

Size-Dependent Intraguild Predation, Cannibalism, and Resource Allocation Determine the Outcome of Species Coexistence

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ABSTRACT: Intraguild predation (IGP), a system in which species compete for resources and prey on each other, is more common than existing theory predicts. In theory, an IG predator and its prey can coexist if the IG predator is a weaker competitor for a shared resource and the predator directly benefits from consuming the prey. However, many species that are IG predators also consume members of their own species (cannibalism). Here, we ask whether cannibalism can help resolve the paradox of IGP systems. Our approach differs from previous work on IGP and cannibalism by explicitly considering the size dependence of predatory interactions and how the benefits of predation are allocated to survival, growth, and fecundity of the predator or cannibal. Our results show that cannibalism facilitates coexistence under conditions that are opposite of those predicted by standard IGP theory: species can coexist when the cannibal is a better competitor on the shared resources, directly benefits little from consuming conspecifics, and allocates resources from predation more toward growth and fecundity over survival. Because the effects of IGP and cannibalism are opposite, when an IGP predator is also a cannibal, coexistence between the IGP predator and its prey is not possible and instead depends on the operation of other coexistence mechanisms (e.g., resource partitioning). These results point to the importance of understanding the relative rates of IGP and cannibalism as well as the resource allocation strategy of the IG predator in determining the likelihood of species coexistence.

Keywords: species coexistence, cannibalism, intraguild predation, alternate stable states, integral projection models, asymmetric competition.

Introduction

Understanding coexistence among species is important because diversity is a defining property of natural communities (Hutchinson 1959, 1961). Theories for species

coexistence invoke a variety of mechanisms, both ecological and evolutionary, operating in diverse contexts (Brown and Wilson 1956; Hutchinson 1961; Stewart and Levin 1973; Koch 1974; Armstrong and McGehee 1980; Slatkin 1980; Chesson and Warner 1981; Taper and Chase 1985; Schluter and McPhail 1992; Taper and Case 1992; Chesson 1994, 2000, 2003, 2008; Schluter 2000; Pfennig and Pfennig 2009). The earliest heuristic theories focused on differences between species in their competitive ability or in their resource niches (e.g., MacArthur and Levins 1967). More sophisticated theory has incorporated the potential for population structure to promote coexistence. This work includes studies of how changes in competitive ability and resource use across discrete (Haefner and Edson 1984; Loreau and Ebenhoeh 1994; Moll and Brown 2008; Ackleh and Chiquet 2011; Miller and Rudolf 2011; de Roos and Persson 2013; Nakazawa 2015) and continuous (Bassar et al. 2017b) life cycle stages affect the likelihood of coexistence. The general rule that has emerged from these studies is that two competing species may coexist even if one species is a dominant competitor as long as there are some stages in the life cycle in which the inferior competitor can escape competition with the dominant competitor.

Competing species often interact in an additional important manner, in which one of the species is also a predator of the other (intraguild predation [IGP]; Fagan 1997; Holt and Polis 1997; Holyoak and Sachdev 1998; Polis et al. 1989; Diehl and Feiße 2000; Mylius et al. 2001; Diehl 2003; Arim and Marquet 2004; Tanabe and Namba 2005). In other cases, each species is both competitor and predator of the other (bidirectional IGP; Polis et al. 1989). These interactions also frequently play out across discrete life stages and/or a continuous range of body sizes; typically, the older or larger individuals of one species consume the younger or smaller individuals of the other (Polis

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et al. 1989; Schellekens and van Kooten 2012). The coexistence of intraguild predators is challenging to explain because interspecific predation often destabilizes otherwise stable interactions, leading to the emergence of alternative stable states wherein either species can exclude the other and a narrower range of situations in which two species may stably coexist. Theory has suggested that for species engaged in IGP to coexist, the predator must be a weaker competitor for the shared resource and must gain a significant direct benefit (i.e., consumption and conversion to body mass, survival, or offspring) from the killing of the prey in addition to the indirect benefit of reduced competition (Holt and Polis 1997).

Because nature is rarely simple, the complete story of IGP and its role in species coexistence cannot be told without acknowledging the role of its less often discussed analog, intraspecific predation (Claessen et al. 2004; Rudolf 2007). Often referred to as cannibalism, intraspecific predation is a common feature of many animal populations (Fox 1975; Polis 1981; Elgar and Crespi 1992), particularly those strongly structured by body size (Polis 1981; Claessen et al. 2004), and may even regulate some populations (Van Buskirk 1989). Because body size so often determines who eats whom, particularly in fish and many arthropods, intraguild predators are also often cannibals, leading to a situation where interspecific and intraspecific predation are inextricably linked (Polis et al. 1989; Claessen et al. 2004).

Can the addition of cannibalism to IGP systems lead to coexistence between an IG predator and its IG prey? There is some theoretical evidence to suggest that it can. Using a continuous-time model of dynamics of a single resource, an IG predator, and an IG prey, Rudolf (2007) showed that when the IG predator is also a cannibal, coexistence between the IG predator and prey is possible even when the IG predator is competitively superior on the shared resource. This contrasts starkly with classical results from studies of IGP systems in which coexistence is possible only if the IG prey is the superior competitor. When the IG prey is the cannibal, then the classical results hold. Toscano et al. (2017) added cannibalism to the model of an IG predator (Hin et al. 2011) and allowed either the IG predator or the IG prey to be competitively superior. As in Rudolf (2007), when the IG predator was competitively superior and a cannibal, then coexistence between the IG predator and prey was possible.

These results suggest that cannibalism in the IG predator can act to facilitate coexistence in IGP systems that classic theory predicts to be unstable. However, the existing models address only a subset of the possible situations in which cannibalism can occur. There are three challenges to finding those conditions.

First, who eats whom in IGP systems with or without cannibalism is largely determined by differences in size be-

tween the interacting individuals. However, most theory for IGP and cannibalism employs either unstructured models or a simplified age structure, with age considered a proxy for size. For example, the models of Rudolf (2007) and Toscano et al. (2017) incorporate a simple two-age structure for the cannibal but no structure for the other species. Neither model addressed bidirectional IGP systems or systems in which each participant is also a cannibal. Ecological systems are replete with a variety of population structures, and ecological theory indicates that population dynamics in structured populations depends heavily on the nature of the structure (Caswell 2001; de Roos and Persson 2013). The same is true for the outcome of species interactions (de Roos 2021). For IGP systems with cannibalism, where size dictates who eats whom, the distribution of intra- and interspecific predation across continuous sizes is likely to be important in determining the outcome of the interaction and deriving predictions that can be tested in the field.

