, juvenile predators and adult predators reduce total resource biomass through feeding (table 4.1). Resource consumption by consumers increases their mass-specific net biomass production

$$v_c(R) = \sigma M_c \frac{R}{H + R} - T_c. \quad (4.1)$$

where $\sigma$ represents the conversion efficiency of resources consumed with a Type II functional response ($M_c$ and $H$ represent the mass-specific maximum consumption rate of the consumer and half-saturation constant, respectively) balanced by the mass-specific maintenance rate of the consumer, $T_c$. Thus basic metabolic demands are met before energy is allocated to reproduction. Conversion efficiency, $\sigma$, represents the net effects of assimilation efficiency (i.e. ingestion lost to feces and urine) and specific dynamic action (i.e. thermal energy expenditure due to food processing) (Peters 1983). Consumer biomass is reduced by adult predators (juvenile predators do not feed on the consumer in either LHIGP scenario: figure 4.1) and background mortality, $\mu_c$ (table 4.1).

Juvenile and adult predator stages are directly linked by maturation, reproduction and asymmetric cannibalism (juveniles cannot consume adults; figure 4.1). The mass-specific net biomass production of juvenile predators

$$v_j(R) = \sigma M_p \frac{R}{H + R} - T_p. \quad (4.2)$$

also increases with resource consumption with a Type II functional response ($M_p$ represents the mass-specific maximum consumption rate of the predator) balanced by the mass-specific maintenance rate of the predator, $T_p$. Juvenile predator biomass is reduced by the juvenile mortality rate ($\omega$, subsequently defined eq. 4.5) and altered

73
by demographic transitions between juvenile and adult predator stages (table 4.1) as follows.

Net biomass production of juveniles $\nu_j(R)$ is spent on juvenile growth which adds biomass to the juvenile stage. Conditional upon survival, growth ultimately leads to maturation and transfer of juvenile biomass to the adult stage. The mass-specific maturation rate equals

$$\gamma \left( \nu_j (R), \omega \right) = \frac{\nu_j (R) - \omega \nu_j (R)}{1 - \omega \nu_j (R)} \quad (4.3)$$

and ensures a correct translation between the biomass densities of juvenile and adult predators and a continuously size-structured model under equilibrium conditions from which this stage-structured model is derived (De Roos et al. 2008b). Mass-specific maturation increases with net juvenile biomass production and decreases with $z$, the ratio between predator size at birth and maturation, as well as the juvenile mortality rate, $\omega$. Maturation represents the sole biomass input into the adult predator equation as adults spend all net production on reproduction and are assumed not to grow. Total adult biomass is reduced by predator background mortality ($\mu_p$; table 4.1).

The net biomass production of adults

$$\nu_a \left( R, C, P_j \right) = \sigma M_p \frac{(1 - \phi)R + \phi(C + \beta P_j)}{H + (1 - \phi)R + \phi(C + \beta P_j)} - T_p. \quad (4.4)$$

increases with consumption of resource, consumer and juvenile predator biomass according to a Type II functional response. $\phi$ represents the fraction of time the adult predator spends foraging on the resource versus conspecific and heterospecific (i.e. consumer) prey: at $\phi = 1$, the adult predator forages solely on prey (i.e. complete diet shift with cannibalism depending on $\beta$: figure 4.1A), while at $\phi = 0.5$, the adult predator spends equal amounts of time foraging on the resource and prey (i.e. diet broadening with cannibalism depending on $\beta$: figure 4.1B). $\beta$ represents the cannibalistic preference of adult predators feeding on juveniles. This parameter scales the preference for conspecific prey relative to heterospecific prey: at $\beta = 1$, adults have no preference for conspecific versus heterospecific prey, while $\beta < 1$ and $\beta > 1$ indicate cannibalistic aversion (i.e. heterospecific preference) or cannibalistic preference, respectively. In empirical studies, cannibalistic preference is often measured by Manly's $\alpha$ (Chesson 1978), which scales from 0 to 1 with $\alpha = 0.5$ indicating no cannibalistic preference (as presented in figure 4.2). Thus our $\beta = 1$ corresponds to Manly’s $\alpha = 0.5$.

