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Cannibalism Prevents Evolutionary Suicide of Ontogenetic Omnivores in a Life History Intraguild Predation System

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ABSTRACT

Ontogenetic omnivores are species that change or expand their diet during life. In ontogenetic omnivores without a metamorphosis, genetic correlations can result in a trade-off between resource specialization on early versus late-life resources. We show that such an ontogenetic trade-off has important consequences for persistence and coexistence of ontogenetic omnivores in life-history intraguild predation systems. In these systems, the small omnivores are engaged in resource competition with a specialist consumer species, which is the main prey of large omnivores. In addition, large ontogenetic omnivores are often cannibalistic. Selection on resource specialization under an ontogenetic trade-off leads to evolutionary suicide of the omnivore, but only when levels of cannibalism are low. Evolutionary suicide occurs because directional selection causes increasing resource specialization of one life stage, at the cost of feeding ability in the other life stage. This results in a shift to an alternative community state and extinction of the ontogenetic omnivore. Re-establishment is inhibited by strong competition with consumers in the juvenile phase. Cannibalism stabilizes selection on the ontogenetic trade-off, resulting in persistence of ontogenetic omnivores and coexistence with consumers. Based on these results, we conclude that life-history intraguild predation systems can only persist when levels of cannibalism are not low and (small) ontogenetic omnivores do not suffer from competition with the specialist consumer.

5.1 – Introduction

Ontogenetic or life-history omnivores are species that change or expand their diet during life (Persson 1988; Pimm and Rice 1987). These include organisms with direct development that change resources as a result of body size growth (such as fish and many amphibians), as well as species with indirect development, in which metamorphosis is responsible for the change in diet (*e.g.* holometabolous insects). The majority of all animal species fall within these two categories, with the exception of most birds and mammals (Werner 1988; Werner and Gilliam 1984; Wilbur 1980). The omnipresence of ontogenetic omnivores within the animal kingdom certainly suggests a high evolutionary potential of such a strategy.

The apparent evolutionary success of ontogenetic omnivores seems to be at odds with the insight that ontogenetic omnivores suffer from a trade-off that limits the ability to specialize on different resources (Hjelm et al. 2000, 2003; Robinson et al. 1996; Schluter 1995). Specializing on a specific resource means that body morphology, physiology and behavior (among others) are optimally adjusted to search, capture and process it. Since optimal exploitation of different resources require different sets of phenotypic traits, specialist species are often better adapted to utilize a specific resource than generalists. In ontogenetic omnivores the use of different resources is separated between different life stages. Genetic correlations between life stages are thought to prevent full ecological specialization on each of the resources used in these different life stages (Ebenman 1992; Werner 1988; Werner and Gilliam 1984). Ontogenetic omnivores are hence often considered less efficient foragers on a particular resource than their specialist competitors for that resource (Ebenman 1992; Persson 1988), in particular if they do not have a metamorphosis (Werner and Gilliam 1984). In fact, metamorphosis is hypothesized to have evolved as a mechanism to break these genetic correlations, so that the different life stages can independently specialize on their stage-specific resources (Ebenman 1992; Moran 1994; Ten Brink and De Roos 2017; Werner 1988). Ontogenetic omnivores that do not metamorphose, such as many fish species, have only limited possibility to rearrange their body morphology and physiology along with their change in resource use over ontogeny (Werner 1988; Werner and Gilliam 1984). The use of different resources and the genetic correlations that limit specialization on these different resources creates an ontogenetic trade-off that makes such ontogenetic omnivores vulnerable to being outcompeted by specialist species (Hin et al. 2011; Toscano et al. in press).

Ontogenetic omnivores thus face a trade-off between specializing on resources that are used early versus those that are used late in life (Ebenman 1992; Persson 1988; Werner 1988; Werner and Hall 1977). Within the same species trade-offs in resource specialization have mainly been shown to occur between morphs from dif-

ferent niches, such as benthic and limnetic forms of freshwater fish species (Robinson and Wilson 1996; Robinson et al. 1996; Schluter 1995). An ontogenetic trade-off has been hypothesized to occur between the benthic and piscivorous stages of Eurasian perch (*Perca fluviatilis*), which niches favor different body forms and feeding apparatus (Hjelm et al. 2000; Svanbäck and Eklöv 2002, 2003). However, given the extent of genetic correlations between different life stages (Aguirre et al. 2014; Cheverud et al. 1983; Ebenman 1992; Werner 1988) and the well-studied phenomenon that different resources require different morphologies (Futuyma and Moreno 1988), ontogenetic trade-offs are likely to occur and are probably important in many ontogenetic omnivores that lack metamorphosis.

These ontogenetic trade-offs can have important consequences for persistence and coexistence of ontogenetic omnivores in the context of life-history intraguild predation (LHIGP; Hin et al. 2011; Pimm and Rice 1987; Polis et al. 1989; Toscano et al. in press, 2016). In LHIGP systems, the ontogenetic omnivore (or intraguild predator) competes with a specialist consumer (or intraguild prey) for a shared resource early in life (when small/juvenile), but preys on the consumer later in life (when large/adult). Because of ontogenetic trade-offs the intraguild predator is often considered an inferior resource competitor compared to the consumer (Byström et al. 2013; Holt and Polis 1997; Persson 1988; Werner and Gilliam 1984). In such a case, the consumer potentially limits persistence of the intraguild predator, by suppressing the resource to a level that is insufficient for growth and successful maturation of juvenile intraguild predators (Byström et al. 1998; Hin et al. 2011; Persson and Greenberg 1990; Van de Wolfshaar et al. 2006; Walters and Kitchell 2001). This can occur irrespective of whether the intraguild predator completely changes its diet to exclusive foraging on consumer prey over ontogeny (diet shift LHIGP; Hin et al. 2011; Toscano et al. in press) or merely expands its diet to include consumer prey when large (diet broadening LHIPG; Rudolf 2007; Toscano et al. in press; Van de Wolfshaar et al. 2006). Alternatively, persistence of the intraguild predator can be promoted by adult predators suppressing consumers and thereby increasing resource availability for their juveniles (cultivation hypothesis; Walters and Kitchell 2001). The dominant process in LHIGP systems that ultimately determines the resulting community structure is hence either predation by adult intraguild predators on consumers, or competition between juvenile intraguild predators and consumers, but both processes do not play a major role at the same time (Hin et al. 2011; Persson and De Roos 2012). The selection on feeding specialization in ontogenetic omnivores is hence expected to depend on whether predation or competition is the dominant mode of interaction between the intraguild prey and predator. How these alternative structuring forces impact the evolutionary dynamics of ontogenetic omnivores that are subject to a trade-off between early versus late foraging success is currently unknown.

Cannibalism, or intraspecific predation, further complicates dynamics of LHIGP systems. Cannibalism often is a size-related interaction (Polis 1981), which makes it likely for adult intraguild predators to cannibalize juvenile intraguild predators, in addition to interspecific predation on the consumer (Byström et al. 2013). Also, because of the interconnectedness of the LHIGP food web all species generally occupy the same habitat, which further adds to the likelihood of cannibalism occurring. The common occurrence of cannibalism in LHIGP systems is supported by Byström et al. (2013) who show that 8 out of 11 fish species that shift from feeding on zooplankton or macrobenthic invertebrates to piscivory select conspecific over interspecific piscivorous prey. Theoretical work shows that the effect of cannibalism on persistence of the intraguild predator depends crucially on the competitive hierarchy between intraguild predator and prey (Toscano et al. in press). When the prey is the superior resource competitor, cannibalism in the predator releases top-down control of the prey by the predator, which breaks down the cultivation effect. This substantially limits the possibility for predator persistence (Toscano et al. in press). In contrast, when the predator is the superior resource competitor cannibalism promotes coexistence of intraguild prey and predator because it reduces top-down control of the predator on the resource (Toscano et al. in press). In LHIGP systems the rate of cannibalism is generally linked to the rate of interspecific predation, because both types of predation require the same set of morphological and behavioral adaptations and all species tend to share the same habitat. Therefore, adaption to interspecific predation is likely to also increase rates of cannibalism and, depending on the competitive hierarchy between consumers and intraguild predators, this can hinder predator persistence even further.

Here we study the consequences of an ontogenetic trade-off between early and late foraging success for persistence of an intraguild predator and its coexistence with intraguild prey. We simulate evolutionary dynamics of resource specialization of intraguild predators depending on the level of cannibalism and whether intraguild predators exhibit a diet shift or a diet broadening over ontogeny (Toscano et al. in press). Previous theoretical studies on resource specialization under an ontogenetic trade-off have shown the influence of productivity of early and late life resources and the non-linearity of the trade-off function (Ebenman 1992; Ten Brink and De Roos 2017). Therefore, next to evaluating qualitatively different trade-off forms we also vary productivity of the shared resource, which determines the ratio between consumer and resource abundance. Our findings reveal that non-cannibalistic intraguild predators evolve towards an abrupt threshold in the ecological dynamics beyond which they go extinct. Such evolutionary suicide of the intraguild predator occurs in both diet broadening and diet shift scenarios. Cannibalism, however, can stabilize evolutionary dynamics and prevent evolutionary suicide, irrespective of resource productivity and

the shape of the trade-off function. Cannibalistic ontogenetic omnivores can stably coexist with specialist consumers only when juveniles are specialized on the shared resource and do not suffer from competition. We conclude that the evolutionary success of non-metamorphosing ontogenetic omnivores in a life-history intraguild predation system can be explained by cannibalism and the resource specialization of juveniles.

5.2 – Model and method

Model formulation

We build upon the LHIGP model of Hin et al. (2011) and Toscano et al. (in press), who both use the stage-structured bio-energetics modeling approach as described by De Roos et al. (2007, 2008*b*). This approach is a stage-structured extension of the bio-energetic model presented by Yodzis and Innes (1992), separating the total population biomass into juvenile and adult biomass. Only the stage structure of the intraguild predator is explicitly represented, whereas population stage structure is ignored for the shared resource (R) and the consumer (C) on the grounds that juveniles and adults in these latter two populations do not differ from a dynamical, energetics perspective. In the predator life history we distinguish a juvenile (P_j) and an adult stage (P_a), where adults are assumed to only reproduce and do not grow.

