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Complementary predation on metamorphosing species promotes stability in predator–prey systems

Ezer Miller · Moshe Coll · Lewi Stone

Abstract Functionally redundant predation and functionally complementary predation are both widespread phenomena in nature. Functional complementary predation can be found, for example, when predators feed on different life stages of their prey, while functional redundant predation occurs when different predators feed on all life stages of a shared prey. Both phenomena are common in nature, and the extent of differential life-stage predation depends mostly on prey life history; complementary predation is expected to be more common on metamorphosing prey species, while redundant predation is thought to be higher on non-metamorphosing species. We used an ordinary differential equation model to explore the effect of varying degree of complementary and redundant predation on the dynamic properties of a system with two predators that feed on an age-structured prey. Our main finding was that predation on one stage (adult or juvenile) resulted in a more stable system (i.e., it is stable for a wider range of parameters) compared to when the two predators mix the two prey developmental stages in their diet. Our results demonstrate that predator–prey dynamics depends strongly on predators' functionality when predator species richness is fixed. Results also suggest that systems with metamorphosing prey are expected to be more diverse compared to systems with non-metamorphosing prey.

Keywords Predator–prey population dynamics ·
Age-structured predation · Functional redundancy/
complementary · Metamorphosis

Introduction

Functionally redundant organisms do similar things in the ecosystem, while functionally complementary species do different things (Casula et al. 2006). Functionally complementary predation can be found for example when predators feed on different life stages of their prey, while functionally redundant predation happens when different predators attack all life stages of their shared prey (Casula et al. 2006; Wilby and Thomas 2002). Since many organisms occupy different habitats at different developmental life sages, their predators may be operating in complementary or redundant ways (Casula et al. 2006; Wilby and Thomas 2002). It is not clear, however, how these modes of predation affect the dynamics of predator–prey systems. The degree by which predators are redundant or complementary in their actions is central for ecosystem functioning and is likely to be influenced by the prey's life history.

Indeed, many animals exploit markedly different habitats as juveniles and adults. This is particularly apparent in amphibians, fish, marine invertebrates, and many holometabolous insects (Fox et al. 2001; Gilbert and Frieden 1981; Margulis and Schwartz 1997). It is common for marine invertebrates to live as free swimmers in the juvenile stage and as bottom dwellers as adults (Fox et al. 2001; Gilbert and Frieden 1981; Thorson 1950), and adult amphibians are

E. Miller (✉) · M. Coll
Department of Entomology,
The Hebrew University of Jerusalem,
P.O. Box 12, Rehovot 76100, Israel
e-mail: miller@agri.huji.ac.il

M. Coll
e-mail: coll@agri.huji.ac.il

L. Stone
Department of Zoology, Faculty of Life Sciences,
Tel Aviv University,
Tel Aviv, Israel
e-mail: lewi@post.tau.ac.il

usually riparian while their immatures are aquatic (Gilbert and Frieden 1981; Pough et al. 1996; Wilbur and Collins 1973). Most species displaying this stage structuring are holometabolous insects, a group which composes more than 50% of all animal species (Price 1997). Some hemimetabolous insects also occupy different habitats during the adult and immature stages; in the Odonata and Ephemeroptera, for example, juveniles are aquatic while adults are terrestrial (Gilbert and Frieden 1981; Gullian and Cranston 1994). Yet, the use of similar habitats by the adults and juveniles is not rare in nature. In many hemimetabolous insects such as Orthoptera, Dictyoptera, and Hemiptera, the adults and juveniles share the same habitat and resources (Borror et al. 1976). This is also the case in many vertebrate taxa, such as fish and reptiles (Pough et al. 1996).

The high prevalence of species with an ontogenetic change in habitat use suggests an adaptive value of the trait. Indeed, much discussion centered on the ways and under what conditions metamorphosing is advantageous (Gillot 1995; Truman and Lynn 1999; Wilbur 1980; Pechenik 1999; Gullian and Cranston 1994; Relyea 2007). From the community perspective, adults that are ecologically distinct from the larvae are expected to be exposed to a different set of predatory interactions (Fox et al. 2001; Istock 1967), i.e., the predators of metamorphosing species can usually be divided to several functional groups, each attacking a specific life stage. Metamorphosing species are expected therefore to suffer primarily from complementary predation, whereas non-metamorphosing taxa are more likely to be preyed upon by redundant predators, where each predator attacks all life stages of the prey (Wilby and Thomas 2002). In the current study, we used an ordinary differential equation model to explore the effect of varying degree of complementary and redundant predation on the dynamic properties of a system with two predators and one age-structured prey.