Lastly, cannibalism increases the juvenile mortality rate

$$\omega = M_p \frac{\phi \beta P_a}{H + (1 - \phi)R + \phi(C + \beta P_j)} \quad (4.5)$$

which sums the effects of cannibalism and background predator mortality. Juvenile mortality rate reduces juvenile biomass, $P_j$ (table 4.1), as well as the mass-specific
# Table 4.1 – Model Equations

<table>
<thead>
<tr>
<th>Dynamic equation</th>
<th>Description</th>
</tr>
</thead>
</table>
| \[
\frac{dR}{dt} = \delta (R_{\text{max}} - R) - M_c \frac{R}{H + R} C - M_p \frac{R}{H + (1 - \phi)R} P_j \\
- M_p \frac{(1 - \phi)R}{H + (1 - \phi)R + \phi(C + \beta P_j)} P_a
\] | Resource biomass                        |
| \[
\frac{dC}{dt} = \nu_c (R) C - M_p \frac{\phi C}{H + (1 - \phi)R + \phi(C + \beta P_j)} P_a - \mu_c C
\] | Consumer biomass                        |
| \[
\frac{dP_j}{dt} = \nu_a (R, C, P_j) P_a + \nu_j(R) P_j - \gamma (\nu_j(R), \omega) P_j - \omega P_j
\] | Juvenile pred. biomass                 |
| \[
\frac{dP_a}{dt} = \gamma (\nu_j(R), \omega) P_j - \mu_p P_a
\] | Adult pred. biomass                    |

maturation rate, \(\gamma (\nu_j(R), \omega)\) (eq. [4.3]), since it determines juvenile survival and hence the fraction of newborn biomass that survives to the adult stage.

**Model parameterization and analysis**

This model was parameterized following [Hin et al. 2011], which we refer the reader to for more thorough biological justification of parameter settings. Briefly, this parameterization (see figure [4.3] caption for settings) assumes quarter-power scaling relationships of mass-specific parameters ([Brose et al. 2006], [Peters 1983], [Yodzis and Innes 1992]), where adult predators are assumed to be 100 times the mass of consumers. Notably, the predator maximum consumption rate, \(M_p\), is set at 2.5, while the consumer maximum consumption rate, \(M_c\), is set at 10. This parameterization ensures that the consumer is a superior resource competitor in both complete diet shift and diet broadening LHIGP scenarios ([Hin et al. 2011]). Consumer competitive superiority is likely in nature due to morphological or behavioral tradeoffs associated with the predator ontogenetic diet shift ([Toscano et al. 2016], see ‘Discussion’ for explanation), but we later relax this condition and assume the opposite to examine the effects of cannibalism on both LHIGP scenarios when the predator is the superior resource competitor.

We used MatCont ([Dhooge et al. 2003]), a MatLab package for numerical bifurcation analysis of ODEs, to calculate equilibrium biomass densities and assess equilibrium stability. We analyze the model scenarios \(\phi = 1\) and \(\phi = 0.5\), representing a complete ontogenetic diet shift and ontogenetic diet broadening, respectively (figure [4.1]). While predators in nature likely occur along a continuum between these two diets, our initial model explorations demonstrated a continuous transition between the dynamics.
of these different diet scenarios (not shown here). Therefore, modeling the two separate scenarios (complete diet shift and diet broadening) as we do here captures all possible qualitative dynamics. To examine potential effects of enrichment, we first explore equilibrium dynamics of these two parameterizations over a gradient in resource productivity (i.e. $R_{max}$). This analysis also allows us to compare dynamics to that of classic (i.e. unstructured) tri-trophic systems evaluated over gradients in productivity (Oksanen et al., 1981). We then apply numeric continuation methods to these equilibria, evaluated at $R_{max} = 3$, as a function of cannibalistic preference, $\beta$, to assess how resource, consumer and predator equilibrium biomasses respond to increasing cannibalism.

We additionally examined equilibrium states over gradients in $R_{max}$ and $\beta$ in four different LHIGP situations (i.e. parameterizations): (1) complete diet shift with the consumer as the superior resource competitor ($M_p = 2.5$); (2) complete diet shift with the predator as the superior resource competitor ($M_p = 5$); (3) diet broadening with the consumer as the superior resource competitor ($M_p = 2.5$); and (4) diet broadening with the predator as the superior resource competitor ($M_p = 5$). These analyses allowed us to explore the effects of cannibalism across a broader spectrum of potential LHIGP systems, notably when consumers are competitively inferior to predators (in contrast to the prior analyses), and extended productivity and cannibalism gradients within each of these four systems.

4.3 – Results

Complete diet shift LHIGP scenario

The dynamics of LHIGP in which the predator undergoes a complete diet shift between stages (without cannibalism) were previously described by Hin et al. (2011). We recapitulate the dynamics here to set the stage for introducing cannibalism to this LHIGP scenario (figure 4.1A).