Second, although classic predictions about the coexistence of IGP predators and their prey hinge critically on the amount of direct benefit the predator receives from consuming its prey (Holt and Polis 1997), predictions about this effect for cannibalism are lacking. When cannibalism depends on age or size, there are positive effects on larger individuals but negative ones on smaller individuals. The balance between these effects will determine how much direct benefit cannibalism is conferring. This reflects the more general challenge: cannibalism introduces direct and indirect effects on fitness that change across the life cycle, and we do not have theory that embraces this complexity.

Third, because competitive ability and predation rates are likely to depend on size distributions, the outcome of species interactions can be heavily influenced by how individuals of each species allocate their resources among competing demands of survival, growth, and reproduction. This is because different allocation strategies will change size distributions. There is little theory about how allocation of the resources gained through predatory interactions (i.e., how the direct benefits are used) alters species coexistence predictions in IGP and cannibalistic species assemblages. Prior work has assumed that direct benefits are used for reproduction. As a result, there is currently little scope for understanding how organisms with different resource allocation strategies (survival vs. growth and reproduction) across their life cycles contributes to species coexistence.

Here, we develop a framework to model the role of IGP and cannibalism in species coexistence in structured populations that addresses these three challenges. Our framework is distinguished from previous efforts by explicitly considering how the traits of individuals (e.g., body

size) interact through competitive and predatory interactions. In doing so, we work directly with body size distributions in both species and model the interactions as size dependent. This work generalizes earlier models in which only one of the interacting species is structured and the interactions are based on age (Rudolf 2007), models based on mean-field approximations at equilibrium (Toscano et al. 2017), and models allowing direct predatory benefits to affect only the birth rate (Holt and Polis 1997; Rudolf 2007; Toscano et al. 2017).

The framework extends our previous approach of using continuous trait-structured discrete-time models of competing species (Bassar et al. 2016, 2017b). We extend our previous models by incorporating uni- and bidirectional IGP and cannibalism. We then parameterize the model using data from fish in Trinidadian streams and perturb the predation parameters to ask three questions. How does the introduction of cannibalism into a unidirectional IGP system change the conditions necessary for coexistence? How does altering the allocation strategy of the direct benefit (survival vs. growth and reproduction) alter the conditions necessary for coexistence? And do the effects of cannibalism on coexistence in a unidirectional system also operate in a bidirectional IGP system?

Our modeling framework expands the range of conditions under which theoreticians can study IGP and cannibalism and simultaneously gives empirical researchers the tools to test predictions with data that can be readily collected in the field.

Material and Methods

To address these questions, we extended models for size-dependent competitive asymmetry and niche differentiation originally described in Bassar et al. (2017b). We summarize these models here. The complete set of functions for the models is given in table 1, and the parameter values used in the analyses are given in table 2. A simple single-species, single-sex (female-only) integral projection model is written

$$n(z', t + 1) = \int_L^U [G(z'|z)S(z) + D(z'|z)M(z)S(z)]n(z, t)dz, \quad (1)$$

where $n(z, t)$ is a function describing the number of individuals of body size z at time t and $n(z', t + 1)$ is a function describing the number of individuals of z' at time $t + 1$. The demographic rate functions S , G , M , and D represent, respectively, survival, growth, fecundity, and size of offspring of parents as functions of body size z at time t . The integration is limited to the lower, L , and upper, U , possible sizes of the species. The body size variable, z , in

principle can represent many different measures of body size. In the work below, we use assume z is a measure of length, such as standard or fork length in fish or snout-vent length in reptiles. For predatory interactions, z must then be translated to body mass for scaling purposes, which we detail below. When working directly with body mass as z , these scaling functions are not needed.

Each of the demographic rate functions depends on size-specific interactions with resources and size-specific predatory interactions (table 1). The interactions with resources are summarized using an interaction surface approach, which naturally arises from a single-consumer/multiple-resource model where resource use and acquisition depend on a trait of the consumer—in this case, body size. The interactions between the predator and the prey (interspecific and/or intraspecific) are explicit in the model. Each of the demographic rates of a predator are functions of the positive effects of acquiring alternative resources and predation. For example, the mean somatic growth increment of species i is modeled as

$$g_i(z'_i|z_i) = g_i^R(z_i) + g_i^P(z_i), \quad (2)$$

where $g_i^R(z_i)$ and $g_i^P(z_i)$ are the amount of growth that is due to acquisition and use of the basal resources (R) and consumption of intra- and/or interspecific prey (P), respectively. Acquisition and use of the resources is modeled as

$$g_i^R(z_i) = g_{i0} + g_{iz}z_i + g_{iN} \sum_{j=1}^k \int \alpha_{ij}(z_i, z_j)n_j(z_j, t)dz_j, \quad (3)$$

where z_i is the body size of the species i individual whose demographic rate is being described, z_j is the body sizes of the species j competitors, $\alpha_{ij}(z_i, z_j)$ is an interaction surface, and $n_j(z_j, t)$ is the distribution of body sizes of species j at time t (Bassar et al. 2017b). The g parameters represent the density-independent growth increment (g_{i0}), how the growth increment changes with increased body size (g_{iz}), and the density-dependent decrease in the growth increment due to competition for a common resource (g_{iN}). The summation is across k species, which allows for the inclusion of multiple species competing for overlapping resources. Here, we limit our analysis to two species ($k = 2$). Acquisition and allocation of resources from captured prey toward somatic growth is modeled as

$$g_i^P(z_i) = \left(z_i^{2.7} + \sum_{j=1}^k \int_{L_j}^{z_j=z_i-w} \kappa_G(z_j)\psi(z_i)(1 - \eta_i)\delta_i\gamma_{ji}(z_i, z_j)\theta_{ji}n_j(z_j, t)dz_j \right)^{1/2.7} - z_i. \quad (4)$$

The overall structure of the equation translates gain in mass (g) from predation to gain in body size measured as length (mm). The net gain in mass of the predator/cannibal is