Although studies of predator–prey systems with age-structured populations are abundant in the literature, most have either (a) employed predator–prey models in which the predator population is age-structured (Cushing and Saleem 1982; Oaten and Murdoch 1975; Smith and Wolkind 1983; Wollkind et al. 1982; McCauley et al. 1996), (b) not provided details of the system's population dynamics (Wilby and Thomas 2002), or (c) assumed aged-structured prey in addition to specifically defined interactions between predators (de Roos et al. 2008; Briggs 1993). Hastings (1983), however, analyzed a system in which the prey population is age-structured while the predators are indifferent with respect to each other. His analysis of one predator–one age-structured prey indicates that for certain functional responses, the system is always stable for either juveniles or adult predation. Other forms of functional responses may destabilize the system unless maturation rate is above or below a certain threshold depending on whether predation is on juveniles or adults stage.

Our current study considers a system with two predators and examined various degrees of differential predation on the adult and juvenile stages of their prey. This way, we explored how variation in the degree of mixing juvenile and adult prey in predators diet affects system dynamics, i.e., how varying predator functionality, be they redundant or complementary, affects community dynamics.

Model description

The model's equations are based on Lotka–Volterra predator–prey theory (Lotka 1925). We consider a two predator–one prey system, where the prey has two stages: juvenile and adult. The complete dynamics is thus described by a system of four coupled ordinary differential equations. Each prey stage can be predated upon by each predator, at different rates of attack. A major goal was to compare a situation in which each predator feeds exclusively on one prey stage to a situation where both predators feed on both prey stages. The equations are similar to those used in previous models on age-dependent predation (Hastings 1983; Hastings and Wollkind 1982; Liu et al. 2002; Zhang et al. 2000). Here, however, we extend the system to include two predators instead of one, and each predator consumes the two prey stages in a proportion defined by the parameter q.

The following assumptions have been adopted: (1) Predation and aging are the only source of mortality for the prey; (2) juvenile preys disappear through predation or molt to the adult stage; (3) adult prey may die due to either predation or aging; (4) in the prey population, only the adults reproduce; (5) the predator exhibits a type I functional response, which is most appropriate in situations where prey densities are low, and handling time is negligible (Hassel 1978; Holling 1959, 1966); (6) for the purposes of our work, rates of growth, mortality, and maturation are all assumed to be density-independent. This assumption is useful generally under reasonable habitat conditions. However, it should be noted that density-dependent rates in age-structured consumer-resource systems have been found to yield complex dynamics including multiple stable states, hysteresis, and counterintuitive changes in population sizes (Schreiber and Rudolf 2008) which will not be studies here; (7) there are no direct interactions, such as competition, intraguild predation, or mutualism, between the two predators in the system; (8) reproduction occurs during overlapping generations.

The basic model may be written as follows:

$$\frac{dN_1}{dt} = r_2 N_2 - r_1 N_1 - a_1 q N_1 P_1 - a_2(1-q)N_1 P_2,$$

$$\frac{dN_2}{dt} = r_1 N_1 - d_n N_2 - a_1(1-q)N_2 P_1 - a_2 q N_2 P_2,$$

$$\frac{dP_1}{dt} = [k_{11}a_1 q N_1 + k_{12}a_1(1-q)N_2]P_1 - d_1 P_1,$$

$$\frac{dP_2}{dt} = [k_{21}a_2(1-q)N_1 + k_{22}a_2 q N_2]P_2 - d_2 P_2,$$

(1)

The key parameter q ($0 \le q \le 1$) quantifies the extent of complementary (redundancy) predation on the two prey stages and represents the efficiency of searching rate in catching juvenile or adult prey. As formulated above, when $q=1$, predator P_1 feeds exclusively on juvenile prey (N_1) while the other predator P_2 feeds exclusively on adult prey (N_2). Conversely, when $q=0$, predator P_1 feeds exclusively on adult prey (N_2) while P_2 feeds exclusively on juvenile prey (N_1). For $q=0.5$, the searching rate of each predator is divided evenly between N_1 and N_2, that is, predator 1 attacks juvenile and adult prey with an efficiency of $0.5a_1$, and predator 2 attacks juvenile and adult prey with an efficiency of $0.5a_2$. This way, the functionality of the two predators varies continuously from complementarity (where $q=0$ or $q=1$) to redundancy (where $q=0.5$). We restrict our analysis to the case where the two predators have the same value of q, i.e., they both behave as specialists or generalists in consuming prey stages. Extending the model to a case where one predator is a generalist and the other is a specialist, by assigning different q values for each predator, is, therefore, beyond the scope of the present study.