Starting from low resource productivity ($R_{max}$), consumers invade the resource-only equilibrium before predators (at productivity threshold $BP_{C\rightarrow R}$) due to their superior competitive ability (figure 4.3A-C). This invasion point marks the start of a consumer-resource equilibrium that is stable (i.e. robust to predator invasion) over increasing resource productivity. At higher resource productivity, predator existence becomes possible (at productivity threshold $LP_{PCR}$) as an alternative stable predator-consumer-resource state (figure 4.3A-C). In this coexistence state, adult predators regulate consumer biomass (figure 4.3), while resource biomass increases with $R_{max}$ (figure 4.3C). Thus coexistence equilibrium dynamics follow that of a traditional top-down food chain (Hin et al., 2011; Oksanen et al., 1981).
The predator stage distribution is dominated by adults in this coexistence state: adult biomass increases with resource productivity while juvenile biomass remains roughly constant (figure 4.3A). This stage-specific response to resource productivity arises because juveniles feed at a higher rate than adults, and thus maturation (i.e. biomass transition to the adult stage) occurs at a faster rate than reproduction. This asymmetry forms a reproductive bottleneck behind which adult biomass accumulates (i.e. reproduction-regulation), leading to an adult-dominated population structure. Specifically, juveniles feed at a higher rate than adults because their food source is more abundant than that of adults: resource biomass increases with resource productivity (figure 4.3C) because adults regulate competitively-dominant consumers (consumer biomass remains constant with increasing resource productivity: figure 4.3B). Thus, when predators exhibit a complete diet shift in LHIGP systems, reproduction is the limiting life-history process, and the preponderance of adults (and resulting top-down control) is necessary to maintain the coexistence state.

**Complete diet shift with cannibalism**

The consumer-resource equilibrium remains unchanged by cannibalism ($\beta$) due to the absence of predators (figure 4.3D-F). In contrast, the three species (predator-consumer-resource) coexistence equilibrium is highly sensitive to cannibalism ($\beta$); when a threshold of cannibalistic preference ($LP_{PCR}$) is exceeded, this equilibrium is no longer possible (figure 4.3D-F). Given the present model parameterization, this threshold occurs at a cannibalism level of $\beta \approx 0.27$ (i.e. heterospecific preference). At values of $\beta$ beyond $LP_{PCR}$, the only equilibrium possible is the consumer-resource equilibrium (figure 4.3D-F). Thus moderate levels of cannibalism in the predator can actually prevent predator persistence in the complete diet shift LHIGP scenario, precluding potential alternative stable states.

A shift in the predator stage distribution is the mechanism behind the collapse of the coexistence state: cannibalism reduces total biomass of adult predators, but increases total biomass of juvenile predators (figure 4.3D). This seemingly counterintuitive effect, a reversal in the predator stage distribution, is potentially driven by two processes. First, cannibalism adds an exclusive food resource for adults (conspecific prey) that is not available to juveniles. Thus cannibalism can help free adults from resource limitation, increasing the rate of reproduction relative to maturation. Second, cannibalism induces stage-specific mortality of juvenile predators. Such mortality can alter population stage distribution independent of which life stage is subjected to increased mortality (De Roos et al. 2007). As explained above, the coexistence equilibrium of predators and intermediate consumers is dependent on adult predator-driven top-down control. Accordingly, the reduction in adult predators and increase in com-
Figure 4.3 — Equilibrium biomasses as a function of resource productivity ($R_{\text{max}}$) when the predator undergoes a complete ontogenetic diet shift (left panels: A-C) and effects of cannibalistic preference ($\beta$) on these equilibria (calculated at $R_{\text{max}} = 3$; right panels: D-F). The consumer is competitively dominant in resource consumption. Juvenile predator biomass is indicated with gray lines and adult predator biomass with black lines. Solid lines depict stable predator-present equilibria and dotted lines unstable predator-present equilibria. Dark gray dashed lines depict equilibria with zero predator density (i.e. stable resource-only and consumer-resource equilibria). Vertical (dotted) lines mark different productivity (panels A-C) and cannibalistic (panels D-F) thresholds at which a qualitative change in equilibria occurs. In panels A-C, the consumer invasion (branching) point, $BP_{C\rightarrow R}$, marks the productivity threshold at which consumers invade the resource-only equilibrium, while $LP_{PCR}$ (a limit point) marks the lowest productivity at which coexistence is possible. In panels D-F, $LP_{PCR}$ marks the level of cannibalism at which coexistence is no longer possible. Parameter values are as follows: (panels A-C) $R_{\text{max}}$ = varied, $\delta = 1$, $\sigma = 0.5$, $M_c = 10$, $M_p = 2.5$, $T_c = 1$, $T_p = 0.3$, $\mu_c = 0.1$, $\mu_p = 0.03$, $H = 1$, $\phi = 1$, $z = 0.01$, $\beta = 0$; (panel D-F) all parameters the same as in panels A-C except $R_{\text{max}} = 3$ and $\beta$ is varied.
Figure 4.4 – Equilibrium biomasses as a function of resource productivity ($R_{\text{max}}$) when the predator undergoes ontogenetic diet broadening (left panels: A-C) and effects of cannibalistic preference ($\beta$) on these equilibria (calculated at $R_{\text{max}} = 3$; right panels: D-F). The consumer is competitively dominant in resource consumption. Lines are as in figure 4.3. In panels A-C, the consumer invasion (branching) point, $BP_{C\rightarrow R}$, marks the productivity threshold at which consumers can invade the resource-only equilibrium, while $BP_{P\rightarrow R}$, the predator invasion (branching) point, marks the productivity threshold at which predators can invade the resource-only equilibrium. A second branching point of the consumer, $BP_{C\rightarrow PR}$, marks the productivity threshold at which a stable predator-resource equilibrium becomes possible (as a function of $R_{\text{max}}$ in panels A-C) or disappears (as a function of $\beta$ in panels D-F). Stability of this predator-resource equilibrium branch changes due to the unstable consumer-resource equilibrium that originates at $BP_{C\rightarrow PR}$. Parameter settings are as in figure 4.3 except $\phi = 0.5$. 