Table 1: Parameter definitions and demographic rate functions

Description	Equation
Body size at $t + 1$, given body size at t	$G_i(z'_i z_i) = z_i + g_i^R(z_i) + g_i^P(z_i) + \mathcal{N}(0, G_{\text{var}})$
Growth in length due to resource acquisition	$g_i^R(z_i) = g_{i_0} + g_{i_z} z_i + g_{i_N} \sum_{j=1}^k \int \alpha_{ij}(z_i, z_j) n_j(z_j, t) dz_j$
Growth in length of predator/cannibal due to consumption of prey	$g_i^P(z_i) = \left(z_i^{2.7} + \sum_{j=1}^k \int_{L_j}^{z_j=z_i-w} \kappa_G(z_j) \psi(z_i) (1 - \eta_i) \delta_i \gamma_{ji}(z_i, z_j) \theta_{ji} n_j(z_j, t) dz_j \right)^{1/2.7} - z_i$
Per-prey increase in the mass of predator/cannibal due to consumption of prey	$\kappa_G(z_j) = z_j^{2.7}$
Survival from t to $t + 1$	$S_i(z_i) = s_i^{R,P^+}(z_i) s_i^{P^-}(z_i)$
Probability of survival due to resource and prey acquisition	$s_i^{R,P^+}(z_i) = \text{invlogit}[s_i^R(z_i) + s_i^{P^+}(z_i)]$
Survival due to resource acquisition	$s_i^R(z_i) = s_{i_0} + s_{i_z} z_i + s_{i_N} \sum_{j=1}^k \int \alpha_{ij}(z_i, z_j) n_j(z_j, t) dz_j$
Increase in survival of predator/cannibal due to consumption of prey	$s_i^{P^+}(z_i) = \sum_{j=1}^k \int_{L_j}^{z_j=z_i-w} \kappa_S(z_i, z_j) \eta_i \delta_i \gamma_{ji}(z_i, z_j) \theta_{ji} n_j(z_j, t) dz_j$
Probability of surviving predation	$s_i^{P^-}(z_i) = 1 - \sum_{j=1}^k \int_{z_j=z_i+w}^{U_j} \gamma_{ij}(z_i, z_j) \theta_{ij} n_j(z_j, t) dz_j$
Per-prey increase in the survival of the predator/cannibal due to consumption of prey; based on scaling to mass	$\kappa_S(z_i, z_j) = q \left(\frac{z_j}{z_i} \right)^{2.7}$
Reproduction	$M_i(z_i) = e^{m_i^R(z_i)} + m_i^P(z_i)$
Fecundity due to resource acquisition	$m_i^R(z_i) = m_{i_0} + m_{i_z} z_i + m_{i_N} \sum_{j=1}^k \int \alpha_{ij}(z_i, z_j) n_j(z_j, t) dz_j$
Increase in fecundity of predator/cannibal due to consumption of prey	$m_i^P(z_i) = \sum_{j=1}^k \int_{L_j}^{z_j=z_i-w} \kappa_M(z_j) (1 - \psi(z_i)) (1 - \eta_i) \delta_i \gamma_{ji}(z_i, z_j) \theta_{ji} n_j(z_j, t) dz_j$
New predator/cannibal offspring per prey	$\kappa_M(z_j) = \left(\frac{z_j}{D_i} \right)^{2.7}$
Size of new offspring	$D_i(z'_i) = d_{i_0} + \mathcal{N}(0, D_{\text{var}})$
Resource-related functions:	
Interaction surface due to resource competition; can be interpreted as the number of z_j individuals that have the same competitive effect as 1 z_i -sized individual	$\alpha_{ij}(z_i, z_j) = \exp(\phi_j(z_j - \nu) - \phi_i(z_i - \nu))$
Predation-related functions:	
Interaction surface between predator and prey; defines the probability of prey of size z_j being captured by a predator of size z_i over the interval	$\gamma_{ji}(z_i, z_j) = \Gamma(1 - \exp(-[c_{ji}(z_j - (z_i + w))]^2))$
Energetic trade-off between growth and fecundity; fraction of acquired prey devoted to growth	$\psi(z_i) = \text{invlogit}[-\psi_z(z_i - \psi_m)]$

Note: Parameters for the functions are listed in table 2. $\mathcal{N}(0, G_{\text{var}})$ and $\mathcal{N}(0, D_{\text{var}})$ are normal distributions with mean of zero and variances equal to the residual variances in the growth and offspring size analyses, respectively. Fecundity functions include both the probability of reproducing (size- and resource-dependent maturation) and the number of offspring in a brood.

Table 2: Parameters for each of the demographic rates for both species

Parameter	Description	Value
Demographic rate parameters:		
s_0	Density independent	.29
s_z	How demographic rate changes with size	.06
s_N	Density-dependent effect on demographic rate	-.03
g_0	Density independent	7.26
g_z	How demographic rate changes with size	-.31
g_N	Density-dependent effect on demographic rate	-.13
G_{var}	Variance in the growth increment	.51
m_0	Density independent	-.93
m_z	How demographic rate changes with size	.22
m_N	Density-dependent effect on demographic rate	-.06
d_0	Density independent	6.35
D_{var}	Variance in the offspring size at birth	.17
Resource competition parameters:		
ϕ_j	Size-dependent intake rate of the victim on the common resources	.02
ϕ_i	Size-dependent intake rate of the predator/cannibal on the common resources	0 to .04
v	Size at which the intake rates or resources used are equal between the species	6.35
Predation/cannibalism parameters:		
θ_{ji}	Propensity for predation to be interspecific; pure IGP when 1	0 to 1
θ_{ii}	Propensity for predation to be intraspecific; pure cannibalism when 1	$1 - \theta_{ji}$
η	Proportion of captured prey devoted to increased survival	.15 or .9
ψ_z	Slope of trade-off between growth and fecundity	-.25
ψ_m	Mean size at maturity	15
δ	Conversion efficiency	0 to 1
Γ	Maximum predation rate	.05
c	Size-dependent predation	.5
w	Minimum difference in size for predation to be successful	15
q	Scales survival benefit of predator for consuming prey to the common resource	50

Note: Estimates are based on field and mesocosm experiments in Bassar et al. (2013, 2015). Intercept terms were estimated at 6.3-mm standard length (z).