Model analysis

Case I: a single predator system

We first examine a simpler but related configuration to gain insights into the dynamics of Eq. 1. We assume that one of the predators, without loss of generality, say P_2, is absent from the system; so model (1) collapses to:

$$\frac{dN_1}{dt} = r_2 N_2 - r_1 N_1 - a_1 N_1 q P_1,$$

$$\frac{dN_2}{dt} = r_1 N_1 - d_n N_2 - a_1 N_2(1-q)P_1,$$

(2)

$$\frac{dP_1}{dt} = [k_{11}a_1 N_1 q + k_{12}a_1 N_2(1-q)]P_1 - d_1 P_1,$$

Again, the juvenile to adult ratio in the diet of predator P_1 is quantified by the parameter q. Equation 2 have three nonnegative equilibria which may be found by setting all

rates on the left-hand side to zero (i.e., $\frac{dN_i}{dt} = \frac{dP_1}{dt} = 0$). These equilibria are:

- E_1: $N_1^* = N_2^* = P_1^* = 0$, the trivial equilibrium. This equilibrium exists for all parameters and can be shown to be locally stable when $r_2 < d_n$ and unstable when $r_2 \ge d_n$.
- E_2: $N_1^* > 0$, $N_2^* > 0$, $P_1^* = 0$ When $r_2 = d_n$, there is a line of equilibria given by $N_2 = \frac{r_1 N_1}{r_2}$. Those equilibria are neutrally stable for the prey subsystem but unstable with respect to Eq. 2 where the predator is involved.
- E_3: $N_1^* > 0$, $N_2^* > 0$, $P_1^* > 0$, The internal equilibrium. The equilibrium exists when $r_2 > d_n$ (i.e., prey offspring's production per capita per unit time > death rate of adult prey).

The above internal equilibrium (E_3) can always be expressed explicitly as a function of the model's parameters, but the general expressions for the predator and the prey equilibrium populations are complicated. Appendix 1 provides a stability analysis showing that the unique internal equilibrium E_3 is always locally stable near $q=0$ and $q=1$. For $q \cong 0.5$, however, the system is always unstable to the left or to the right of $q=0.5$, i.e., there exists an instability interval of size R, $R = |0.5 - q'|$, for a unique q' ($0 < q' < 1$), so the instability region is wedged between the points $q=0.5$ and $q=q'$ (Figs. 1, 2, and 3).

The exact value of q' where the equilibrium changes from stable to unstable depends on the model's parameters and has a value between $0 < q' < 1$.

Numerical calculations (see Figs. 2 and 3) indicate that q' has the following characteristics: (1) when $k_{12} \le k_{11}$, $q' < 0.5$ and the unstable region lie to the left of $q=0.5$ (Fig. 2); (2) when $k_{12} > k_{11}$, $q' > 0.5$ and the unstable region lie to the right of $q=0.5$ (Fig. 3); (3) it is a decreasing function (Fig. 3) of r_2 (the per capita number of prey
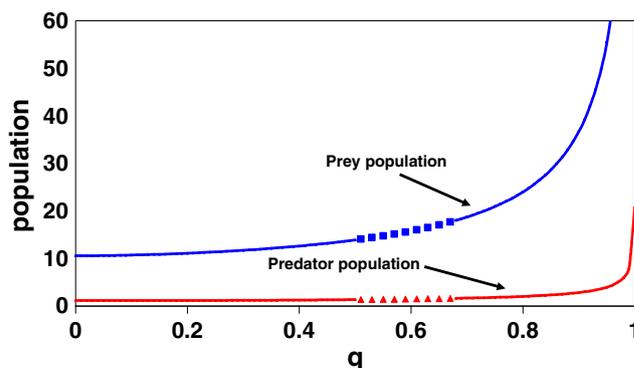

Fig. 1 Bifurcation diagram showing the stability region of the internal equilibrium point E_3 of Eq. 2 where $k_{11} < k_{12}$. The total prey and predator populations are plotted as a function of q. *Solid* and *dotted lines* denote stability and instability, respectively. Parameter values are: $k_{12}=0.009$, $k_{11}=0.002$, $d_1=0.03$, $a=0.72$, $r_2=0.9$, $r_1=0.7$, $d_n=0.04$. The equilibrium is unstable when $0.5 < q < 0.67$, i.e., $q'=0.67$ and $R=[0.5, 0.67]$
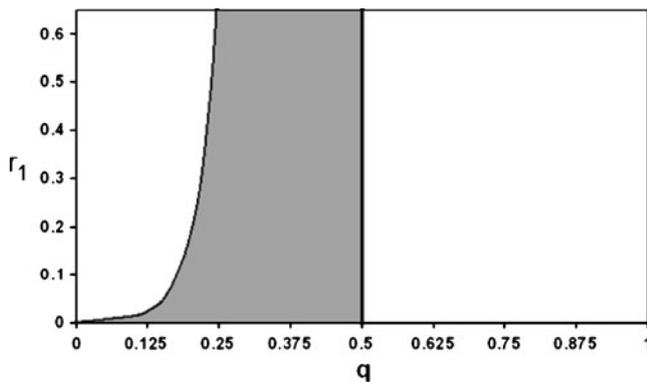
Fig. 2 Stability of the internal equilibrium E_3 as a function of r_1 and q. The *dark zone* denotes parameters for which the model is unstable as found from numerical simulations of Eq. 2 and predicted by the analysis. Parameters are: k_{11}=0.68, k_{12}=0.3, d_1=0.03, a=0.72, r_2=0.99, d_n=0.04. Since $k_{12}<k_{11}$, the instability region lies to the left of q=0.5 and becomes narrower as r_1 increases. The model is stable in the *white regions*