4.3 – Results
petitively inferior juvenile predators due to cannibalism (i.e. a shift from reproduction-to maturation-regulation: De Roos et al. [2007]) reduces top-down control, leading to competitive exclusion of the predator and loss of the three species coexistence state.

Additional analyses indicate that juvenile-specific mortality, rather than energy gain for adults, is the primary driver of the effect of cannibalism on predator stage distribution (appendix figure 4.A1A-C, appendix figure 4.A2A-C). Even when energy gain for adult predators from cannibalism is prevented, cannibalism has the same qualitative effect on predator stage distribution (a shift from adult to juvenile biomass dominance) (appendix figure 4.A1A-C). Furthermore, an increase in juvenile-specific mortality alone, in the absence of cannibalism, captures this same qualitative effect (appendix figure 4.A2A-C). Thus it appears that juvenile-specific mortality due to cannibalism acts to shift biomass dominance to the juvenile stage, ultimately eliminating the coexistence equilibrium.

Diet broadening LHIGP scenario

When predators broaden their diet over ontogeny (i.e. consume both the intermediate consumer and the resource as adults: figure 4.1B) alternative stable states are again possible, but these states are different than in the complete diet shift scenario (figure 4.1A). In diet broadening, consumer-resource and predator-resource states co-occur over a range of $R_{\text{max}}$. Thus coexistence in the diet broadening scenario when the consumer is competitively dominant is not possible.

Starting at low resource productivity, competitively-superior consumers again invade the resource-only equilibrium before predators (at productivity threshold $BP_{C \rightarrow R}$) leading to a stable consumer-resource equilibrium over increasing resource productivity (figure 4.4A-C). At higher resource productivity, however, predator invasion (at productivity threshold $BP_{P \rightarrow R}$) and then stable existence (at productivity threshold $BP_{C \rightarrow PR}$) becomes possible as an alternative predator-resource state (figure 4.4A-C). While the predator-resource equilibrium branch originates at $BP_{P \rightarrow R}$, it only becomes stable at $BP_{C \rightarrow PR}$ due to an unstable coexistence equilibrium originating at this threshold (figure 4.4A-C). In this alternative stable state, adult and juvenile predators persist solely of resource biomass, regulating resource biomass with increasing resource productivity (figure 4.4C).

As in the complete diet shift scenario, this predator-present state is dominated by adult biomass. Specifically, adult biomass increases at a faster rate than juvenile biomass with increasing resource productivity (figure 4.4A). This occurs because generalist adults, which split their time foraging for resources and prey ($\phi = 0.5$), feed at half the rate of juveniles in the absence of consumers. Accordingly, reproduction occurs at a lower rate than maturation, driving biomass accumulation in the adult stage. Thus, just as in the complete diet shift scenario, the predator-present state in the diet
broadening scenario is reproductively-regulated (dominated by adult biomass) and this condition is necessary to ward off consumer invasion.