described by the central term with the summation across prey species and integral that defines the sizes of prey that can be captured. Reading from right to left under the integral, $n_j(z_j, t)$ is the density distribution of the prey at time t , and θ_{ji} determines the propensity for the predatory habitat of the predator to be inter- or intraspecific. When $\theta_{ji} = 0$, the whole term under the integral is zero, and there is no gain from predation on species j . The function $\gamma_{ji}(z_i, z_j)$ is a predation surface giving the feeding rate of z_i -sized individuals of species i on z_j -sized individuals of species j (fig. 1). The parameter δ_i describes the fraction of prey mass that can be used by the predator for growth, survival, and reproduction. The fraction of consumed prey that is allocated to survival is η_i . The fraction that is not allocated to survival ($1 - \eta_i$) can be allocated to growth and reproduction. The fraction of $(1 - \eta_i)$ devoted to growth was modeled as

$$\psi(z_i) = \text{invlogit}(-\psi_z(z_i - \psi_m)), \quad (5)$$

where ψ_m is the mean size at maturity in the population. Equation (5) has the property that the amount that is devoted to growth has a maximum of 1 at birth and declines

to zero as the predator grows. The fraction that is not devoted to growth ($1 - \psi(z_i)$) is then allocated to reproduction. The function $\kappa_G(z_j)$ describes the conversion of captured prey into predator tissue. While $\gamma_{ji}(z_i, z_j)$ is common to each of the demographic rates, $\kappa_G(z_i, z_j)$ is specific to each. For growth,

$$\kappa_G(z_j) = z_j^{2.7}, \quad (6)$$

which simply relates mass to length (mass = length^{2.7}). The limits of the integration in equation (4) are such that predators must be at a minimum size w greater than the prey for the successful killing of the prey. Overall, $g_i^P(z_i)$ has properties such that smaller prey contribute less to predator growth than larger prey, that for a given size prey larger predators gain less of a benefit, and that the gain in mass is always less than or equal to the mass of the consumed prey.

Mean growth is then translated to a probability density distribution to project the size at the next time step using

$$G_i(z'_i|z_i) = z_i + g_i^R(z_i) + g_i^P(z_i) + \mathcal{N}(0, G_{\text{var}}), \quad (7)$$

where $\mathcal{N}(0, G_{\text{var}})$ is a normal distribution with a mean of zero and variance G_{var} .

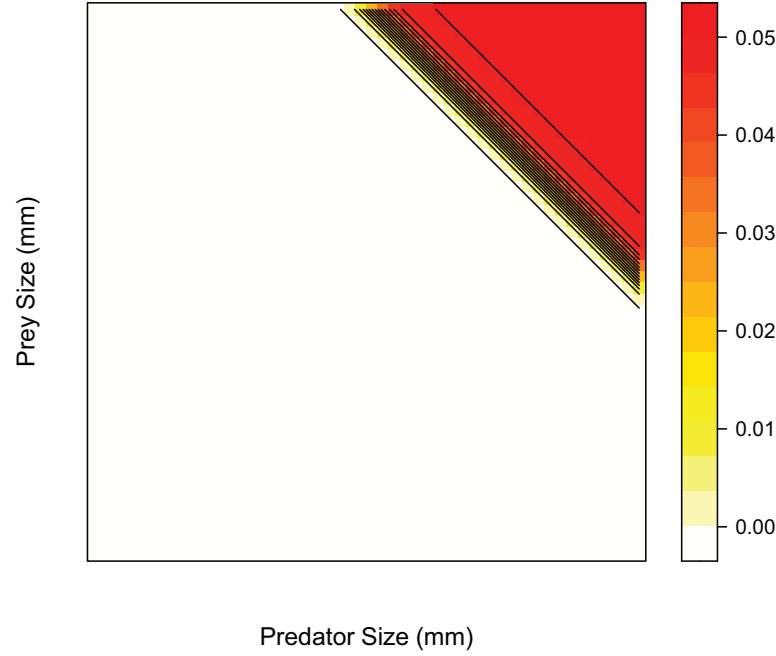


Figure 1: Example size-dependent predation surface, $\gamma_{ij}(z_i, z_j)$. The units for the z -axis are the prey's probability of being consumed per predator over the time interval. Colors denote different intensities of predation, and the black lines show contours.

Similar equations describe the other demographic rates with the exception of offspring size, which for simplicity is assumed to be independent of resources (table 1). The critical difference between the predator components of the demographic rates is how the mass of the consumed prey is converted to these functions, which is given by the κ 's. For fecundity, a predator cannot make more offspring (more mass) than is consumed and allocated to offspring production. We therefore formulated the conversion of prey mass into offspring as

$$\kappa_M(z_j) = \left(\frac{z_j}{\bar{D}_i} \right)^{2.7}, \quad (8)$$

which describes the relative mass of the prey and the mean offspring mass at birth, $\bar{D}_i$, and yields the number of new offspring a predator/cannibal can produce per consumed prey. Modeling how the consumption of prey translates into survival is less straightforward because it is not a mass for mass conversion. Yet larger prey should yield a higher survival benefit, and this benefit should decline with an increase in the size of the predator. The latter of these is because larger predators require more total resources for maintenance. We modeled this as a simple ratio between the relative mass of the predator and the prey as

$$\kappa_S(z_i, z_j) = q \left(\frac{z_j}{z_i} \right)^{2.7}, \quad (9)$$

where q translates the relative captured prey mass into a survival benefit.

Predation or cannibalism also must decrease the survival of the size classes subject to predation. Overall, survival was modeled as

$$S_i(z_i) = s_i^{R,P^+}(z_i) s_i^{P^-}(z_i), \quad (10)$$

where $s_i^{R,P^+}(z_i)$ and $s_i^{P^-}(z_i)$ represent the probabilities of survival due to consuming the common resources (R) and inter- or intraspecific prey (P^+) as well as the probability of surviving predation (P^-). The term s_i^{R,P^+} follows the same logic as growth, with the appropriate transformation to a probability (see table 1). The probability of surviving predation was modeled as

$$s_i^{P^-}(z_i) = 1 - \sum_{j=1}^k \int_{z_j=z_i+w}^{U_j} \gamma_{ij}(z_i, z_j) \theta_{ij} n_j(z_j, t) dz_j, \quad (11)$$

where the second term describes the probability of an individual of species i dying from predation by species j . Note that the limits of integration are switched such that only individuals of species j larger than $z_i + w$ can prey on species i . Likewise, the subscripts on θ and γ are switched such that this now reads as the propensity of an individual of species j to prey on species i .