offspring per unit time); (4) it is an increasing function (Fig. 2) of r_1 (prey maturation rate).

The above characteristics show that r_2 and r_1 affect R, the range of instability, in opposing ways (Figs. 2 and 3) depending on k_{ij} (the conversion ratios of prey into predators, see Table 1). For $k_{12} \leq k_{11}$, increasing r_2 increases R, while increasing r_1 reduces R (Fig. 2). The opposite is true when $k_{12} > k_{11}$: increasing r_2 reduces R (Fig. 3) while increasing r_1 increases R.

Numerical simulations of Eq. 2 indicate that the local stability of E_3 is also global for trajectories with positive initial conditions. Simulations also suggest that when the equilibrium is unstable, population trajectories get infinitely
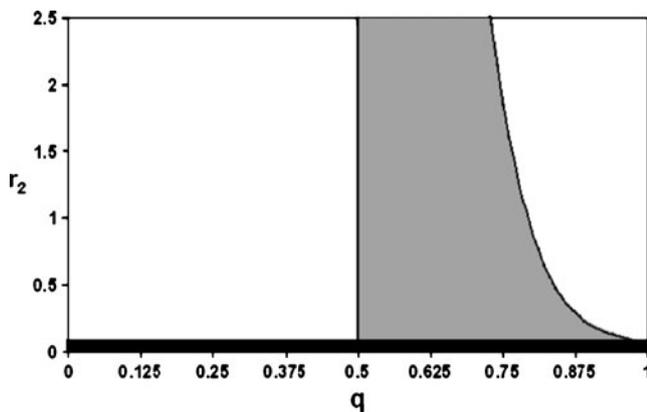

Fig. 3 Stability of the internal equilibrium E_3 as a function of r_2 and q. *Black and gray zones* denote parameters where equilibrium is impossible (i.e., $r_2 < d_n$) and unstable, respectively, as found from numerical simulations of Eq. 2 and predicted by the analysis. Parameters are: k_{11}=0.68, k_{12}=20, d_1=0.06, a=0.72, r_1=0.05, d_n=0.08. Since $k_{12} > k_{11}$, the instability region lies to the right of q=0.5 and becomes narrower as r_2 increases. The model is stable in the *white regions*

close to the axes, implying that the system is impersistent, i.e., populations are not positively bounded, and they oscillate in time in an unstable cycle of increasing amplitude (Fig. 4).

The full two-predator system

We begin the analysis of the two-predator system, Eq. 1, by studying the special case of identical predators (henceforth, "case II"). Later, we extend the analysis to nonidentical predators ("case III"). The following analysis focuses only on the internal equilibrium points, i.e., the equilibrium where all species coexist, and all equilibrium populations are thus strictly positive. However, inspection of Eq. 1 reveals the existence of other equilibrium points. Moreover, the dynamic solutions of the model must also be addressed in addition to the equilibrium points. These issues are dealt with at the end of this section.

Case II: two identical predators

The analysis begins with symmetrical predation in which the predators P_1 and P_2 are identical except for their prey preference. This case is worthy of attention for two reasons. First, a difference in dynamics may only be attributed to differences in diet mixing when the two predators are identical. Second, results for systems with identical predators are simpler and more intuitive and will serve as a reference for subsequent analysis of systems with nonidentical predators.