**Diet broadening with cannibalism**
Similar to the complete diet shift LHIGP scenario, cannibalism ($\beta$) has no effect on the consumer-resource equilibrium, but quickly destabilizes (at the threshold in cannibalistic preference $BP_{C\rightarrow PR}: \beta \approx 0.26$) the predator-present (predator-resource) state ($BP_{C\rightarrow PR}$). Thus at values of $\beta$ beyond $BP_{C\rightarrow PR}$, the only stable state possible is the consumer-resource equilibrium (figure 4.4-D-F). Therefore, just as in the complete diet shift LHIGP scenario, low levels of cannibalism (i.e. maintaining a heterospecific prey preference) in the diet broadening scenario again prevent predator persistence and thus potential alternative stable states.

The mechanism behind this effect of cannibalism on community structure also involves a shift in the predator stage distribution. Specifically, where adult biomass outweighs juvenile biomass in the absence of cannibalism, cannibalism reverses this asymmetry (figure 4.4-D). We show that juvenile-specific mortality, and not addition of an exclusive resource for adults, is again the primary driver of the effect of cannibalism on predator stage distribution (appendix figure 4.A1-D-F, appendix figure 4.A2-D-F). Thus juvenile-specific mortality due to cannibalism releases adults from resource limitation and shifts biomass dominance to the juvenile stage. Ultimately, this reduction in adult predators and the preponderance of competitively inferior juveniles destabilizes the predator-resource equilibrium (figure 4.4-D-F) because predators can no longer resist consumer invasion.

**Importance of consumer competitive ability**
The aforementioned dynamics occur when consumers are competitively dominant over predators in resource competition. We further show that these same dynamics remain qualitatively unchanged over a wider range of cannibalism ($\beta$) and resource productivity ($R_{max}$) values (figure 4.5A, B). Specifically, predator persistence is limited to low cannibalistic preference and higher resource productivity in both complete diet shift (figure 4.5A) and diet broadening (figure 4.5B) LHIGP scenarios. At high cannibalistic preference and low resource productivity, a consumer-resource state is the only possible equilibrium (figure 4.5A, B) due to competitive exclusion of predators.

In contrast, when the predator is superior in resource competition, a juvenile competitive bottleneck and thus predator exclusion is no longer possible. Instead, a predator-present equilibrium always occurs at low resource productivity and remains robust to cannibalism (figure 4.5C, D). Specifically, in the complete diet shift scenario, the consumer invades the resource-only equilibrium first despite the competitive superiority of the predator (figure 4.5C); this is because adult predators specialize on
consumers and thus predators cannot exist in their absence. The predator, however, invades soon thereafter, leading to coexistence as the only equilibrium state (figure 4.5C). Cannibalism has no effect on qualitative dynamics in this scenario, but does stabilize oscillations (figure 4.5C; note Hopf bifurcation).

In the diet broadening scenario, the predator-resource equilibrium occurs as the only equilibrium state when predators are superior in resource competition in the absence of cannibalism. Interestingly, in contrast to all other scenarios, high cannibalism actually allows consumer invasion into this equilibrium at high resource productivity (i.e. three species coexistence: figure 4.5D). Again, this is due to the previously described shift in predator stage distribution due to cannibalism; cannibalism reduces adult biomass and increases juvenile biomass, which in turn permits consumer invasion due to a reduction in top-down control (appendix figure 4.A3). Thus in total, when the predator is the superior resource competitor, cannibalism either has no effect on qualitative equilibria (complete diet shift: figure 4.5C) or promotes coexistence (diet broadening: figure 4.5D).