In the original formulation by Hin et al. (2011) both consumers and predators feed according to Holling type II functional responses with a mass-specific maximum ingestion rate (M) and a half-saturation constant (H). The half-saturation constant indicates the resource density at which the functional response equals half the maximum ingestion rate. This parameter equals the ratio of the mass-specific maximum ingestion and the mass-specific attack rate or searching efficiency and therefore is a compound parameter. To perform evolutionary analysis on components of the functional response it is appropriate to choose a formulation that has parameters with a clear interpretation at the individual level (Rueffler et al. 2006*a*). Accordingly, we choose to avoid the formulation with the maximum ingestion rate and half-saturation constant and instead use an attack rate formulation in combination with a handling time constant (Persson et al. 1998; Ten Brink and De Roos 2017). In this formulation the attack rate or searching efficiency represents the amount of space or area that a predator can search for prey per unit of time, which is assumed to scale linearly with the body mass of the individual predator by Hin et al. (2011). Similarly, the handling time equals the inverse of the maximum ingestion rate, where the latter is also assumed to scale linearly with predator body mass (Hin et al. 2011). The handling time thus scales inversely with predator body size and amounts to the time required to handle

or digest one unit resource (or prey) biomass. Because of these scalings with predator body mass, the attack rate of species i feeding on species j will be represented by the mass-specific attack rate, denoted by a_{ij}, while the handling time will be represented by the scalar relating handling time to the inverse of individual body mass, denoted by h_i. The latter is assumed equal across all prey types.

All model equations are summarized in table 5.1. Mass-specific ingestion rate of resource biomass by consumers is hence given by:

$$I_{cr} = \frac{a_{cr}R}{1 + h_c a_{cr} R}$$

and ingested biomass is converted to net-biomass production (v_c) after multiplication with conversion efficiency σ and subtraction of mass-specific maintenance rate T_c

$$v_c = \sigma I_{cr} - T_c$$

Similar to consumers, juvenile intraguild predators solely feed on resource biomass and their mass-specific ingestion and net-biomass production rates are hence given by:

$$I_{jr} = \frac{a_{jr}R}{1 + h_p a_{jr} R}$$

and

$$v_j = \sigma I_{jr} - T_p$$

respectively.

Adult intraguild predators feed on resource with attack rate a_{ar} and on consumers with attack rate a_{ac}. Additionally, adult predators are cannibalistic by feeding on juvenile predators. The attack rate for cannibalism is assumed equal to the attack rate for interspecific predation. Following Toscano et al. (in press), the intensity of cannibalism relative to interspecific predation is represented by a scaling factor β. Mass-specific ingestion rate of resource biomass by adult intraguild predators is therefore given by:

$$I_{ar} = \frac{a_{ar}R}{1 + h_p \left(a_{ar}R + a_{ac}\left(C + \beta P_j\right)\right)}$$

Ingestion rates of adults feeding on consumer biomass, (I_{ac}), and for cannibalistic feeding, (I_{aj}) follow similar expressions and are shown in table 5.1. The mass-specific net-biomass production rate of adult predators equals the difference between the sum of the three mass-specific ingestion rates, multiplied by conversion efficiency σ, and the mass-specific maintenance rate for predators, T_p.

$$v_a = \sigma \left(I_{ar} + I_{ac} + I_{aj}\right) - T_p$$

Table 5.1 – Model Equations

Description	Equation
Pred. attack rate trade-off	$a_{ac} = \dfrac{a_p - a_{jr}}{1 + \varepsilon a_{jr}/a_p}$
Consumer ingestion	$I_{cr} = \dfrac{a_{cr}R}{1 + h_c a_{cr}R}$
Juvenile pred. ingestion	$I_{jr} = \dfrac{a_{jr}R}{1 + h_p a_{jr}R}$
Adult pred. ingestion on resource	$I_{ar} = \dfrac{a_{ar}R}{1 + h_p \left(a_{ar}R + a_{ac}\left(C + \beta P_j\right)\right)}$
Adult pred. ingestion on consumer	$I_{ac} = \dfrac{a_{ac}C}{1 + h_p \left(a_{ar}R + a_{ac}\left(C + \beta P_j\right)\right)}$
Adult pred. ingestion on juvenile pred.	$I_{aj} = \dfrac{a_{ac}\beta P_j}{1 + h_p \left(a_{ar}R + a_{ac}\left(C + \beta P_j\right)\right)}$
Consumer net-biomass production	$\nu_c = \sigma I_{cr} - T_c$
Juvenile pred. net-biomass production	$\nu_j = \sigma I_{jr} - T_p$
Adult pred. net-biomass production	$\nu_a = \sigma\left(I_{ar} + I_{ac} + I_{aj}\right) - T_p$
Juvenile pred. mortality rate	$D_j = \mu_p + \dfrac{a_{ac}\beta P_a}{1 + h_p\left(a_{ar}R + a_{ac}\left(C + \beta P_j\right)\right)}$
Juvenile pred. maturation rate	$\gamma\left(\nu_j, D_j\right) = \dfrac{\nu_j - D_j}{1 - z^{1-D_j/\nu_j}}$
Resource biomass dynamics	$\dfrac{dR}{dt} = \delta\left(R_{max} - R\right) - I_{cr}C - I_{jr}P_j - I_{ar}P_a$
Consumer biomass dynamics	$\dfrac{dC}{dt} = \nu_c C - I_{ac}P_a - \mu_c C$
Juvenile pred. biomass dynamics	$\dfrac{dP_j}{dt} = \nu_a P_a + \nu_j P_j - \gamma\left(\nu_j, D_j\right)P_j - D_j P_j$
Adult pred. biomass dynamics	$\dfrac{dP_a}{dt} = \gamma\left(\nu_j, D_j\right)P_j - \mu_p P_a$

Ingestion, production and biomass production rates are mass-specific

To study the evolutionary dynamics of late versus early foraging success we implement a trade-off between the juvenile attack rate on the resource (a_{jr}) and the adult attack rate (a_{ac}) for predation (both interspecific and cannibalism) as follows:

$$a_{ac} = \frac{a_p - a_{jr}}{1 + \varepsilon a_{jr}/a_p} \tag{5.1}$$

with $\varepsilon > -1$. This trade-off is a modified version of the trade-off function used by Ebenman (1992). In eq. 5.1 a_p is the maximum value that the attack rates a_{jr} and a_{ac} can adopt, while ε controls the shape of the trade-off. For $\varepsilon = 0$, the trade-off between the attack rates a_{jr} and a_{ac} is linear, for $\varepsilon < 0$ the trade-off is weak and concave from below, while for $\varepsilon > 0$ the trade-off is strong and convex from below. In order to study both diet shift and diet broadening LHIGP systems the adult attack rate for the resource a_{ar} is not part of the trade-off and can be set independently.

Juvenile and adult predator mortality include the stage-independent background mortality rate μ_p. Juvenile predators furthermore suffer from mortality due to cannibalistic feeding by adult predators, which amounts to:

$$\frac{a_{ac}\beta P_a}{1 + h_p \left(a_{ar}R + a_{ac} \left(C + \beta P_j \right) \right)}$$

Dynamics of resource, consumer, juvenile predator and adult predator biomass are described by four ordinary differential equations (table 5.1). Resource biomass increases following semi-chemostat dynamics (De Roos and Persson 2013) with turnover rate δ and maximum resource density R_{max} and decreases due to ingestion by consumers and juvenile and adult predators. Consumer biomass increases with total consumer net-biomass production, $\nu_c C$ and decreases through total feeding by adult predators, $I_{ac}P_a$ and consumer background mortality $\mu_c C$. Juvenile biomass increases through reproduction, which depends on the net-biomass production of adult predators and equals $\nu_a P_a$. Juvenile predators use their own net-biomass production rate, ν_j, exclusively for somatic growth. Growth increases juvenile biomass and, when positive, growth ultimately leads to maturation of juveniles to the adult stage. The rate of maturation, $\gamma\left(\nu_j, D_j\right)$, hence depends on the net-biomass production, but also on the juvenile mortality rate and the ratio between size at birth and size at maturation, z. The exact functional form of the maturation function is shown in table 5.1 and is derived such that the stage-structured biomass model in equilibrium is identical to a model with a continuous size-structure, as derived in De Roos et al. (2008b). The stage-structured biomass model studied hence implicitly accounts for the population size-structure dynamics of both the consumer and the predator population (see De Roos et al. 2008b, for details). Adult biomass only increases through maturation as adult predators spend all net-biomass production on reproduction. Adult biomass decreases through background mortality.

Model parameterization

Model parameterization follows Hin et al. (2011), in which a more in-depth motivation about the default parameter values (shown in table 5.2) can be found. To transform the functional response parameters of Hin et al. (2011) to our formulation we use the fact that the handling time equals the inverse of the maximum ingestion rate and the half-saturation constant equals the ratio between maximum ingestion and attack rate. The default parameterization of Hin et al. (2011) is derived from the observed power law scaling of the rates of mass-specific maximum ingestion, mass-specific maintenance and mortality with adult body size raised to the power of -0.25 (see also De Roos and Persson 2013). The constants of these scaling relationships approximately differ one order of magnitude; the mass-specific maximum ingestion equals 10 times the maintenance rate, which in turn equals 10 times the background mortality rate. Since Hin et al. (2011) adopt a value of 1 for the half-saturation constant we adopt $a_{cr} = 10$, $h_c = 0.1$, $T_c = 1$ and $\mu_c = 0.1$. The difference in the mass-specific rates between predators and consumer stems from the difference in their adult body mass. Hin et al. (2011) and Toscano et al. (in press) assume adult predators to be 100 times the mass of consumers. However, because predators grow in body mass 2 orders of magnitude during their life (the newborn-adult size ratio, $z = 0.01$; table 5.2) such a large mass difference would imply that only newborn predators overlap in body size with consumers, which is in contrast to the fact that species competing for a resource often have similar body sizes. We therefore assume a larger size overlap between consumers and juvenile predators and adopt a predator-consumer body mass ratio of 40. This value is close to the geometric average predator-prey body-mass ratio of 42 as reported by Brose et al. (2006). Consequently, the default values for the predator maintenance and mortality rate become $T_p = 0.4$ and $\mu_p = 0.04$, respectively, and for predator handling time $h_p = 1/4$.

The value of a_{ar} controls whether the intraguild predator has a diet shift ($a_{ar} = 0$) or a diet broadening ($a_{ar} > 0$). In addition, a_{ar} together with a_{jr} influence the competitive hierarchy between the intraguild predator and the consumer. This competitive hierarchy is of crucial importance for persistence and coexistence in (life-history) intraguild predation systems (Hin et al. 2011; Holt and Polis 1997; Mylius et al. 2001; Toscano et al. in press). Competitive ability is inversely related to resource density in the population-dynamical equilibrium containing only the resource and the focal population. The species with the lowest equilibrium resource density is hence considered the superior competitor, sensu Tilman (1980). For the intraguild predator we asses the competitive ability in absence of cannibalism. In case of a diet shift ($a_{ar} = 0$) the competitive ability of the intraguild predator is not defined, because predators cannot persist solely on the resource. However, juvenile intraguild predators can still compete with the consumer and to asses the competitive hierarchy between

TABLE 5.2 – Model Parameters

Description	Intraguild Predators		Consumer	Resource
	Juveniles	Adults		
Attack rate on resource	a_{jr} = varied	a_{ar} = varied	$a_{cr} = 10$	
Attack rate on consumer		a_{ac} = varied		
Cannibalism		β = varied		
Attack rate in trade-off	$a_p = 6$			
Shape of trade-off	$\varepsilon = 0$			
Handling time	$h_p = 0.25$		$h_c = 0.1$	
Maintenance rate	$T_p = 0.4$		$T_c = 1.0$	
Background mortality	$\mu_p = 0.04$		$\mu_c = 0.1$	
Juvenile/adult size ratio	$z = 0.01$			
Conversion efficiency	$\sigma = 0.5$		$\sigma = 0.5$	
Resource productivity				$R_{max} = 3$
Resource turn-over rate				$\delta = 1$

Attack and maintenance parameters are mass-specific. Handling time parameter inversely mass-specific

them requires an individual-level measure of the juvenile predator's competitive ability. For this we use the resource density that is needed for positive growth ($v_j > 0$). Juvenile predators are considered superior to consumers when they have a positive net-biomass production rate and can grow in the consumer-resource equilibrium.