The outcome of these equations is that increased predation/cannibalism decreases the survival of smaller and

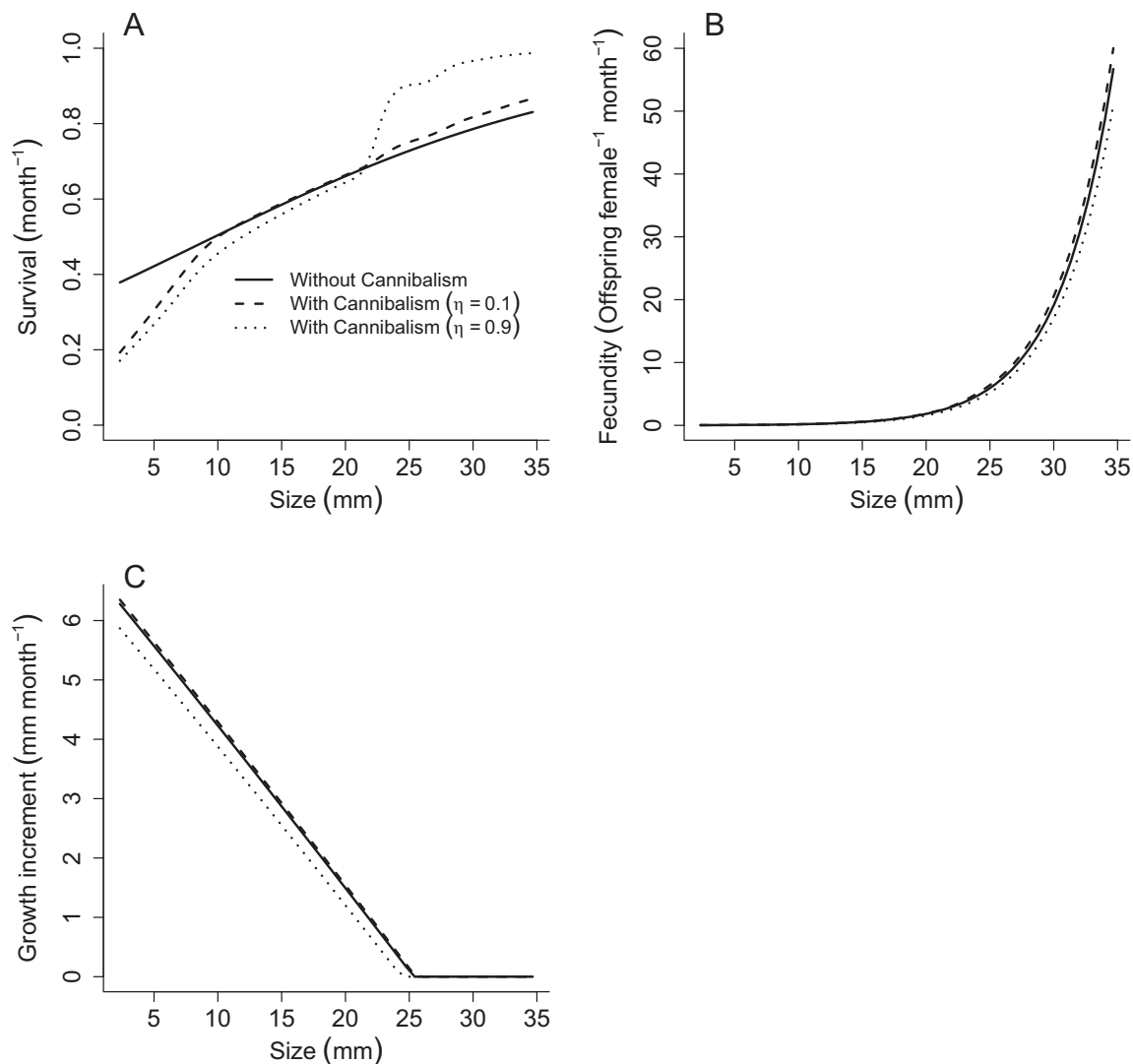


Figure 2: Size-dependent survival (A), fecundity (B), and somatic growth increment (C) with and without cannibalism. Rates were determined in a cannibalistic species at its demographic equilibrium ($\Gamma = 0.25$, $\delta = 0.5$, $\phi = 0.02$). The rest of the parameters are set at their default values.

increases the survival of larger predators/cannibals (fig. 2A), increases the fecundity of larger predators/cannibals (fig. 2B), and increases the growth increment of larger predators/cannibals (fig. 2C).

Model Parameterization and Analysis

We examined our model for two competing species and parameterized the resource competition parts of the demographic equations with data from experiments with Trinidadian guppies (table 2; Bassar et al. 2013). Guppies are small, stream-dwelling fish with strongly size-structured populations. Guppies live in stream communities that are comprised a diversity of other fish species. In some com-

munities, they live only with Hart's killifish (*Rivulus hartii*). Killifish populations are also strongly structured by body size. The two species are born at roughly the same size, become better competitors as they grow (Potter et al. 2019; Anaya-Rojas et al. 2021), and shift the resources they use with increasing body size. There is some evidence that larger individuals of both species consume intra- and interspecific individuals (Goldberg et al. 2022). To coexist, both species must navigate size-dependent competition, resource use, predation, and cannibalism (Travis et al. 2014). Yet current theory does not cover situations such as these.

To explore whether there are important differences in the conditions that are necessary for coexistence in IGP systems with or without cannibalism, we assumed that

all individuals of both species have the same baseline life history (pattern/parameters of/for size-dependent survival, somatic growth, and reproduction) and compete for the same limiting resources. We asked whether the predatory and competitive interactions determine coexistence or exclusion when (1) one species was an either IG predator or cannibal (or both) and (2) whether the direct benefit of predation was allocated primarily to growth and reproduction ($\eta = 0.15$) or to survival ($\eta = 0.9$). The degree of preference for interspecific or intraspecific prey was modified by altering the preference parameter of one or both of the species. For example, when species i is a predator of species j , then $\theta_{ji} = 1$ and $\theta_{ii} = 0$; when species i is a cannibal, then $\theta_{ji} = 0$ and $\theta_{ii} = 1$; and when species i is a predator and a cannibal with no preference for either, then $\theta_{ji} = 0.5$ and $\theta_{ii} = 0.5$. In all cases, $\theta_{ji} + \theta_{ii} = 1$.