4.4 – Discussion

A hallmark of structured predator-prey systems is that different predator sizes or stages often engage in different types of species interactions (Rudolf and Lafferty 2011; Werner and Gilliam 1984). Thus influences on predator population stage distribution have the capacity to shift the balance of interactions that shape long-term system dynamics. We present the novel finding that predators can short-circuit their own persistence in LHIGP systems through cannibalism, a nearly ubiquitous interaction in structured predator-prey systems (Byström et al. 2013; Rudolf 2007; Toscano et al. 2016). This occurs via a cannibalism-induced shift in the predator stage distribution from adult to juvenile biomass dominance. The loss of adult predators, solely responsible for regulating consumers, frees competitively-dominant consumers from top-down control, ultimately leading to predator exclusion. Predator extinction via cannibalism is only possible because of the feedback loop between predators and competitors; in a single-species system, cannibalism, a negatively density-dependent process, cannot drive extinction. We further show that this effect hinges upon the competitive superiority of consumers; when predators are competitively superior, cannibalism either has no effect on coexistence (in the complete diet shift scenario) or actually drives coexistence (in diet broadening). Thus while previous work emphasizes the (positive) effects of cannibalism in promoting coexistence (Ohlberger et al. 2012; Rudolf 2007), our study demonstrates a diversity of effects of cannibalism on long-term LHIGP dynamics, depending on system properties.
Figure 4.5 – Equilibria dependent on resource productivity \( (R_{max}) \) and cannibalistic preference \( (\beta) \) within four life-history intraguild predation (LHIGP) scenarios: (panel A) complete diet shift in predator \( (\phi = 1) \), consumer as superior resource competitor \( (M_p = 2.5) \); (panel B) diet broadening in predator \( (\phi = 0.5) \), consumer as superior resource competitor \( (M_p = 2.5) \); (panel C) complete diet shift in predator \( (\phi = 1) \), predator as superior resource competitor \( (M_p = 5) \); (panel D) diet broadening in predator \( (\phi = 0.5) \), predator as superior resource competitor \( (M_p = 5) \). Other parameter settings are as in figure 4.3. Solid lines indicate shifts between different qualitative equilibria. Narrow white region on the left-hand side of all four panels represents the resource-only equilibrium. Gray shading indicates the presence of a consumer-resource (CR) equilibrium. Letters indicate the presence of different predator-present equilibria (PR [predator-resource] or PCR [predator-consumer-resource]). An addition sign (+) preceding letters indicates that these predator-present equilibria occur alternatively to a CR equilibrium. The dashed lines in panels A and C mark the transition from a stable equilibrium point to a stable limit cycle (Hopf bifurcation), with the limit cycle occurring at higher resource productivity.
Ontogenetic asymmetry in LHIGP systems

We show that while the community-level effects of cannibalism can be diverse, they are all driven by a single mechanism: cannibalism (and specifically juvenile predator mortality) switches the predator stage distribution from adult to juvenile biomass dominance. The loss of adult predators (and thus top-down control) either eliminates, destabilizes, or allows consumer invasion into predator-present equilibria. Such asymmetries in biomass distribution arise when the key life-history transitions, development (i.e. maturation) and reproduction, differ in their rate of biomass transfer, a phenomenon termed ontogenetic asymmetry \cite{DeRoos2013,DeRoos2007, Persson2013}. Predator populations in LHIGP systems are dominated by adult biomass at equilibrium due to the relatively greater energy intake rate of juveniles compared to adults. Thus maturation occurs at a greater rate than reproduction (i.e. reproduction-regulation). Our analyses indicate that cannibalism actually enhances the rate of reproduction relative to maturation by increasing juvenile mortality (i.e. a positive effect of mortality: \cite{Schoeder2014}), reversing the ontogenetic distribution of biomass. Previous analyses support this finding, that mortality can alter population stage distribution independent of which life stage is subjected to increased mortality \cite{DeRoos2007}. Such ontogenetic asymmetry is an underappreciated characteristic of structured populations that is likely widespread in nature \cite{DeRoos2013, Persson2013, Reichstein2015}. Our work thus provides a striking example of the importance of ontogenetic asymmetry for long-term system dynamics, and further suggests that natural LHIGP systems could be more sensitive to changes in predator stage distribution than previously recognized, whether due to cannibalism or other means (e.g. human harvesting of adults: \cite{Walters2001}). Specifically, any factor that increases juvenile-specific mortality (e.g. disease or a size-dependent predator) could elicit similar effects in LHIGP systems without cannibalism.

Cannibalistic preference and coexistence

We found that the degree of cannibalism necessary to inhibit predator persistence in LHIGP is surprisingly low: the loss of predator-present equilibria occurs at a 3 : 1 preference for heterospecific versus conspecific prey in both complete diet shift and diet broadening scenarios. While this precise cannibalistic preference is dependent on our model parametrization, the important finding is that adults can short-circuit their own persistence while still exhibiting preference for heterospecific prey. Furthermore, the present parameterization is based on power law scaling of physiological rates with body size and is thus justifiable based on metabolic theory (see \cite{Hin2011} for further explanation). Models based on biomass density, such as the present formulation, allow for a much more realistic parameterization than typical consumer-resource models.
based on individual density \cite{Yodzis1992}. Thus our results are certainly within the realm of biological possibility.