Based on the above considerations we distinguish three different cases of competitive hierarchy: *i*) the consumer is superior to the intraguild predator and juveniles cannot grow in the consumer-resource equilibrium, *ii*) the consumer is superior to the intraguild predator, but juvenile predators can grow in the consumer-resource equilibrium and *iii*) the intraguild predator is superior to the consumer. In the last case juveniles are always able to grow in the consumer-resource equilibrium (appendix 5.A). These three cases apply for the diet broadening scenario ($a_{ar} > 0$), while in the diet shift scenario ($a_{ar} = 0$) we can only distinguish the first two cases. Figure 5.1 shows how these three cases of competitive hierarchy correspond to the values that determine the resource feeding of the intraguild predator (a_{ar} and a_{jr}). The derivation of
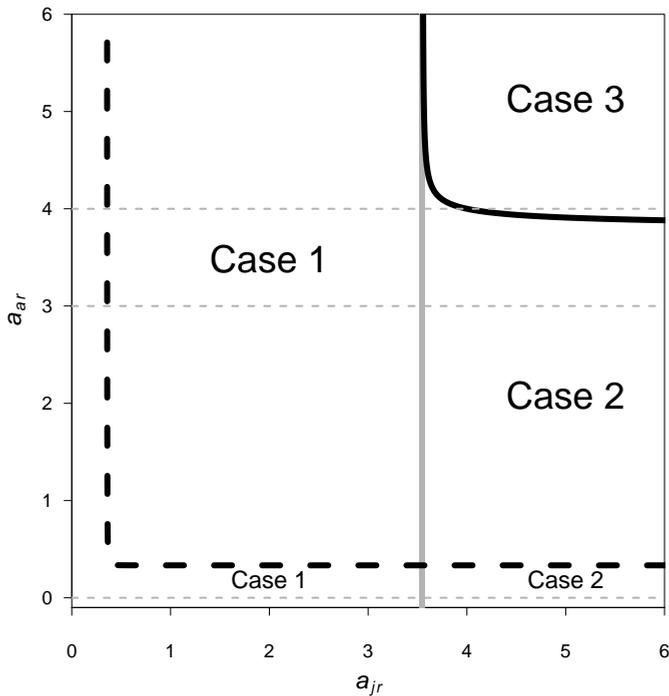
FIGURE 5.1 – Different cases of competitive hierarchy between consumers and intraguild predators as a function of a_{jr} and a_{ar}. The solid black line indicates the boundary between the overall competitive superiority of consumers vs. intraguild predators, with predators being superior at the upper-right of this line (case 3). The dashed black line indicates the region in which intraguild predators can persist solely on the resource if $R = R_{max}$, with persistence possible at the upper-right of this line. The vertical gray solid line separates the region where juvenile predators are superior to consumers (able to grow in the equilibrium resource density of consumers), with juveniles being superior to the right of this line. In case 1 the consumer is overall superior in resource competition. This also holds for case 2, but with the exception that juveniles are now superior to consumers. Horizontal dashed lines indicate the three different values of a_{ar} that are chosen in the analysis.

the boundaries shown in figure 5.1 is discussed in appendix 5.A. Based on figure 5.1 we choose three values of a_{ar} that, together with changes in a_{jr}, cover all three cases of competitive hierarchy in addition to the diet shift and diet broadening scenarios. For $a_{ar} = 0$ the intraguild predator has a diet shift and juvenile predators are superior to consumers for $a_{jr} > 3.55$. For $a_{ar} = 3$ intraguild predators have a diet broadening and can persist solely on the resource, but consumers are superior resource competitors. Again juvenile intraguild predators are superior to consumers for $a_{jr} > 3.55$. For $a_{ar} = 4$ the intraguild predator also has a diet broadening. Again, the juvenile intraguild predator is superior to the consumer for $a_{jr} > 3.55$ and, in addition, for

$a_{jr} > 4$ the intraguild predator outcompetes the consumer (figure 5.1). Finally, a_p controls the maximum value of a_{jr} and we take $a_p = 6$. By default the strength of the trade-off is set to $\varepsilon = 0$ (linear trade-off), but variation in this parameter is explored.

Model analysis

We used PSPManalysis (https://bitbucket.org/amderoos/pspmanalysis) to study equilibrium and evolutionary dynamics. PSPManalysis is a software package with numerical procedures to perform demographic, bifurcation and evolutionary analysis of physiologically structured population models. More details about the package can be found at https://bitbucket.org/amderoos/pspmanalysis. In addition to PSPManalysis we used MatCont (Dhooge et al. 2003), a Matlab package for numerical bifurcation analysis to asses equilibrium stability.

PSPManalysis uses adaptive dynamics as the framework for evolutionary analysis (Dieckmann and Law 1996; Geritz et al. 1998; Metz et al. 1995). In adaptive dynamics evolutionary change occurs by mutant phenotypes (y') that invade and take over the population-dynamical attractor of the resident phenotype (y). Invasion and replacement is only successful for mutants with phenotypes in the direction of the selection gradient. The selection gradient is sign equivalent with the derivative of the mutant's lifetime reproductive success, $R_0(y, y')$, with respect to the mutant's phenotype and evaluated at $y' = y$: $\left(\partial R_0(y',y)/\partial y'|_{y'=y} \right)$ (Durinx et al. 2008; Geritz et al. 1998). Evolutionary change can come to a halt when the selection gradient vanishes. Such an evolutionary singular strategy (ESS) can either be convergence unstable (an evolutionary repeller; ERP), convergence stable and evolutionary stable (a continuously stable strategy; CSS) or convergence stable but evolutionary unstable (an evolutionary branching point; EBP). Convergence stability tells whether gradual evolution moves towards the ESS (convergence stable) or away from the ESS (convergence unstable). Evolutionary stability refers to whether the monomorphic population can evolve towards a dimorphic population, in which the mutant and resident can coexist (evolutionary unstable; see also Geritz et al. 1998). PSPManalysis calculates the selection gradient numerically and detects and classifies evolutionary equilibria according to the above classification.

Our primary interest lies with the two values of a_{ar} where consumers outcompete intraguild predators, $a_{ar} = 3$ and $a_{ar} = 0$ (figure 5.1), which, respectively, correspond to the diet broadening and diet shift scenarios as studied by Toscano et al. (in press). Next we adopt $a_{ar} = 4$, in which case intraguild predators can outcompete consumers for $a_{jr} > 4$. We analyze the equilibrium and evolutionary dynamics as a function of a_{jr} in case of no cannibalism ($\beta = 0$) and with cannibalism ($\beta = 1$). We furthermore check robustness of the results with respect to a continuous change in the level of cannibalism (β), system productivity (R_{max}) and the strength of the trade-off (ε).

5.3 – Results

In our three species community we can have four different types of equilibria: a resource only equilibrium (R-equilibrium), a consumer-resource equilibrium (CR-equilibrium), a predator-resource equilibrium (PR-equilibrium) and a predator-consumer-resource-equilibrium (PCR-equilibrium). In the following we will use the above abbreviations to refer to the different types of equilibria. Except for very low values of resource productivity ($R_{max} < 0.2820$), the R-equilibrium is unstable because it can always be invaded by consumers. We will not pay further attention to this equilibrium. The PCR-equilibrium is also referred to as the coexistence equilibrium, or coexistence state. With the term 'stability' we refer to the stability of the population dynamical equilibrium and stable equilibria are those that are (locally) stable against invasion or extinction of a certain species (all eigenvalues have a real part less then zero). Limit cycles only occur in a small region of parameter space and their amplitude is insignificant, for which reason we will not consider them further below.

Diet broadening without cannibalism ($a_{ar} = 3$, $\beta = 0$)
For $a_{ar} = 3$ the intraguild predator exhibits a broadening of its diet throughout ontogeny and can persist on the resource alone. However, the intraguild predator is an inferior resource competitor compared to the consumer, irrespective of the value of a_{jr} (figure 5.1, case 1 or 2). Without cannibalism ($\beta = 0$) there is no stable coexistence between the intraguild predator and the consumer as a function of a_{jr} (figure 5.2; Toscano et al. in press). When the ontogenetic trade-off of the intraguild predator is directed towards late foraging success (low a_{jr} and consequently high a_{ac}), predator persistence is not possible and only the CR-equilibrium is stable. Although a PR-equilibrium is possible for low a_{jr}-values it is unstable due to the low food availability for juvenile predators. Food limitation in the juvenile stage leads to low adult biomass and, consequently, low predation pressure of adult predators on consumers (figure 5.2, left panels). Consumers can therefore invade this PR-equilibrium and outcompete the predator. An increase in a_{jr} changes the size distribution of the predator towards adult dominated. This initially increases predation pressure that invading consumers would experience, despite the decrease in predatory attack rate a_{ac} associated with the increase in a_{jr} (equation 5.1). In addition, the increase in a_{jr} leads to a decrease in equilibrium resource density and these processes stabilize the PR-equilibrium against invasion of the consumer. Initially, the stable PR-equilibrium co-occurs with a stable CR-equilibrium as an alternative stable state. A further increase in a_{jr} destabilizes the CR-equilibrium, as the higher a_{jr}-value allows predators to invade it. This makes the PR-equilibrium the only stable equilibrium state. At $a_{jr} \approx 6$, the adult predation rate on consumers reaches zero and consumers and intraguild predators only

interact through competition for the shared resource. Since consumers are superior competitors, the CR-equilibrium becomes the only stable outcome here.

In the PR-equilibrium, selection is always positive on a_{jr} and negative on a_{ac} (arrows along the predator equilibrium in figure 5.2; top left panel). Due to the lack of consumers in this state and the absence of cannibalism, predators derive no benefits from retaining a predatory morphology. Therefore, intraguild predators become increasingly specialized as resource foragers by increasing a_{jr}. Eventually this destabilizes the PR-equilibrium and allows consumers to invade and outcompete the intraguild predator. Selection on resource specialization of juveniles ultimately leads to the extinction of the intraguild predator (evolutionary suicide).