Within each general scenario, we altered the direct benefit of the predatory interaction for the predator by manipulating the conversion efficiency (δ) from 0 to 1. When $\delta = 0$, the IG predator (or cannibal) gains no direct benefit from consuming the prey but does gain an indirect benefit through the decrease in competition due to the death of the intra- or interspecific prey. For example, male lions kill the offspring of other males (Packer and Pusey 1983). This can be generalized to other situations such as extreme contest competition, where one of the competitors dies as a result of the contest but is not consumed. When $\delta = 1$, the predator gains the indirect benefit from the decrease in competition as well as a direct benefit because all of the resources from the prey that was consumed are available to increase the survival, growth, and fecundity of the predator. Independently of the change in this parameter, we altered the size-dependent feeding rate of the predatory species on the shared resource such that it increased at a slower rate, was no different from, or increased faster than that of the competing species. We assumed the baseline size-dependent relative feeding rate of the prey (species 1) on the shared resources (ϕ) was equal to 0.02 mm^{-1} , based on empirical data (Potter et al. 2019). We then altered the predator/cannibal (species 2) feeding rate from 0 to 0.04 mm^{-1} . This means that the predator could be considered to not increase its feeding rate on the shared resource with increased size when $\Delta\phi_z = \phi_{z_2} - \phi_{z_1} = -0.02 \text{ mm}^{-1}$ and to increase its feeding rate with size twice as much with increased body size when $\Delta\phi_z = 0.02 \text{ mm}^{-1}$.

We derived the coexistence predictions using invasion analysis. The invasion growth rate of each of the species was calculated as the dominant eigenvalue of the projection matrix with the resident at its demographic equilibrium and the vector describing the population density of the invader containing zeros. The demographic equilibrium of the resident species was calculated by numerically

iterating the resident population through time until the population size and distribution of body sizes in the resident did not change across time steps. All iterations resulted in stable point equilibria.

Results

How Does the Introduction of Cannibalism into a Unidirectional IGP System Change the Conditions Necessary for Coexistence in a Qualitative Fashion?

Consistent with general IGP theory, when size-dependent predation is unidirectional, coexistence between an IG predator and its prey is possible only when larger predatory individuals are inferior competitors ($\Delta\phi_z < 0$; fig. 3A, 3B, light gray regions). When large predatory individuals are only slightly worse competitors ($-0.01 < \Delta\phi_z < 0$), then there are alternative stable states in which each species can exclude the other (fig. 3A, 3B, black areas). If larger predatory individuals are also better competitors for common resources ($\Delta\phi_z > 0$), the predatory species will always exclude the competitor (fig. 3A, 3B, dark gray areas). If larger predatory individuals are very poor competitors for common resources ($\Delta\phi_z < -0.01$), then the competitor will exclude the predatory species (fig. 3A, 3B, white areas).

In contrast, when cannibalism facilitates coexistence, it does so in the diametrically opposite region of parameter space (fig. 3D, 3E, light gray areas). Cannibalism facilitates coexistence when cannibalistic individuals are superior competitors for the shared resources ($\Delta\phi_z > 0$). When the larger cannibals are inferior competitors ($\Delta\phi_z < 0$), then either species can exclude the other from the habitat (fig. 3D, 3E).

The ability of cannibalism alone to facilitate coexistence might suggest that adding cannibalism to an IGP system will enhance coexistence beyond what either agent can do on its own. Exactly the opposite is true. Because predation and cannibalism each facilitate coexistence separately in opposing regions of parameter space, their combined effects nearly cancel each other and make coexistence impossible (fig. 3G, 3H). The range of conditions under which the predator will exclude the competitor are much greater than those in which the competitor excludes the predator. Along the boundary between the two outcomes, a region of priority effects, where either species can exclude the other, is also possible.

How Does Altering the Allocation Strategy of the Direct Benefit (Survival vs. Growth and Reproduction) Alter the Conditions Necessary for Coexistence?

The opposing predictions of IGP and cannibalism are affected differently by changes in the allocation of the