We can use empirical estimates of cannibalistic preference to speculate on whether predator taxa would inhibit their own persistence in LHIGP systems. Our literature review shows that cannibalistic preference varies considerably among a wide range of invertebrate and vertebrate predator taxa, and can rival or even exceed interspecific predation rates \cite{Burgio2005, Gerber2000, Rudolf2008, Yasuda2001, Bystrom2013}. For example, found that freshwater fish often exhibit a strong preference for conspecific relative to heterospecific prey. Interestingly, this same study found that fish predators are typically competitively inferior to their prey (intermediate fish consumers: \cite{Bystrom2013}). Our results suggest that in these fish systems, there is a high likelihood of predator exclusion from LHIGP interactions. Thus it appears that the conditions for predator exclusion from LHIGP interactions are met in a number of natural LHIGP systems.

Reconciling theory with nature

Given these empirical patterns of cannibalism, our work thus poses an apparent conundrum: how can LHIGP systems with cannibalism be common in nature \cite{Bystrom2013, Rudolf2007}? The sensitivity of LHIGP to cannibalism is due in part to consumer competitive superiority: any factor that frees consumers from top-down control leads to a juvenile competitive bottleneck that inhibits predator persistence. This assumption (consumers superior to predators in resource competition) is likely upheld in many natural systems due to an ontogenetic tradeoff associated with continuous growth \cite{Bystrom2013, Hin2011, Werner1984}: continuously-growing predators retain the same basic morphology while switching among resource types, and thus juvenile predators may be “burdened” by adult predatory morphology \cite{Werner1984}. In contrast, specialist consumers feed solely on the basal resource over ontogeny and are thus not faced with such a trade-off.

This condition, however, is not necessarily true for species that undergo complete metamorphosis \cite{Werner1984} but see \cite{Toscano2016}. Metamorphosis allows predators to completely “rebuild” their morphology over ontogeny, allowing them to potentially circumvent the same phenotypic trade-off. Thus as an alternative scenario, we present the effects of cannibalism on LHIGP dynamics when predators are competitively superior to consumers in resource competition, showing that the juvenile competitive bottleneck and concomitant loss of predator-present equilibria is no longer possible. Instead, a predator-present equilibrium is the sole equilibrium state in both complete diet shift and diet broadening scenarios. In the complete diet shift scenario, this predator-present state occurs as full (three species) coexistence, while in the diet broadening scenario, this occurs as a predator-resource equilibrium. Nevertheless,
strong cannibalism in the diet broadening scenario actually allows consumer invasion into this predator-resource equilibrium, thus promoting coexistence. Rudolf (2007) demonstrates this same effect of cannibalism in a diet broadening LHIGP model with a fixed (i.e. non-food-dependent) maturation rate, showing that this result is robust to model formulation. Thus, when the predator is superior in resource competition, coexistence is a likely outcome of LHIGP with cannibalism. More broadly, consumer versus predator competitive superiority is critical to predicting the long-term outcome of LHIGP interactions, and could depend in part on the details of predator life-history (e.g. continuous growth versus metamorphosis).

Other mechanisms could also allow for predator persistence in cannibalistic LHIGP systems when consumers are superior in resource competition, though these require an increase in system complexity beyond the basic LHIGP module. An extraneous (i.e. non-predator-driven) increase in consumer mortality, for example, permits predator persistence in both complete diet shift and diet broadening LHIGP scenarios, despite strong cannibalism (Toscano, unpublished results). In this scenario, increased mortality reduces consumer population growth (i.e. competitive ability) and thus the ability of consumers to competitively exclude predators. Thus it is possible that natural LHIGP interactions nested within complex food webs are more complicated than suggested by current model formulations, and this additional complexity begets the apparent stability of these interactions in nature.

Empirical ecologists may begin to test the theory we present using multigenerational community-scale experiments. Specifically, to test the effects of cannibalism on LHIGP system dynamics, we suggest using congeneric predators that differ in their degree of cannibalism (e.g copepods: Toscano et al. 2016) nested in otherwise identical LHIGP systems. While different predator species may vary in their precise life-history parameters or feeding rates, our theory is robust to these differences, predicting qualitatively different dynamics in the absence and presence of cannibalism. Specifically, predator persistence should not be possible in the presence of a cannibalistic predator, whereas in the absence of cannibalism, predator-present community states are predicted. Juvenile mortality is the primary process behind the collapse of predator-present stable states, and thus the experimental harvest of juveniles should elicit the same community response as cannibalism while corroborating the stage-dependent mechanism.

Cannibalism is predicted to result in predator-absent LHIGP states, and so the effects of cannibalism could be more difficult to test within intact natural communities. Nevertheless, additional analyses suggest that in LHIGP systems with low cannibalism, increasing consumer mortality (e.g. via a removal manipulation) should shift the predator to a more adult-dominated stage distribution (i.e. resembling the dynamics of an LHIGP system without cannibalism). Furthermore, consumers should exhibit
complete biomass compensation in response to increased mortality. Such community responses to increased consumer mortality would identify cannibalism as a key regulatory interaction. We emphasize, however, that long-term multigenerational studies of LHIGP dynamics are rare, and any such study would significantly advance our understanding of stage-structured community dynamics.