Diet broadening with cannibalism ($a_{ar} = 3$, $\beta = 1$)
When intraguild predators are cannibalistic the properties of the ecological equilibria are different (figure 5.2; right panels). The PR-equilibrium now becomes stable against invasion by the consumer at a value of a_{jr} that is higher than the value at which the CR-equilibrium destabilizes and can be invaded by the predator. The latter point has remained at the same a_{jr}-value compared to the non-cannibalistic situation. In between these two threshold values of a_{jr} a stable PCR-equilibrium occurs. Although adult predators benefit from feeding on the consumer in this coexistence state, selection on a_{jr} is still positive. This leads to a lower per capita predation rate on consumers, but total mortality of consumers still increases due to an increase in adult predator density. Along with an increase in a_{jr} the PCR-equilibrium changes into a PR-equilibrium when consumers go extinct. In this PR-equilibrium selection on a_{jr} reaches an evolutionary endpoint (arrows along predator equilibrium in figure 5.2; top right panel). As adult predators cannibalize juveniles, they benefit from maintaining a predatory morphology and the intraguild predator therefore does not completely specialize towards the highest possible resource foraging ability of juvenile predators. The stabilizing selection on a_{jr} as a result of cannibalism prevents the evolutionary suicide of the intraguild predator.

Diet shift without cannibalism ($a_{ar} = 0$, $\beta = 0$)
Equilibrium properties of LHIGP systems with a full ontogenetic diet shift have been described before by (Hin et al. 2011) and (Toscano et al. in press). Because adult predators do not feed on the resource ($a_{ar} = 0$; complete diet shift, see figure 5.1), reproduction, and therefore predator persistence, is only possible in the presence of consumers. Figure 5.3 shows the ecological equilibria as a function of resource specialization, parameterized by a_{jr} with concomitant changes in a_{ac} following the trade-off relation in equation 5.1. At the two extremes of this trade-off ($a_{jr} \approx 0$ or $a_{jr} \approx 6$) the intraguild predator cannot persist and there is only a stable CR-
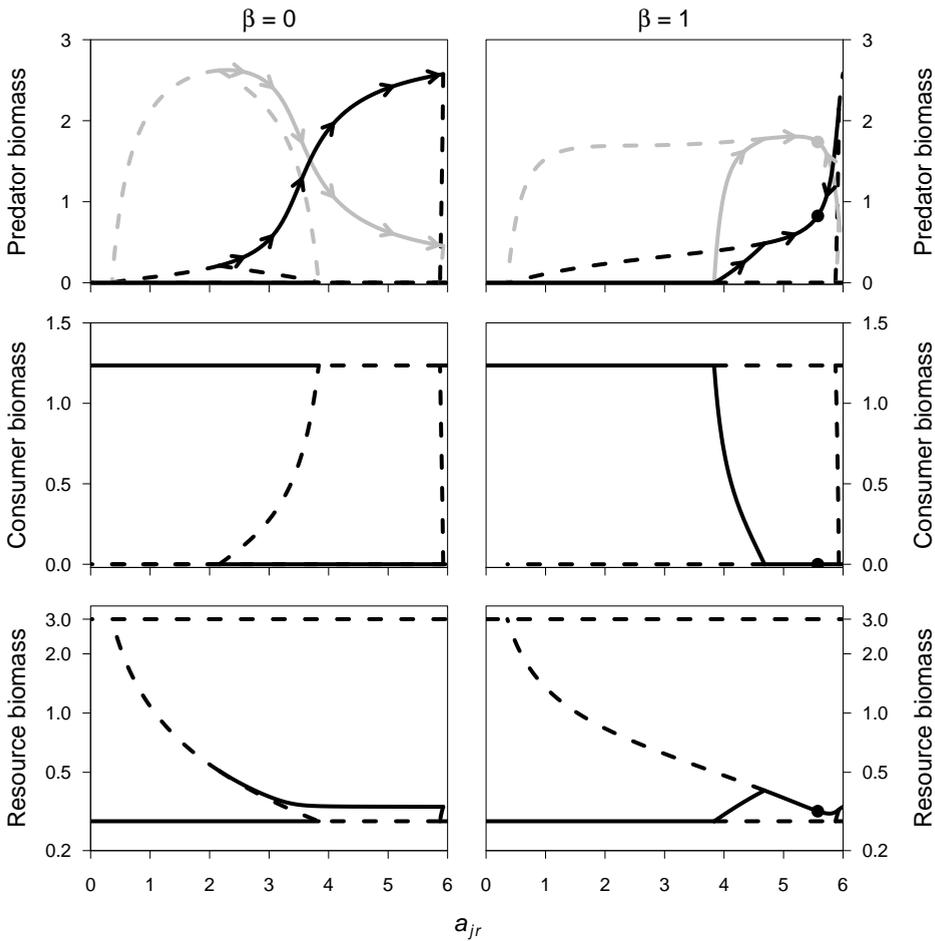
Figure 5.2 – Evolutionary dynamics of resource specialization (plotted as a function of a_{jr}, which is negatively related to a_{ac} through the trade-off in equation (5.1)) leads to evolutionary suicide of the intraguild predator when cannibalism is absent ($\beta = 0$; left panels) and to a stable evolutionary equilibrium when cannibalism is present ($\beta = 1$; right panels). Adult intraguild predators are able to feed on the shared resource (diet broadening scenario: $a_{ar} = 3$). All other parameters have default values (table 5.2). Solid (dotted) lines depict stable (unstable) equilibria of the ecological dynamics. Direction of selection on a_{jr} in the stable equilibrium with intraguild predators is indicated with arrowheads. Filled dots indicate evolutionary endpoints for a_{jr}, which are convergence and evolutionary stable. Black and gray curves in top panels represent adult and juvenile predator biomass, respectively.
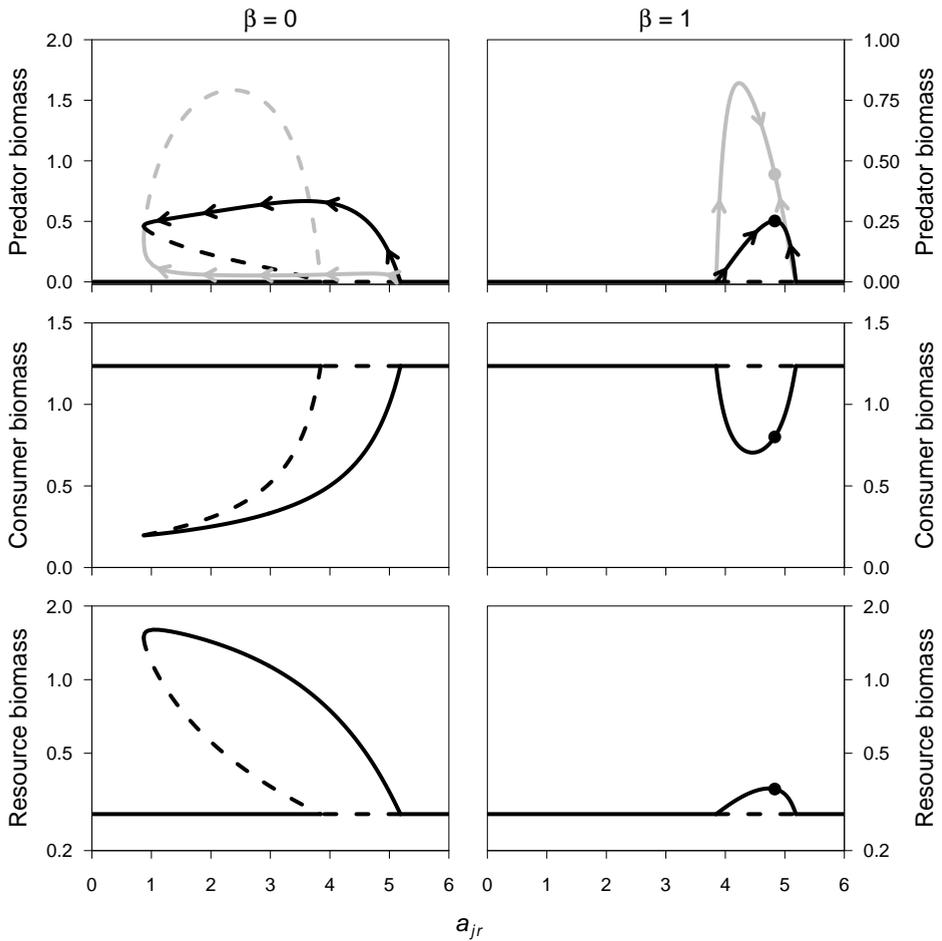
FIGURE 5.3 – Evolutionary dynamics of resource specialization (a_{jr} with concomitant change in a_{ac} following the trade-off in equation (5.1)) in the diet shift scenario (adult intraguild predators do not feed on the shared resource: $a_{ar} = 0$) leads to evolutionary suicide of the predator when cannibalism is absent ($\beta = 0$; left panels) and to a stable evolutionary equilibrium when cannibalism is present ($\beta = 1$; right panels). All other parameters have default values (table 5.2). All lines and symbols as in figure 5.2. Note the difference in y-axis scaling for predator biomass between left and right panels.

equilibrium. Persistence is possible when adult predators suppress consumers, thereby increasing resource availability for juvenile predators (figure 5.3; Hin et al. 2011; Walters and Kitchell 2001). This coexistence state is stable from $a_{jr} \approx 1$ until $a_{jr} \approx 5$, but co-occurs as an alternative stable state next to a stable CR-equilibrium for part of this parameter range. The CR-equilibrium can be invaded by predators when juveniles specialize on the resource (a_{jr} is high), which allows for positive juvenile predator growth for resource densities as present in the CR-equilibrium. However, for very high values of a_{jr} ($a_{jr} \leq 5$) invasion of the CR-equilibrium by predators is no longer possible, as adults no longer feed on consumers ($a_{ac} \approx 0$).

In the coexistence state, the suppression of consumers by adult predators leads to a high resource biomass density at equilibrium. Consequently, there is strong competition in the adult stage and little competition among juveniles. Maturation rates are high and reproduction rates are low, resulting in a low juvenile-adult biomass ratio. The fierce competition between adults favors a higher adult predation efficiency, at the expense of juvenile foraging ability. Thus, selection leads to lower values of a_{jr} and higher values of a_{ac} (arrows along PCR-equilibrium in figure 5.3; top left panel). Ultimately, this drives the predator population beyond the ecological threshold (fold bifurcation) that marks the minimum level of a_{jr} for which predator persistence is possible. Also in the case of a complete diet shift of the intraguild predator we therefore observe evolutionary suicide as a consequence of resource specialization in a non-cannibalistic LHIGP system, but remarkably enough now through selection towards adult as opposed to juvenile resource specialization.