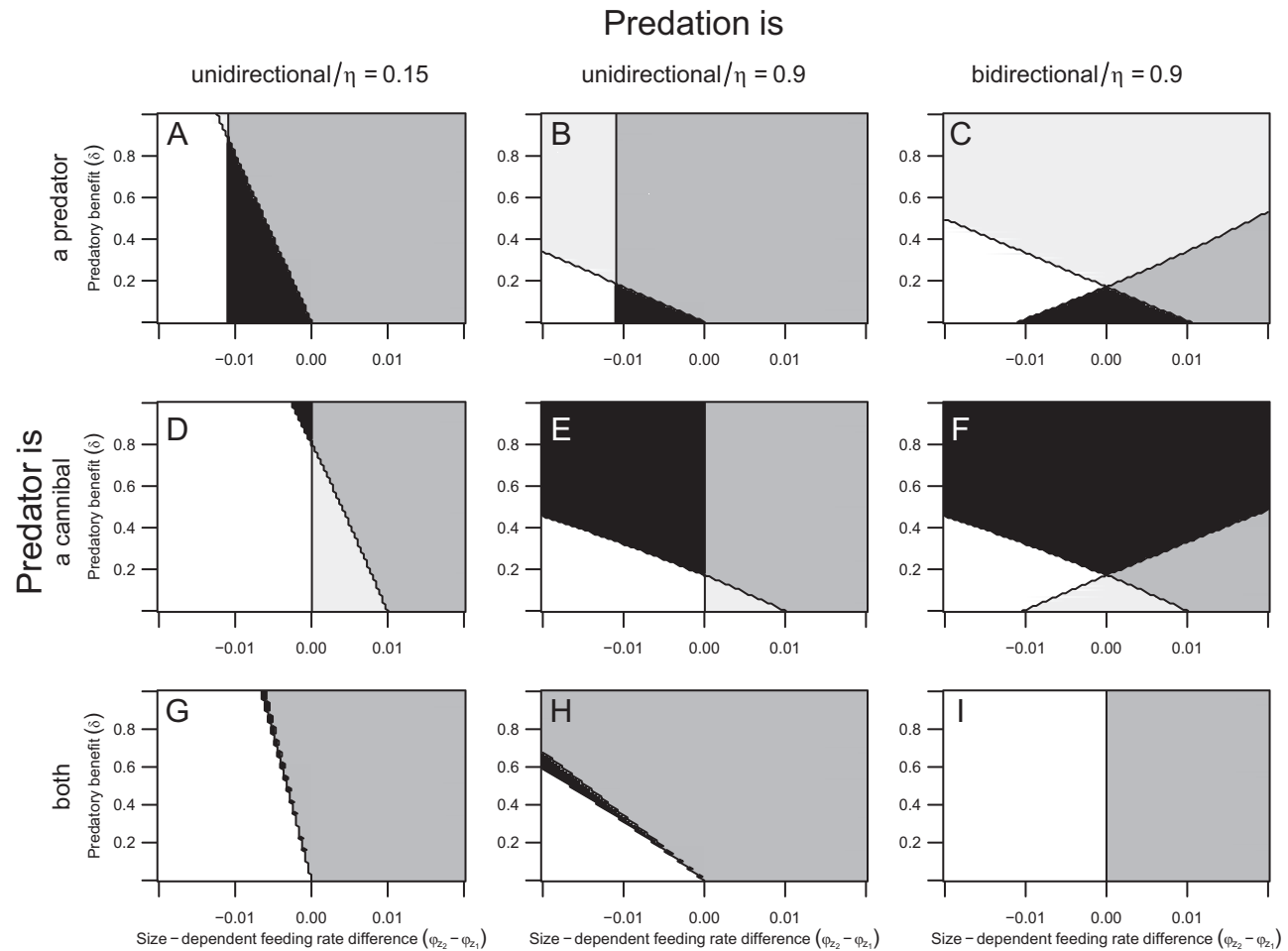


Figure 3: Predictions for species coexistence, competitive exclusion, and alternative stable states when size-dependent predatory interactions involve one species being an interspecific predator, cannibal, or an interspecific predator and a cannibal (A, B, D, E, G, H) or both species are interspecific predators, cannibals, or interspecific predators and cannibals (C, F, I). The first row (A–C) shows the predictions when the predatory interactions are interspecific only (intraguild predation). The second row (D–F) shows the predictions when the predation is intraspecific only. The third row (G–I) shows the results when the predator consumes inter- and intraspecific prey with equal frequency. The first (A, D, G) and second (B, E, H) columns show the predictions for when the predator devotes captured energy mostly toward somatic growth and fecundity or toward survival, respectively. For each plot, the y-axis gives the direct predatory benefit (conversion efficiency: δ) ranging from 0 (where the predator or cannibal does not consume the prey and hence does not directly increase in its survival, growth, or reproduction) to 1 (where the prey are consumed and there is perfect transfer of resources from the prey to the predator). The x-axis gives the difference in the size-dependent feeding rate of the two species. Positive values indicate where the predator or cannibal in the unidirectional cases increase their feeding rate with body size to a greater degree than the other species. Negative values indicate where the predator or cannibal have lower feeding rates at larger sizes than the other species. White areas of the plots are areas where species 1 (the prey) can exclude species 2 (the predator/cannibal). Dark gray areas of the plots are where species 2 can exclude species 1. Light gray areas of the plots are parameter combinations where the models predict stable coexistence. Black areas of the plots show regions of priority effects where either species can repel invasion of the other.

consumed prey toward survival or growth and reproduction (i.e., the direct benefit). When the predatory species is an IGP predator and resources from consumed prey are allocated mostly to growth and fecundity, coexistence is predicted only under extreme upper values of the conversion efficiency (fig. 3A, light gray regions). This means that most of the prey biomass needs to be converted by the predator into new somatic tissue and offspring. How-

ever, species coexistence is likely under a wider range of conversion efficiencies when the predator allocates consumed prey toward survival (fig. 3B, light gray regions). This means that species coexistence may be much more likely when the predator is a longer-lived species that prioritizes intrinsic survival over reproduction and growth.

In contrast, when the predatory species is solely a cannibal, the combinations of competitive ability and conversion

efficiency that allow species coexistence are more limited when the resources are allocated to survival over growth and reproduction (fig. 3D vs. 3E, light gray regions). Increased allocation toward survival creates a region of parameter space where priority effects are likely when the cannibal is also an inferior competitor (fig. 3E, black region). Increasing allocation of the consumed prey toward survival also makes the exclusion of the competitor/prey by the predator more likely (fig. 3G, 3H, dark gray regions).

*Do the Effects of Cannibalism on Coexistence
in a Unidirectional System Also Operate
in a Bidirectional IGP System?*

The regions in which a competitor can coexist with either predation or cannibalism are more diverse when the predatory interaction is bidirectional (fig. 3C, 3F, 3I). When the IGP interaction is bidirectional such that larger individuals of each species consume smaller individuals of the other species, coexistence is possible over a much broader range of competitive differences (fig. 3C, light gray regions). In this scenario, coexistence is not so dependent on one particular species increasing its competitive ability with body size to a greater degree than the other; the region of coexistence revolves around $\Delta\phi_z = 0$. Coexistence emerges only when both species benefit directly from the consumption of the other.

Similarly, when both species are cannibals, coexistence depends less on which species is a better competitor and more on the direct benefit the cannibals receive from consuming conspecifics (fig. 3F). When the cannibals receive little direct benefit, coexistence is possible, similar to the case in a unidirectional IGP system. And just as was the case in a unidirectional IGP system, when both species are IG predators and cannibals, then coexistence is not possible (fig. 3I). In this case, however, the prediction from the model is the same as a model of pure resource competition: the better competitor will exclude the weaker competitor.

Discussion

Theories of species coexistence with IGP suggest that IG predators and their prey can coexist only when the IG predator is an inferior competitor and directly benefits in a significant way from consuming the IG prey. Previous work has shown that intraspecific predation (cannibalism) can modify these predictions such that IG predators and their prey can stably coexist when the IG predator is also a cannibal (Rudolf 2007; Hin et al. 2011; Ohlberger et al. 2012; Toscano et al. 2017). Our results show that in both uni- and bidirectional IGP systems, cannibalism alone acts as the reciprocal of interspecific predation, leading

to coexistence or alternative stable states under conditions that are the opposite of those that do so with IGP alone. Because these conditions oppose each other, there is no possibility of coexistence when both species compete for the same resources and one or both species are simultaneously an IG predator and cannibal. Moreover, the ability of either of these ecological interactions to result in the coexistence of the interacting species hinges critically not just on whether the direct benefits are large or small but also on how the benefits are allocated to survival, growth, and reproduction.