Symmetrical predation is defined by the following identities of Table 1 parameters:

$$
\begin{aligned}
a_1 &= a_2 = a, \\
k_{11} &= k_{21} = k_1, \\
k_{12} &= k_{22} = k_2, \\
d_1 &= d_2 = d,
\end{aligned}
\tag{3}
$$

Under Eq. 3, the unique internal equilibrium of Eq. 1 is found to be:

$$
N_1^* = \frac{d}{k_1 a} > 0, \quad N_2^* = \frac{d}{k_2 a} > 0,
$$

$$
P_1^* = \frac{k_2(1-q)[k_2 r_1 - k_1 d_n] + k_1 q[k_2 r_1 - k_1 r_2]}{k_1 k_2 a(1-2q)},
$$

$$
P_2^* = \frac{k_1(1-q)[k_1 r_2 - k_2 r_1] + k_2 q[k_1 d_n - k_2 r_1]}{k_1 k_2 a(1-2q)},
$$

$\quad$ (4)

The equilibrium values for juvenile N_1^* and adult N_2^* prey densities depend neither on q nor on prey parameters (r_1, r_2, d_n), but rather on the predator parameters (k_1, k_2, d, a), which are always real and positive. The conditions for existence of the positive internal equilibrium can be found

Table 1 The definition of parameters used in Eq. 1

Parameters/Variables	Meaning
N_1	Juvenile prey density
N_2	Adult prey density
P_i	Population density of predator i
r_1	Maturation rate—the rate at which juveniles prey N_1 metamorphose to adult stage N_2
r_2	Average number of offspring per capita for adult prey (only adult preys have offspring—see assumption 4 in text)
d_n	Death rate of adult prey due to maturation
d_i	Death rate of predator i
k_{ij}	Conversion coefficient of prey stage j into predator i
a_i	Searching efficiency or searching rate of predator i
q	The extent of complementary (or redundant) predation on the two prey stages

The indices i and j may take on the integer values 1 or 2

by solving the inequalities: $P_1^* > 0$; $P_2^* > 0$ (N_1^* and N_2^* are always positive). First, define the following parameters:

$$X_1 = k_1(k_1 r_2 - k_2 r_1), \quad X_2 = k_2(k_2 r_1 - k_1 d_n),$$
$$U_1 = \frac{X_1}{X_1 + X_2}, \quad U_2 = \frac{X_2}{X_1 + X_2}, \tag{5}$$

Note that $U_1 + U_2 = 1$. Following Eqs. 4 and 5, the necessary and sufficient conditions for the existence of the unique internal equilibrium are:

$$r_2 > \frac{k_2}{k_1} r_1 > d_n,$$
$$q \le \min(U_1, U_2) \ or \ q \ge \max(U_1, U_2), \tag{6}$$

Define $U = |U_1 - 0.5| = |U_2 - 0.5|$, Eq. 6 indicates that the internal equilibrium is possible for every q except for
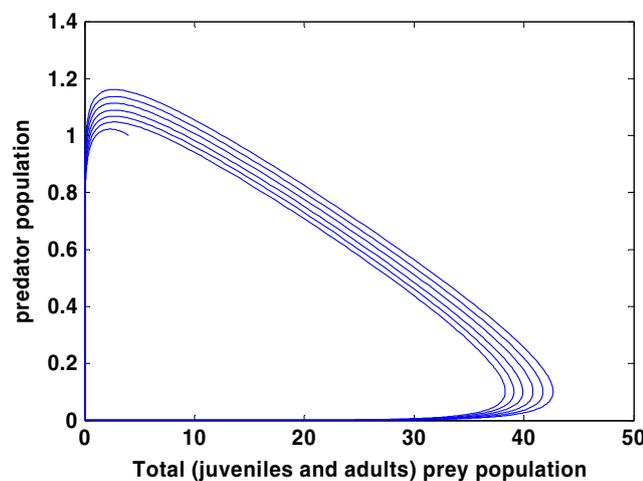

Fig. 4 Phase plane diagram of a dynamic solution of Eq. 2 when $r_2 > d_n$ and E_3 is unstable. The trajectory encircles the phase plane and slowly grows in amplitude with time. Note that the solution is not positively bounded; therefore, it is not persistent. Parameter values are: $k_{11}=0.09$, $k_{12}=0.02$, $d_1=0.03$, $a=0.72$, $r_2=0.09$, $r_1=0.7$, $d_n=0.04$, and $q=0.36$

those which belong to the neighborhood of size U around $q=0.5$.