Conclusions

The present work demonstrates the potential for strong effects of cannibalism on the long-term outcomes of stage-structured species interactions, adding to just a handful of studies that have investigated the effects of cannibalism on complex communities (Ohlberger et al. 2012, Persson et al. 2003, Rudolf 2007, Wahlström et al. 2009). Such a paucity of research attention is surprising, given that cannibalism is nearly ubiquitous in structured populations (Fox 1975, Polis 1981, Polis and Myers 1985). Claessen et al. (2004) suggest this lack of study is because “the complexity of (structured) cannibalistic-population models makes extensions to multi-species systems a daunting task.” Nevertheless, we feel this is a task worth taking on, in order to better understand how communities might respond to the full range of biotic interactions in nature.

Acknowledgments

We wish to thank André de Roos for helpful feedback that improved this work. This work was supported by an Arnold O. Beckman Postdoctoral Fellowship to B.J. Toscano and NSF DEB-1256860 to V.H.W. Rudolf. V. Hin was supported by funding from the European Research Council under the European Union’s Seventh Framework Programme (FP/2007-2013) / ERC Grant Agreement No. 594 322814.
APPENDIX 4.A  ADDITIONAL EFFECTS OF CANNIBALISM ON PREDATOR EQUILIBRIA

Figure 4.A1 – Effects of cannibalistic preference ($\beta$) without energy gain for adults on equilibria when the predator undergoes a complete ontogenetic diet shift (left panels: A-C) or ontogenetic diet broadening (right panels: D-F) (calculated at $R_{\text{max}} = 3$). The consumer is competitively dominant in resource consumption. Solid lines depict stable equilibria and dotted lines unstable equilibria. Juvenile predator biomass is indicated with gray lines and adult predator biomass with black lines. Dashed dark gray lines depict stable consumer-resource equilibrium where predators are absent. Parameter values are as follows: (panels A-C) $R_{\text{max}} = 3$, $\delta = 1$, $\sigma = 0.5$, $M_c = 10$, $M_p = 2.5$, $T_c = 1$, $T_p = 0.3$, $\mu_c = 0.1$, $\mu_p = 0.03$, $H = 1$, $\phi = 1$, $z = 0.01$, $\beta$ = varied; (panels D-F) all parameters the same as in panels A-C except $\phi = 0.5$. 
**Figure 4.A2 –** Effects of juvenile-specific mortality ($\omega$) in the absence of cannibalism on equilibria when the predator undergoes a complete ontogenetic diet shift (left panels: A-C) or ontogenetic diet broadening (right panels: D-F) (calculated at $R_{\text{max}} = 3$). The consumer is competitively dominant in resource consumption. Solid lines depict stable equilibria and dotted lines unstable equilibria. Juvenile predator biomass is indicated with gray lines and adult predator biomass with black lines. Dashed dark gray lines depict stable consumer-resource equilibrium where predators are absent. Parameter values are as follows: (panels A-C) $R_{\text{max}} = 3$, $\delta = 1$, $\sigma = 0.5$, $M_c = 10$, $M_p = 2.5$, $T_c = 1$, $T_p = 0.3$, $\mu_c = 0.1$, $\mu_p = 0.03$, $H = 1$, $\phi = 1$, $z = 0.01$, $\beta = 0$; (panels D-F) all parameters the same as in panels A-C except $\phi = 0.5$. 

89
Figure 4.A3 – Consumer invasion into predator-resource equilibrium due to cannibalistic preference ($\beta$) when the predator is dominant in resource consumption and undergoes diet broadening over ontogeny. Solid lines depict stable equilibria and dotted lines unstable equilibria. Juvenile predator biomass is indicated with gray lines and adult predator biomass with black lines. Dashed dark gray lines depict (unstable) consumer-resource equilibrium where predators are absent. Parameter values are as follows: $R_{\text{max}} = 3$, $\delta = 1$, $\sigma = 0.5$, $M_c = 10$, $M_p = 5$, $T_c = 1$, $T_p = 0.3$, $\mu_c = 0.1$, $\mu_p = 0.03$, $H = 1$, $\phi = 0.5$, $z = 0.01$, $\beta$ varied.
APPENDIX 4.B STUDIES MEASURING CANNIBALISTIC PREFERENCE

Preference estimates are shown in figure 4.2 (main text)