Diet shift with cannibalism ($a_{ar} = 0$, $\beta = 1$)
Cannibalism among intraguild predators that exhibit a diet shift during ontogeny prohibits the occurrence of a PCR-equilibrium and a CR-equilibrium as alternative stable states (Toscano et al. in press). This is revealed by figure 5.3 (right panels), which shows the ecological equilibria as function of resource specialization. The range of a_{jr}-values for which the CR-equilibrium is unstable against invasion by predators remains identical to the case without cannibalism. However, persistence of the predator is not possible for a_{jr}-values outside this range. Cannibalism thus greatly diminishes the possibility of ecological persistence for the intraguild predator (Toscano et al. in press). Similar to the diet broadening scenario, cannibalism does stabilize selection on the resource specialization trade-off. From an evolutionary point of view cannibalism promotes predator persistence, by preventing the evolutionary suicide that results from strong selection towards adult specialization.

For values of a_{jr} below its evolutionary equilibrium value (indicated with the dot in figure 5.3, right panels) there is positive selection on a_{jr} in case of cannibalism, where in the non-cannibalistic case the selection gradient for similar values of a_{jr} is negative.

This change in the direction of selection with cannibalism can be explained by the change in predator size-structure that cannibalism induces. Cannibalism disrupts the top-down control of adult predators on consumers by shifting their foraging efforts toward juvenile predators (Toscano et al. in press). Consumer density is therefore higher and resource density lower than in the absence of cannibalism. The decrease in resource density as a consequence of cannibalism is so substantial that competition is most severe in the juvenile as opposed to the adult stage. As a consequence of cannibalism, the predator population therefore changes from being reproduction regulated, where competition is most severe in the adult stage, towards maturation regulated, where competition is most severe in the juvenile stage (De Roos and Persson 2013; De Roos et al. 2007). In a maturation regulated predator population, selection will tend to decrease juvenile competition through an increase in juvenile performance.

The effect of resource productivity (R_{max}) and trade-off shape (ε) in a diet broadening scenario ($a_{ar} = 3$)

The consequences of changes in resource productivity (R_{max}) and the shape of the trade-off (ε) on the model outcomes for the diet broadening scenario ($a_{ar} = 3$) are summarized in figure 5.4. Earlier studies have shown that an increase in resource productivity in a LHIGP system translates into an increased ecological persistence of the intraguild predator (Hin et al. 2011; Toscano et al. in press). In the diet broadening scenario this translates into an increase in the parameter range, for which a stable PR-equilibrium is possible (figure 5.4). Qualitatively, however, the parameter ranges of resource specialization and cannibalism that lead to different model outcomes do not change with changes in productivity (R_{max}) and trade-off shape (ε) (figure 5.4). Weak trade-offs (low ε-values) and high productivity decrease the threshold level of cannibalism (β) below which evolutionary suicide occurs and thus increase the region where selection on a_{jr} is stabilizing. For high levels of cannibalism the predator persists in a PCR-equilibrium, as the consumer can invade the PR-equilibrium. Also in this equilibrium a stable evolutionary endpoint of a_{jr} is possible (figure 5.4). Irrespective of resource productivity or trade-off shape, resource specialization of the predator is always directed towards juvenile specialization on the resource, at the expense of adult specialization on consumers/juveniles.

The effect of resource productivity (R_{max}) and trade-off shape (ε) in a diet shift scenario ($a_{ar} = 0$)

For the diet shift scenario ($a_{ar} = 0$), the model outcomes as presented in figure 5.3 depend on resource productivity (R_{max}) and trade-off shape (ε), but implications of the results remain the same. Quantitatively, weak trade-offs (low ε-values) and higher resource productivity increase the region of resource specialization for which
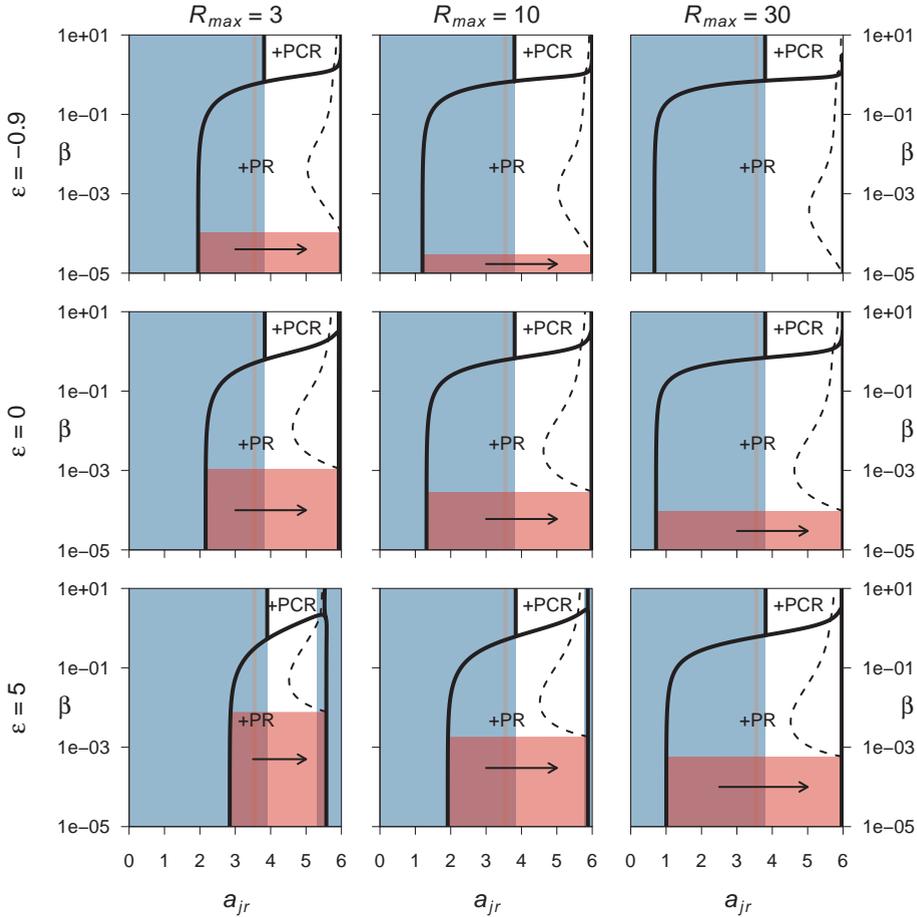
Figure 5.4 – Increasing productivity and decreasing trade-off strength decrease the regions of evolutionary suicide in the diet broadening scenario ($a_{ar} = 3$). Each panel shows the possible stable equilibria of the ecological dynamics as a function of a_{jr} and β, with a_{ac} related to a_{jr} following the trade-off in equation (5.1). The thick black lines indicate boundaries between parameter combinations for which different types of ecological equilibria with predators occur, with the text labels in between these boundaries indicating the type of equilibrium that occurs (+PR = PR-equilibrium, +PCR = predator-consumer-resource equilibrium). The blue shaded parameter regions indicate the presence of a CR-equilibrium that is stable against predator invasion. The dashed lines show the evolutionary equilibrium value of a_{jr}. All evolutionary equilibria are convergence and evolutionary stable (CSSs). In the red shaded regions, the evolutionary equilibrium for a_{jr} either does not exist or is located outside the region in which the ecological equilibrium is stable. Hence, the red shading indicates the parameter range for which selection on a_{jr} leads to evolutionary suicide. Horizontal arrows indicate the direction of selection in the region of evolutionary suicide. Outside the red shaded region the direction of selection is not indicated, but always points towards the evolutionary equilibrium (dashed line). To the right of the vertical gray lines the juvenile intraguild predators can grow at the resource density as set by consumers ($a_{jr} \approx 3.55$). For high values of β the predator persists in coexistence with the consumer and selection on a_{jr} is stabilizing.
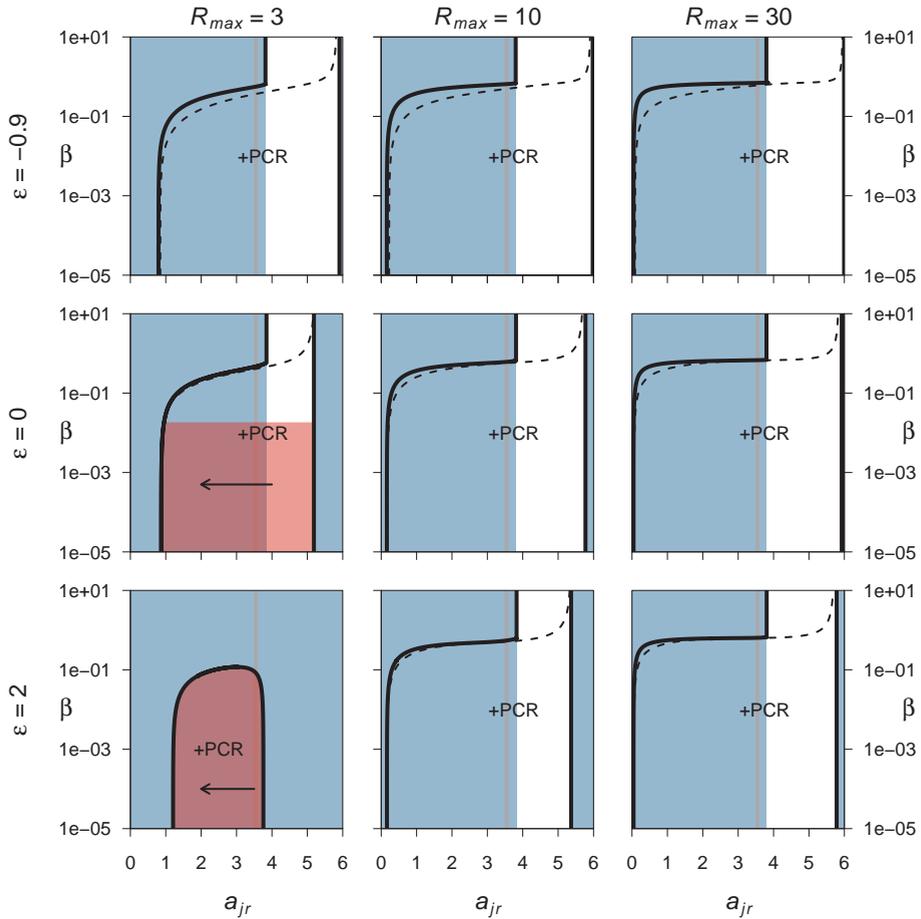
FIGURE 5.5 – In the diet shift scenario ($a_{ar} = 0$) the occurrence of evolutionary suicide depends on resource productivity (R_{max}) and trade-off strength (ε). For default parameter values ($R_{max} = 3$ & $\varepsilon = 0$), evolutionary suicide is, strictly speaking, only possible for low levels of cannibalism (on the y-axis) because there is no evolutionary equilibrium for a_{jr} (indicated by the dashed line) within the parameter range for which the ecological equilibrium with predators is stable (see also figure 5.3). For either a higher productivity or a weaker trade-off, the evolutionary equilibrium is within the parameter range with a stable ecological PCR-equilibrium, but located in close proximity to the persistence boundary of the predator (black solid lines) when cannibalism levels are low. When there is an overlapping stable CR-equilibrium (indicated by blue shading), any perturbation to the system can induce a shift to this alternative stable state and thus extinction of the predator. Only for higher levels of cannibalism the evolutionary equilibrium of a_{jr} is further away from the persistence boundary of the predator, in an area for which there is no overlapping stable CR-equilibrium. For a strong trade-off and low resource productivity the alternative CR-equilibrium is stable, independent of the level of cannibalism or the value of a_{jr}. All symbols and colors as in figure 5.4.