Next, we examine how the size of this neighborhood depends on the model's parameters. Note that if $U_i=0.5$ (for $i=1$ and 2), then the internal equilibrium exists for every q, and according to Eq. 5, this occurs when:

$$r_1 = \frac{k_1(k_1 r_2 + k_2 d_n)}{k_2(k_2 + k_1)} = r_0, \tag{7}$$

From Eqs. 5, 6, and 7, it is not difficult to demonstrate that the greater the deviation of prey's maturation rate r_1 from r_0, the wider the neighborhood U around $q=0.5$ where the equilibrium fails to exist (Fig. 5). We conclude that if the equilibrium exists at all, it must exist in certain neighborhoods around $q=1$ and $q=0$. These neighborhoods are always equal because of the symmetry of the system with two identical predators (Fig. 5).
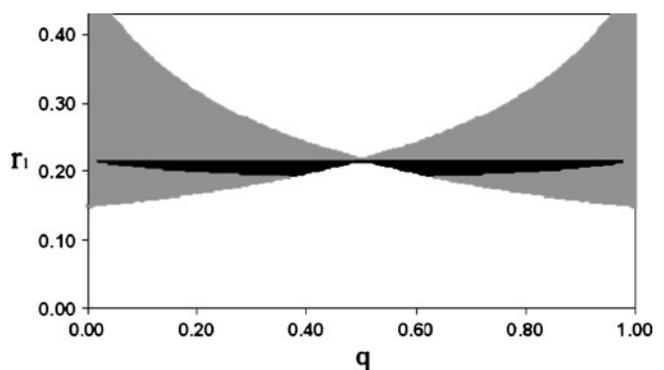

Fig. 5 Existence and stability of the internal equilibrium of Eq. 1 as a function of r_1 and q with two identical predators. *Black*: equilibrium exists but unstable. *Gray*: equilibrium exists and stable. *White*: equilibrium does not exist. Parameter values are: $k_{11}=k_{21}=0.02$, $k_{22}=k_{12}=0.08$, $d_1=d_2=0.07$, $a_1=a_2=0.05$, $r_2=1.9$, $d_n=0.6$, and $r_0=0.215$. Note that the greater the deviation of r_1 from r_0 the wider the range of q where the internal equilibrium fails to exist. This range is symmetrical related to $q=0.5$

Case III: two nonidentical predators

Consider now Eq. 1 in its most general form with nonidentical predators. By setting its derivatives to zero, it is easy to verify that an internal equilibrium, if it exists, is unique. However, the expressions of N_1^* and N_2^*, in contrast with the previous symmetrical case (Eq. 3), depend on q and, therefore, set another necessary (but not sufficient) criterion for the existence of the internal equilibrium. If we demand that both prey stages N_1^* and N_2^* are positive, it is possible to show (Appendix 2) that the internal equilibrium fails to exist only in a certain interval within the [0,1] q's range. However, unlike the previous symmetrical case, this interval is not centered at $q=0.5$.

A necessary and sufficient condition for the existence of the internal equilibrium requires that predator populations be positive as well. For this general case, the predator equilibrium populations are complicated expressions of model parameters, and simple rules are hard to deduce. However, necessary and sufficient conditions for an internal positive equilibrium can be found when $q=0$ and when $q=1$. In these cases, the prey equilibria N_1^* and N_2^* are always positive (see Appendix 2). By writing the expression for predator populations at equilibrium and demanding that they should be positive as well for $q=0$ and $q=1$, the following conditions are obtained for $q=0$ (Eq. 12a) and for $q=1$ (Eq. 12b):

$$r_2 > \frac{k_{22}a_2d_1}{k_{11}a_1d_2}r_1 > d_n, \tag{8a}$$

$$r_2 > \frac{k_{12}a_1d_2}{k_{21}a_2d_1}r_1 > d_n, \tag{8b}$$

Thus, unlike the symmetrical case II, the existence of the internal equilibrium at $q=1$ does not guarantee its existence at $q=0$ and vice versa.

Stability analysis of internal equilibrium (cases II and III)

By writing the Jacobian matrix at the internal equilibrium and applying Routh–Hurwitz criteria for the characteristic polynomial, it is possible to show that if the internal equilibrium exists for $q=0$ or $q=1$, then it is locally stable (Figs. 5 and 6). Numerical calculations show that this is generally not true for other values of q (Figs. 5 and 6). These results are valid irrespective of the symmetry of the system (i.e., whether Eq. 3 holds true or not; see Appendix 2 for details).

Other dynamic behaviors (periodic solutions, chaos, etc.)