Our modeling approach differs from previous work on IGP and cannibalism in two key ways. First, previous work on this topic has focused on two discrete life history stages in which adults prey on juveniles and where only one species is structured. Our models here allow for a broader range of interactions between species that are both structured by continuous traits. The values of these traits then determine the resources that are used, the ability of the individuals that possess them to compete, and the IGP and cannibalistic interactions between individuals. We focused our analysis on body size because it is a trait that often determines how individuals compete with and consume each other. Our modeling approach, using the complete size distributions with competition within and between all sizes, allowed us to generate a more general set of predictions about how cannibalism affects coexistence.

The second way our approach differs from others is that we explicitly consider how variation in the life history of the species can impede or facilitate coexistence. We did so by explicitly considering how resources acquired through the predatory interactions are allocated among competing demographic components. Demographic life history theory predicts that species with low extrinsic rates of mortality should allocate more of their acquired resources toward survival and less toward growth or reproduction compared with species with higher rates of extrinsic mortality (Charlesworth 1994). When the interaction between the species is a unidirectional IGP, coexistence is much more likely when the IG predator is longer lived and allocates more resources toward survival than growth and reproduction. Exactly the opposite is true when the predator is a cannibal: coexistence is more likely when the allocation strategy is more like a shorter-lived species, devoting more resources gained through cannibalism toward growth and reproduction instead of survival. However, these predictions deal only with the allocation strategies themselves and do not explicitly consider how size-dependent mortality wrought by intra- or interspecific predation causes selection for the allocation strategy itself. Doing so would allow a more complete picture of the situations under which we can expect to see IGP with or without cannibalism evolve and the types of life histories we expect to see when they do.

An advantage of our models is that they can be parameterized for specific systems using demographic data that are collected by empirical biologists (Bassar et al. 2013; Bassar et al. 2015, 2017a; Ellner et al. 2016; Potter et al. 2019; Griffiths et al. 2020). Our use of data from the Trinidadian guppy-killifish system illustrates this advantage. We could parameterize the components of resource competition in our models with data obtained via experimentation (Bassar et al. 2013; Potter et al. 2019; Anaya-Rojas et al. 2021). There is more uncertainty surrounding our choices of parameters for predation and cannibalism because there are fewer data available on these components. Each species is thought to prey on the smaller juvenile stages of the other species (Goldberg et al. 2022). The extent of cannibalism is even less well understood. While empirical observation also suggests that older, larger guppies consume juvenile guppies (Nilsson et al. 2011), nearly all observations of guppy cannibalism are drawn from laboratory settings or other artificial settings of overcrowding. The results of our models point to the importance of obtaining stronger data on both predation and cannibalism if we are to understand whether those interactions facilitate or impede coexistence. Our results also show that coexistence is much more likely when both species devote the excess resources gained from IG predation toward future survival and not toward somatic growth or reproduction. Thus, our models point to the importance of obtaining data on specific resource allocation patterns.

More generally, being able to use a model to empirically investigate whether species coexist allows investigators to calculate fitness under a wide range of demographic states, which is especially valuable in populations structured by traits such as body size. This is particularly useful for estimating the invasion criteria, which assumes that there are no or an infinitesimally small number of invaders in the habitat. This scenario is almost impossible to establish in a reasonable experimental context. Experiments can, however, be designed that vary the density and distribution of sizes in a factorial design that allows the parameterization of the models for each of the demographic rates (Bassar et al. 2015, 2016; Potter et al. 2019; Griffiths et al. 2020). Expected invasion growth rates can then be calculated from these parameterized models.

One limitation of the results presented here is that we assume that both species have the same baseline life history (pattern/parameters of/for size-dependent survival, somatic growth, and reproduction). This is certainly not the case for a wide variety of interacting species, including the guppies and killifish that inspired this work. Often one species may be larger or have a very different life cycle than the other species. Does the baseline life history of guppies introduce a bias in the results of the model presented here? Maybe, but probably not, as it is typical of

many species that grow throughout their lives. Whether differences in the baseline life history exaggerate or restrict the predictions presented here is an open question and one that presents another possibly important axis of variation in understanding the persistence of IGP systems.

Does cannibalism resolve the paradox of IGP? The answer is yes, but not in the way that one might expect. While cannibalism alone can lead to coexistence, its larger effect occurs when it is combined with IG predation. When an IG predator is also a cannibal, as is to be expected in strongly size-structured species that consume anything they can fit in their mouths, such as fish, the predictions largely revert to situations where the outcome is dictated by resource competition and not predation. The most extreme form of this is when both species consume both each other (bidirectional IGP) and conspecifics. In that way, species coexistence in IGP systems may not be that difficult to understand after all because they more resemble purely competitive situations in their coexistence requirements than systems of predator-prey interactions. Under these circumstances, other mechanisms of species coexistence, such as niche differentiation (*sensu* MacArthur and Levins 1967) or spatial and temporal storage effects (Chesson 2000; Ellner et al. 2019), may play larger roles in determining the outcome of ecological interactions.

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Statement of Authorship

R.D.B. conceived the research ideas during discussion with T.C. and J.T. R.D.B. developed and analyzed the models and wrote the first draft of the manuscript. All authors discussed the results and contributed to the final draft.

Data and Code Availability

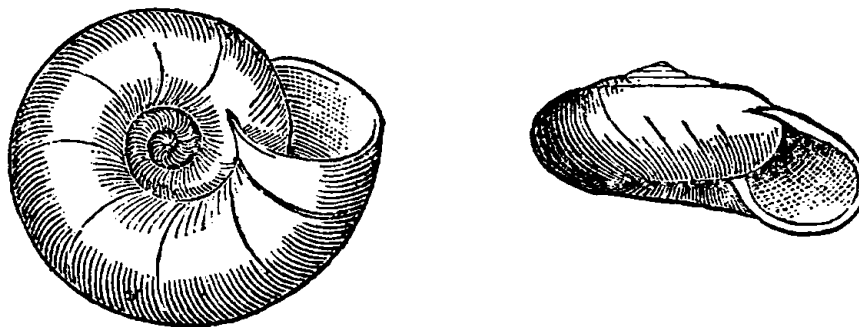
Code for the analyses can be found on Zenodo (<https://doi.org/10.5281/zenodo.7314668>; Bassar 2022).

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Editor: Jennifer A. Lau



“This species is peculiar in its habits. It lives in the dark woods, and is a regular cannibal in its propensities.” Figured: “*Helix concava* Say.” From “The Land Snails of New England (Continued)” by Edward S. Morse (*The American Naturalist*, 1867, 1:411–414).