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a stable PCR-equilibrium exists and decrease the parameter regions for which the CR-equilibrium is stable against predator invasion, in particular for higher values of a_{jr} (figure 5.5). Beside these quantitative changes there are two qualitative differences. In case of a low resource productivity and a strong trade-off ($R_{max} = 3$ and $\varepsilon = 2$) the CR-equilibrium is stable for all values of the resource specializations (a_{jr} on the x-axis). The predator can persist in the PCR-equilibrium that occurs as alternative stable state next to the CR-equilibrium. However, in this PCR-equilibrium there is no stable evolutionary endpoint and negative selection on resource specialization will lead to extinction of the predator (evolutionary suicide). Another noteworthy difference is the absence of evolutionary suicide in the strict sense for values of resource productivity and trade-off shape other than $R_{max} = 3$ and $\varepsilon \leq 0$. Evolutionary suicide technically only occurs when very close to the ecological threshold of predator persistence (the solid black lines in figure 5.5) the selection on a_{jr} is in the direction of this threshold. While this is the case for $R_{max} = 3$ with $\varepsilon = 0$ and $R_{max} = 3$ with $\varepsilon = 2$, for all other cases an evolutionary equilibrium does occur, albeit for a value of a_{jr} close to the ecological threshold of predator persistence (figure 5.5). Therefore, for the value of a_{jr} corresponding to the ecological threshold of predator persistence, the direction of selection on a_{jr} points away from this threshold and evolutionary suicide does, strictly speaking, not occur. However, the evolutionary endpoint occurs in an area of trait space that is very close to the predator's threshold of persistence and any perturbation in resource productivity or large mutational step can push the predator population over this ecological threshold towards extinction.

Diet broadening with superior intraguild predators ($a_{ar} = 4$)

For $a_{ar} = 4$ the intraguild predator is superior in resource competition to the consumer for $a_{jr} > 4$ (appendix 5.A). The evolutionary outcomes for this case are comparable to the diet broadening scenario with $a_{ar} = 3$ (figure 5.2) and we therefore only highlight the main differences. For $a_{ar} = 4$, the PR-equilibrium can no longer be invaded by consumers at high a_{jr}, as was the case for $a_{ar} = 3$ (figure 5.6), and is thus stable. Without cannibalism ($\beta = 0$) positive selection on a_{jr} does not lead to evolutionary suicide and the resource specialization of juveniles becomes constraint by the value of a_p (figure 5.6; left panels). With cannibalism ($\beta = 1$) there is again stabilizing selection for a_{jr}-values in the PR-equilibrium (figure 5.6; right panels), which leads to an evolutionary equilibrium for high resource specialization of juveniles. Even higher values of cannibalism allow for the invasion of consumers in the PR-equilibrium and, consequently, lead to a stable PCR-equilibrium (figure 5.B1; Toscano et al. in press). Also in this PCR-equilibrium selection on resource specialization is stabilized at high
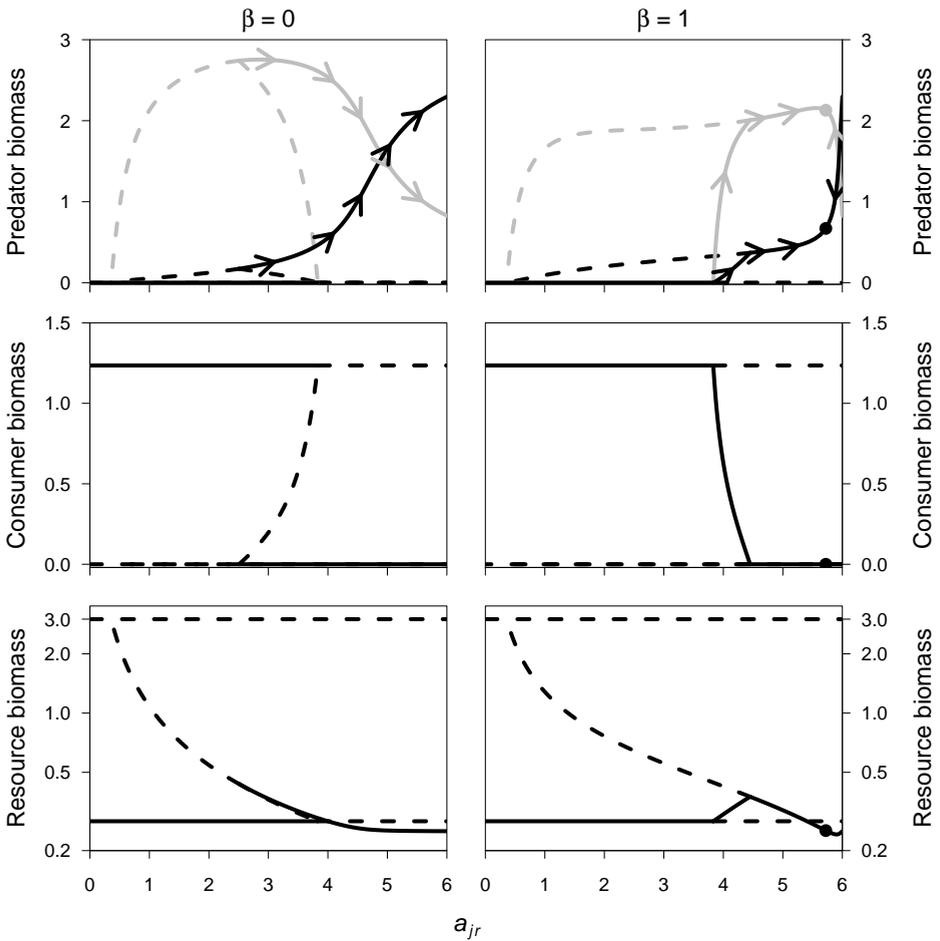
FIGURE 5.6 – Evolutionary dynamics of resource specialization (plotted as a function of a_{jr}, which is negatively related to a_{ac} through the trade-off in equation (5.1)) for $a_{ar} = 4$ with no cannibalism ($\beta = 0$; left panels) and with cannibalism ($\beta = 1$; right panels). For $a_{jr} > 4$, the intraguild predator becomes a better resource competitor compared to the consumer (when $\beta = 0$). Selection on the resource specialization trade-off (equation (5.1)) leads to increasing values of a_{jr}, and a decrease in a_{ar}. In case of cannibalism (right panels), selection is stabilized at high values of a_{jr}. All other parameters have default values (table 5.2). Lines and symbols as in figure 5.2.

juvenile specialization on the resource. Appendix figure 5.B1 shows furthermore that these results are qualitatively independent of the trade-off shape (ε) and resource productivity (R_{max}).

5.4 – DISCUSSION

We study the evolutionary and ecological dynamics of a potentially cannibalistic, onto-genetic omnivore in a life-history intraguild predation system, in which the ontogenetic omnivore (or intraguild predator) competes as a juvenile with a consumer species (or intraguild prey) that becomes its prey later in life (Abrams 2011; Hin et al. 2011; Pimm and Rice 1987; Polis et al. 1989; Van de Wolfshaar et al. 2006). We show that such on-togenetic omnivores (or intraguild predators) when subject to a trade-off in resource specialization between early- and late-life resources can only stably persist over evolu-tionary time when adult intraguild predators cannibalize juvenile predators. Without cannibalism, selection either increases resource specialization of juveniles, which neg-atively affects the feeding ability of adults, or selection favors (predatory) resource specialization of adults at the cost of poor performance of juveniles on the resource that is shared with the consumer. The direction of selection depends on whether adult predators are able to feed on the resource, which distinguishes a diet broadening scenario from a diet shift scenario and determines whether predators persist alone (diet broadening) or in coexistence with consumers (diet shift). In both scenarios, directional selection leads to evolutionary suicide of the intraguild predator because it forces the predator population into an area of trait space where its ecological per-sistence is compromised. Cannibalism prevents evolutionary suicide by stabilizing selection on the resource specialization trade-off. This happens because cannibalism creates a benefit to keep a predatory morphology for adult predators (in the diet broadening scenario) or because cannibalism changes the population regulation of the predator such that resource specialization of juveniles becomes important (in the diet shift scenario).

Our results potentially have broad ecological and evolutionary significance, as the majority of all animal species are ontogenetic or life-history omnivores that undergo an ontogenetic niche shift either because of ontogenetic growth (direct development) or as a result of metamorphosis (indirect development) (Persson 1988; Pimm and Rice 1987; Werner 1988; Werner and Gilliam 1984; Wilbur 1980). In ontogenetic omni-vores without a metamorphosis, the morphological and behavioral adaptations that are related to feeding on the different resources are controlled by a single genetic ar-chitecture or are subject to genetic correlations (Ebenman 1992; Marshall and Morgan 2011; Schluter et al. 1991; Werner 1988). When the different resources require different optimal phenotypes this results in opposing selection pressures between the life stages that feed on different resources (Ebenman 1992; Hjelm et al. 2000, 2003; Robinson et al. 1996; Schluter 1995; Schluter et al. 1991; Werner 1988). Such an ontogenetic trade-off makes persistence of ontogenetic omnivores vulnerable to competition with specialist species, raising the question of how ontogenetic omnivory can be such a widespread strategy.

Persistence of intraguild predators

An ontogenetic trade-off in feeding efficiency was originally proposed as the reason for why intraguild predators are inferior in resource competition compared to their specialist prey (Persson 1988; Werner and Gilliam 1984). Moreover, the competitive superiority of prey was put forward as one of the requirements that enabled coexistence between intraguild predators and prey in the absence of size-specific interactions (Diehl and Feißel 2000; Holt and Polis 1997). The assumption of competitive dominance of the prey is likely to hold in many, but certainly not all systems (Vance-Chalcraft et al. 2007). However, when intraguild predation is the result of an ontogenetic niche shift (life-history omnivory/intraguild predation; Abrams 2011; Hin et al. 2011; Rudolf 2007; Toscano et al. in press; Van de Wolfshaar et al. 2006, *this study*) the predictions about persistence and coexistence in such systems become more complicated and depend on a number of factors. We integrate these predictions in table 5.4, and distinguish between *i*) the extent of diet change during ontogeny of the intraguild predator, *ii*) the three cases of competitive hierarchy between consumers and predators and *iii*) the level of cannibalism. Table 5.4 describes the opportunity for persistence and potential coexistence on an ecological time scale by denoting the stable population dynamical equilibria that occur. In addition, table 5.4 also provides an overview of the evolutionary dynamics that result from selection on the ontogenetic trade-off in resource specialization.