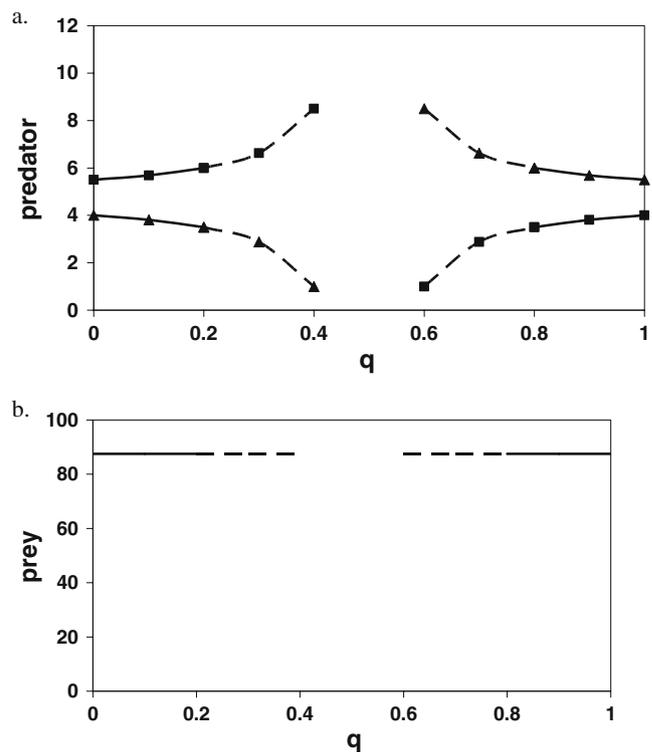No persistent (positively bounded) dynamic solutions (except those that converge to an equilibrium), such as

Fig. 6 Bifurcation diagrams indicating the stability region of the internal equilibrium point of Eq. 1 for the case of two identical predators (case II). **a** *Squares* and *triangles* denote the two distinct predator populations. **b** Prey population. *Solid* and *dashed lines* denote stability and instability, respectively. The equilibrium fails to exist for q in the range [0.4, 0.6]. Parameter values are: $k_{11}=k_{21}=0.02$, $k_{22}=k_{12}=0.08$, $d_1=d_2=0.07$, $a_1=a_2=0.05$, $r_2=1.9$, $d_n=0.6$, $r_1=0.2$. Note that equilibrium is stable only in a neighborhood of $q=0$ and $q=1$ and unstable elsewhere

limit cycle behavior or chaos of Eq. 1, were found via simulations. Every trajectory, which initially contains predators (one or two), either converges to an equilibrium point or gets infinitely close to the state space axis implying that it is not persistent (as in Fig. 4). For systems that do not initially contain predators, the prey population either remains constant, extinct, or explodes depending on whether r_2 is equal, less, or greater than d_n, respectively.

Discussion

We can see from case I (one predator–one prey dynamics) that although the functional response stabilizes the internal equilibrium point at $q=0$ and $q=1$ (provided that $r_2>d_n$), the equilibrium can be unstable in a left/right neighborhood of $q=0.5$ with size depending on r_1 (prey's maturation rate) and r_2 (prey intrinsic rate of increase per capita). This finding extends earlier results which concentrated on age dependent predation where $q=0$ or $q=1$ only (Hastings 1983).

Numerical integration demonstrates that Eq. 1 trajectories which initially include that predator(s) is (are) always attracted to one nontrivial equilibrium point if it exists and is locally stable. This equilibrium is not unique to the system, and different trajectories may end up at different equilibria. When there are no stable nontrivial equilibria in the whole state space, trajectories get close to the state space axis (where the population is extinct), implying that the system is impersistent (Fig. 4). Our results indicate that a mixed diet of juvenile and adult prey may result in the loss of equilibrium points or make existing equilibria unstable. This is a general finding, valid for all the cases we explored. We may conclude, therefore, that complementary predation, where each predator tends to concentrate on one developmental stage, contributes to system stability and persistence (populations which are positively bounded), while predators that mix several prey life stages in their diet tend to reduce the stability and persistence of the system. Splitting of the prey's life stages between different habitats may, therefore, contribute to the persistence and stability of the community.

The effect of predator species richness on prey consumption has been the focus of much attention (Casula et al. 2006; Scmitz 2007; Wilby and Thomas 2002). In contrast, we kept the number of predators constant in our study and demonstrated the importance of predator functionality. We found that differences in predator's functionality may result in different dynamic outcomes even when species richness of the predators in the system remains the same.

Previous studies focused on various mechanisms which affect predator guild richness (Haigh and Smith 1972). It was found that scramble competition within various life stages of the prey can stabilize communities with two predators that feed on one age-structured prey, where each predator attacks a different life stage (de Roos et al. 2008). Likewise, coexistence of two parasitoid species of a single host may persist under certain life history conditions (Murdoch et al. 2003), such as when parasitoid larvae interact negatively within their host or when they differ their ability to attack the host (Briggs 1993; Kakehashi et al. 1984). These studies assume that prey population is not age-structured or that there is a complete differential predation (i.e., each predator/parasitoid attacks the adults or the juveniles, but not both). Our study analyzed the importance of predator's functionality, i.e., their preference in attacking juveniles or adults, for their coexistence. Our results suggest that complementary predation on various life stages of the prey, founded in Holometabolous insects and other important taxa with phenotypically different adults and juveniles, may enable predator's coexistence and, therefore, support more speciose and persistent communities which are less vulnerable to external perturbation.