The assumption that consumers are competitively superior to all predators diminishes the ecological scope for persistence of predators and coexistence with consumers (Hin et al. 2011; Toscano et al. in press). For no or low levels of cannibalism, the superiority of consumers leads to alternative stable states between an equilibrium with predators present (either PR or PCR-equilibrium, depending on the extent of diet change of the intraguild predator) and a CR-equilibrium (table 5.4; Hin et al. 2011; Toscano et al. in press). With higher levels of cannibalism the competitive superiority of consumers is even more detrimental as the equilibrium, in which predators are present, disappears completely and only a CR-equilibrium remains. Cannibalism hence disrupts ecological persistence of intraguild predators in LHIGP systems, in which consumers are superior to juvenile predators, a result that was pointed out by Toscano et al. (in press). Even in cases that non-cannibalistic omnivores in LHIGP systems are predicted to persist ecologically (Hin et al. 2011; Toscano et al. in press), we show here that their potential to persist over evolutionary time-scales is threatened by selection on the ontogenetic trade-off in feeding ability on the different resources. In these cases, cannibalism enhances persistence on evolutionary timescales if intraguild predators can evolve such that the competitive hierarchy changes from consumers being superior towards juvenile predators being superior or even predators being overall superior. The incorporation of evolutionary dynamics into models of LHIGP systems

thus leaves us to conclude that these systems can only persist stably when levels of cannibalism (compared to interspecific predation) are not low and when (juvenile) intraguild predators are competitively superior to consumers.

The occurrence of cannibalism and the competitive hierarchy between juvenile intraguild predators and consumers in LHIGP systems were reviewed for a number of freshwater fish species by Byström et al. (2013). They concluded that large ontogenetic omnivores preferentially select conspecifics over interspecific prey (high values of β in our study) and that consumer species are more efficient zooplankton foragers than juvenile ontogenetic omnivores. The latter conclusion was based on attack rate measurements from separate feeding experiments (Byström et al. 2013). The high cannibalistic preference as observed by Byström et al. (2013) is in accordance with the requirements for predator persistence in LHIGP system that we pose here. However, it is difficult to draw conclusions about competitive inferiority of juvenile ontogenetic omnivores relative to their prey species based on a higher attack rate alone. To be able to compare the results of Byström et al. (2013) to our framework, information on other processes that contribute to competitive ability are required. These processes include handling times, maintenance metabolism and conversion efficiency. The crucial experimental test would be to study whether juvenile ontogenetic omnivores can successfully grow and mature under resource conditions as set by the specialist consumer species they compete with for resources. Besides the role of exploitative competition, other interspecific interactions such as interference or predation can also play an important role in determining to what extent juvenile ontogenetic omnivores suffer from competition with specialist consumers under natural conditions.

Table 5.4 (opposite page) – Theoretical predictions of persistence of (cannibalistic) ontogenetic omnivores and coexistence with specialist consumers in life-history intraguild predation systems. The table distinguishes between 3 types of competitive hierarchy: *i*) consumers are superior, *ii*) juvenile predators are superior to consumers, but adult predators are not and *iii*) both juvenile and adult predators are superior to consumers; 3 levels of cannibalism: *i*) no or low cannibalism, *ii*) medium cannibalism and *iii*) high cannibalism; and whether the intraguild predator undergoes a diet broadening or diet shift over ontogeny (top vs bottom part of the table, respectively). In case of a diet shift predators cannot be competitively superior to consumers since adult predators do not feed on the resource. For each combination of competitive hierarchy, level of cannibalism and ontogenetic diet change the table presents the possible ecological equilibria and the evolutionary process. Evolution acts either to increase resource specialization of juveniles on the shared resource, or of adults on the consumer as studied with the trade-off in equation (5.1). CR; consumer-resource equilibrium; PR: predator-resource equilibrium; PCR: predator-consumer-resource equilibrium; ASS: alternative stable states.

Diet broadening

Level of cannibalism		Competitive hierarchy		
		Consumer > all predators	Juvenile predators > consumers	All predators > consumers
No / low	Ecological	ASS: PR/CR[1]	PR	PR[1]
	Evolutionary	Suicide	Suicide	Persistence[a]
Medium	Ecological	ASS: PC/CR or only CR[1,b]	PR	PR[1]
	Evolutionary	*Evolutionary transient to juvenile predators > consumers*	Persistence	Persistence
High	Ecological	Only CR[1]	PCR	PCR[1]
	Evolutionary	No persistence	Persistence	Persistence

Diet shift

Level of cannibalism		Competitive hierarchy		
		Consumer > all predators	Juvenile predators > consumers	All predators > consumers
No / low	Ecological	ASS: PCR/CR[1,2]	PCR[1,2]	
	Evolutionary	Suicide	Suicide	
Medium	Ecological	ASS: PCR/CR or only CR[1,c]	PCR[1]	
	Evolutionary	Persistence	*Evolutionary transient to consumers > all predators*	
High	Ecological	Only CR[1]	PCR[1]	
	Evolutionary	No persistence	Persistence	

[1] Toscano et al. in press [2] Hin et al. 2011 [a] Evolution toward maximum juvenile specialization and loss of ontogenetic omnivorous life history
[b] Changes from PR/CR to only CR with increasing cannibalism [c] Changes from PCR/CR to only CR with increasing cannibalism

A number of multi-generation laboratory experiments on LHIGP systems studied the factors that determine persistence and coexistence after invasion of *Poecilia reticulata* (Common Guppies; the intraguild predator) into food-limited populations of *Heterandria formosa* (Least Killifish; the intraguild prey) (Reichstein et al. 2013; Schröder et al. 2009*a*). Schröder et al. (2009*a*) showed that in this system invasion success of *P. reticulata* depends on the invader body size: small, juvenile *P. reticulata* do not manage to invade *H. formosa* populations, whereas large *P. reticulata* can successfully invade and after invasion drive *H. formosa* to extinction. Stable, long-term coexistence between *P. reticulata* and *H. formosa* was rarely observed by Schröder et al. (2009*a*), a result that corresponds to theoretical predictions of LHIGP systems if the intraguild predator has a diet broadening during ontogeny (Toscano et al. in press; Van de Wolfshaar et al. 2006, *this study*). The *P. reticulata* used in the experiment of Schröder et al. (2009*a*) were derived from a high predation (HP) environment. By using *P. reticulata* from a low predation (LP) environment, Reichstein et al. (in prep.) showed that weaker predation increases the possibility for coexistence, although only in the absence of spatial refuges. Invasion success still depended on invaders body size in the experiment by Reichstein et al. (in prep.) and coexistence was especially enhanced for the large invaders. Theory on LHIGP can accommodate for this result in case the *P. reticulata* from low predation environments have an enhanced competitive ability and adult/large *P. reticulata* are cannibalistic (Toscano et al. in press, *this study*). The former is indeed the case according the Reichstein et al. (in prep.). Cannibalism also occurs in *P. reticulata* (Reichstein et al. in prep.) and, based on the theory developed here and in Toscano et al. (in press), we hypothesize that the level of cannibalism in each replicate experiment might be the decisive factor that determines whether coexistence or prey extinction results.

Implications for the occurrence of cannibalism in nature

It is recognized that cannibalism is a common interaction in terrestrial and aquatic food webs (Fox 1975; Polis 1981; Polis et al. 1989; Smith and Reay 1991). This holds especially for systems with substantial body size growth, such as the life-history intraguild predation systems studied here. Our results show that non-cannibalistic LHIGP systems do not persist on evolutionary timescales because of the evolutionary suicide of non-cannibalistic intraguild predators as a result of selection on the ontogenetic trade-off in resource specialization. This mechanism thus provides an explanation for the common occurrence of cannibalism in such systems. However, since already small amount of cannibalism (relative to interspecific predation) can stabilize selection on the ontogenetic trade-off (figure 5.4 and figure 5.5), systems that might seem non-cannibalistic could potentially still be persisting because of the stabilizing effect that

results from a small degree of cannibalistic feeding. Furthermore, the incorporation of a small degree of cannibalism can lead to small changes in the population dynamics, but have a large qualitative effect on the evolutionary outcome. This study adds to the idea that cannibalism can have multiple, diverse effects on ecological and evolutionary dynamics of natural populations (Claessen et al. 2000, 2004; Dercole 2003; Getto et al. 2005; Ohlberger et al. 2012*a*; Polis 1981; Rudolf 2007; Smith and Reay 1991) and the true impact of cannibalism is therefore studied best in a specific context when a considerable amount of system-specific detail is available.

Evolution of resource specialization over ontogeny

Evolution of resource specialization has mainly been studied at an interspecifc level, addressing the question under which circumstances species evolve to be specialist or generalist (Futuyma and Moreno 1988; Levins 1962, 1963; Nurmi and Parvinen 2008, 2013; Rueffler et al. 2006*b*, 2007; Wilson and Turelli 1986). A central result from these studies is that under a weak trade-off (or a convex fitness set) generalist should evolve, while under a strong trade-off (or concave fitness set) specialists should evolve (Levins 1962; Ma and Levin 2006; Mazancourt and Dieckmann 2004; Rueffler et al. 2006*b*). However, frequency- and density-dependence have been shown to complicate this picture (Ma and Levin 2006; Mazancourt and Dieckmann 2004; Rueffler et al. 2006*b*, 2007). Resource specialization across ontogeny is much less studied (but see Ebenman 1992 and Ten Brink and De Roos 2017 for a theoretical treatment and German et al. 2014; Hjelm et al. 2000, 2003; Schluter et al. 1991 for empirical work). Ebenman (1992) finds that for strong trade-offs (corresponding to a large difference between juvenile and adult niche) selection favors juvenile specialization, at the expense of adult performance. For a weak trade-off (when niche differences are small) specialization does not occur and an intermediate phenotype evolves. In the study of Ebenman (1992) adult specialization only occurs for weak trade-offs and when the productivity of the adult niche is low in comparison with the juvenile niche. Ten Brink and De Roos (2017) show that ontogenetic niche shifts only evolve when the adult habitat is sufficiently productive and when this does not hamper juvenile performance in the original habitat. Selection even favors maintaining high juvenile growth rates with adults being maladapted to their resource (Ten Brink and De Roos 2017). Both Ebenman (1992) and Ten Brink and De Roos (2017) hence show that juvenile performance is more important than adult performance. Our study is in accordance with this view, since we find that most evolutionary stable outcomes are those with high resource specialization of juvenile intraguild predators (high a_{jr}). Adult specialization is only observed in the diet shift scenario and always occurs in combination with a cultivation effect that nullifies competition in the juvenile stage (figure 5.2 and figure 5.4).

However, in all of these cases there is an imminent risk of extinction for the predator, because the evolutionary equilibrium occurs close to the ecological persistence boundary and there exists an alternative stable CR-equilibrium.

Evolutionary suicide in a community context

Evolutionary suicide or Darwinian extinction is a process in which a population adapts in a way that compromises its own persistence (Ferrière and Legendre 2013; Parvinen 2005, 2016; Rankin and López-Sepulcre 2005; Webb 2003). It has been observed in a diversity of ecological models, but receives only little attention from empirical workers (but see Fiegna and Velicer 2003; Rankin and López-Sepulcre 2005). Parvinen (2005, 2016) distinguishes deterministic evolutionary suicide, in which selection pushes the population across a population dynamical threshold or bifurcation (*e.g.* Ferrière and Legendre 2013; Gyllenberg and Parvinen 2001; Parvinen 2005; Parvinen and Dieckmann 2013), from demographically stochastic evolutionary suicide, where selection reduces population size and this increases the likelihood of extinction due to demographic stochasticity (*e.g.* Matsuda and Abrams 1994). It was shown by Gyllenberg and Parvinen (2001) that deterministic evolutionary suicide can only occur when the population dynamical bifurcation is a discontinuous transition towards extinction (see Webb 2003 or Parvinen 2005 for an overview of such population dynamical bifurcations). A common example of evolutionary suicide is when the population evolves across a saddle-node (or fold) bifurcation towards extinction (Dercole 2003; Ferrière and Legendre 2013; Gyllenberg and Parvinen 2001; Parvinen 2005). Such a bifurcation also occurs in the diet shift scenario of the model studied here, where for low levels of cannibalism two equilibria collide and disappear with decreasing juvenile resource specialization (figure 5.3, left panels). Evolutionary suicide in the diet broadening scenario operates through a different mechanism. In this case, adaptation of the predator drives the system across a continuous transition in population dynamics, namely the invasion boundary of the consumer. Immigration of consumers then leads to an abrupt shift in ecological dynamics (attractor switching) and extinction of the predator. The latter possibility for evolutionary suicide arises because we study evolutionary dynamics of a species (the intraguild predator) in a community context, therefore allowing for alternative community attractors. Since most studies on evolutionary suicide study species in isolation, or merely accompanied by a resource, we postulate that evolutionary suicide might be much more common than currently acknowledged when evolutionary dynamics are studied in a community context.

Conclusions

Size-specific interactions prevail in natural communities and many ontogenetic omnivores are likely involved in a mixed predation/competition interaction with a specialist consumer species (Olson et al. 1995; Persson 1988; Toscano et al. 2016; Wilbur 1988). We extend the current body of theory on persistence and coexistence in these systems by studying evolutionary dynamics under an ontogenetic trade-off in feeding ability between early and late resources. We show that evolutionary suicide limits persistence of a non-cannibalistic intraguild predator, but cannibalism can lead to ecological and evolutionary stable persistence if juveniles can overcome the negative effects of competition with consumers. Our analysis shows that the requirements of species for persistence on ecological and evolutionary time scales differ and advocates for considering both processes simultaneously.

ACKNOWLEDGMENTS

Appendix 5.A Motivation for attack rate parameters

Similar to Hin et al. (2011) we evaluate for which values of a_{ar} and a_{jr} the predator is superior in resource competition compared to the consumer. Based on this we select three value of a_{ar} that distinguish between three qualitatively different cases.

The competitive abilities of the consumer and the predator are quantified by the resource density in the consumer-resource (CR) and predator-resource (PR) equilibrium (Tilman 1980), respectively, provided such an equilibrium exists. This is denoted by R_c^* in case of the consumer-resource equilibrium and R_p^* for the predator-resource equilibrium. The expression for R_c^* follows from solving dC/dt for R, while setting $P_a = 0$, and is given by

$$R_c^* = \frac{T_c + \mu_c}{(a_{cr}\,(\sigma - h_c\,(T_c + \mu_c)))}$$

Next, we evaluate for which combinations of a_{jr} and a_{ar} the predator can persist in case $R = R_c^*$ and $C = 0$ and $\beta = 0$. The condition for predator persistence in a predator-resource equilibrium is $R_0(R_p^*) = 1$, where $R_0(R)$ is the expected lifetime reproduction of a single predator individual and given by De Roos and Persson (2013).

$$R_0(R) = \frac{\nu_a(R)}{\mu_p} z^{D_j/\nu_j(R)-1}$$

To assess the competitive ability of the predator in relation to the consumer we evaluate $R_0(R_c^*) = 1$. This results in the black solid curve that is a function of a_{jr} and a_{ar} (figure 5.1 main text). To the upper-right of this curve predators outcompete consumers ($R_p^* < R_c^*$), while at the other side consumers outcompete predators: ($R_c^* < R_p^*$). We refer to this type of competitive hierarchy as the overall superiority or inferiority of consumers and predators. Furthermore, we assess the persistence boundary for the predator as a function of a_{jr} and a_{ar} in case $R = R_{max}$ by evaluating $R_0(R_{max}) = 1$. This results in the black dashed curve in figure 5.1 (main text). At the bottom-left of this line predators cannot persist solely on the resource.

Besides the overall competitive hierarchy of consumers and intraguild predators, we also distinguish the competitive hierarchy between consumers and juvenile predators alone. To this end we propose that juvenile intraguild predators are competitively superior to consumers when they can grow in the resource density in the consumer-resource equilibrium: $\nu_j(R_c^*) > 0$. Evaluating this expression for the default parameters in table 5.2 leads to the gray solid line in figure 5.1 (main text).

Based on the different regions of competitive ability as shown in figure 5.1 (main text) we choose three values of a_{ar} that, together with changes in a_{jr}, cover all the qualitative competitive hierarchies between consumers and intraguild predators. For $a_{ar} = 0$, adult intraguild predators do not feed on the resource and the overall competitive ability of the predator is not defined. Juvenile predators can grow in the

resource equilibrium as set by consumers and are competitively superior to consumers for $a_{jr} > 3.55$, while for lower values consumers are competitively superior to juvenile predators. This case corresponds to the diet shift scenario as studied by Toscano et al. (in press). For $a_{ar} = 3$, intraguild predators can persist on the resource but they are overall competitively inferior compared to consumers irrespective of a_{jr}. Again, for $a_{jr} > 3.55$ juvenile predators are superior to consumers. Case 3: $a_{ar} = 4$, intraguild predators can persist on the resource and they are overall competitively superior to consumers for $a_{jr} > 4$. Already for $a_{jr} > 3.55$ juvenile predators are superior to consumers. The three different values are indicated in figure 5.1 (main text).

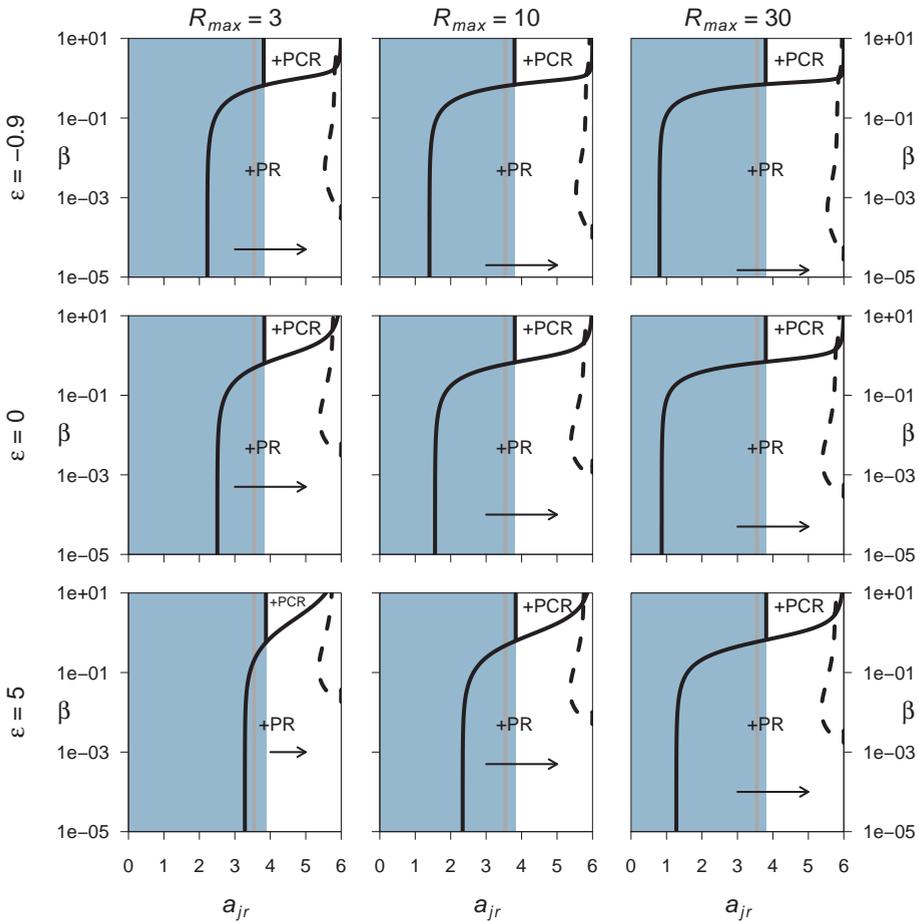## APPENDIX 5.B   SUPPLEMENTARY FIGURE

FIGURE 5.B1 – For $a_{ar} = 4$ intraguild predators can become overall superior in resource competition provided that a_{jr} is sufficiently large, in which case selection on the resource specialization trade-off (equation (5.1)) no longer leads to evolutionary suicide for low levels of cannibalism (β). There is still positive selection on a_{jr} (as indicated by the horizontal arrows), but predators persist in a stable PR-equilibrium at $a_{jr} = a_p = 6$ and, following equation (5.1), $a_{ac} = 0$. Higher levels of cannibalism lead to stabilizing selection on a_{jr}, as indicated by the dashed lines that show the evolutionary equilibria of a_{jr}. All evolutionary equilibria are convergence and evolutionary stable (CSSs). Even higher levels of cannibalism lead to predators persisting in coexistence with consumers. Different panels show the result of changes in productivity (R_{max}) and trade-off shape (ε). The thick black lines indicate boundaries between parameter combinations for which different types of ecological equilibria with predators occur, with the text labels in between these boundaries indicating the type of equilibrium that includes predators (+PR = PR-equilibrium, +PCR = predator-consumer-resource equilibrium). Right to the vertical gray lines the juvenile intraguild predators can grow in the resource density as set by consumers ($a_{jr} \approx 3.55$). The blue shaded parameter regions indicate the presence of a CR-equilibrium that is stable against predator invasion.