Appendix 1: Local stability analysis of the internal equilibrium of Eq. 2—case I

Writing the characteristic polynomial of the Jacobian of Eq. 2 at equilibrium and equate to 0, we have:

$$\lambda^3 + A_2\lambda^2 + A_1\lambda + A_0 = 0,$$

According to Routh–Hurwitz criteria, necessary and sufficient conditions that third-degree polynomial will have stable roots (i.e., have only negative real parts) are:

$$A_2 > 0 \,\&\, A_0 > 0 \,\&\, A_1A_2 - A_0 > 0,$$

A_i's are complicated expressions. However, it can be verified according to the signs of the factors consisted in each A_i that, provided that all system parameters are positive and $r_2 > d_n$ (the condition for the existence of the internal equilibrium), it is always true that:

$$A_2 > 0 \,\&\, A_0 > 0 \text{ for every q } (0 \leq q \leq 1).$$

The third condition: $A_1A_2 - A_0 > 0$ is not valid for every q. We, therefore, defined a function $f(q) = A_1A_2 - A_0$.

This function has all the information of the local stability properties of the internal equilibrium. When $f(q) > 0$, the system is locally stable, when $f(q) < 0$, it is locally unstable. Although it consists of complicated expressions, it can be shown that it is always true that $f(q = 1) > 0$ and $f(q = 0) > 0$. Matlab found the exact symbolic expressions for the roots of $f(q) = 0$. It was found that: (1) $f(q) = 0$ has only four roots; (2) two roots are always complex, provided $r_2 > d_n$ and all other parameters are positive; (3) two roots are always real, provided all parameters are positive and $r_2 > d_n$; (4) One root is always 0.5, i.e., $f(q = 0.5) = 0$.

Aided by these findings, we can see that $f(q)$ has only two roots in the range $0 \leq q \leq 1$. One is always 0.5 (i.e., $f(q = 0.5) = 0$) and the other is q' which can take any number between 0 to 1 ($0 < q' < 1$) (Fig. 7). Since $\frac{df(q)}{dq}(q = q') \neq 0$ for $q' \neq 0.5$ and $f(q)$ is C^1, we conclude that $f(q) < 0$ in the interval $R = [q', 0.5]$ or $[0.5, q']$ and $f(q) > 0$ elsewhere in the interval $[0,1]$ (Fig. 7).

The location and the size of R in the $[0,1]$ interval is determined by q' according the following rules: (1) if $q' > 0.5$, the range R lies to the right of $q = 0.5$, i.e., the internal equilibrium is unstable focus for $0.5 < q < q'$ and stable focus everywhere else ($0 < q < 0.5$ or $q > q'$); (2) if $q' < 0.5$, the range R lies to the left of $q = 0.5$ (Fig. 7), i.e., the internal equilibrium is unstable focus for $q' < q < 0.5$ and stable focus everywhere else ($0 < q < q'$ or $q > 0.5$); (3) if $q' = 0.5$, then the internal equilibrium is a stable focus for every $q \neq 0.5$; (4) for $q = 0.5$ or $q = q'$, i.e., when q lies on the boundaries of the interval R, the internal equilibrium is neutrally stable.
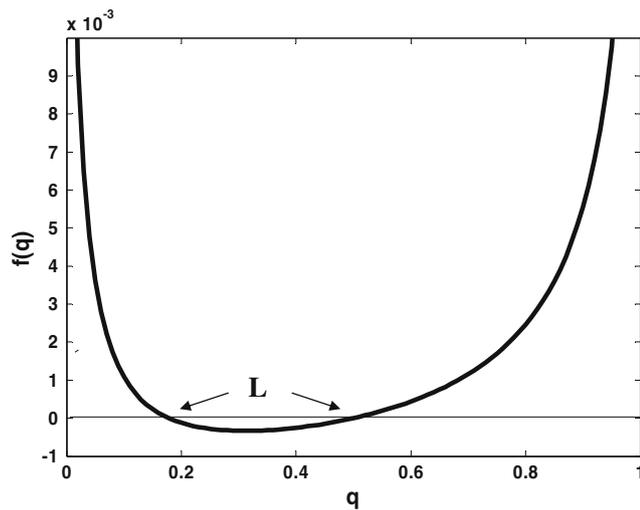
Fig. 7 Stability pattern for the internal equilibrium E_3 of Eq. 2 as determined by the function $f(q)$ (see text for details). The parameter q describes the degree of mixing by the predator of two life stages of its prey. When $f(q)>0$, the system is stable; when $f(q)\leq0$, the system is unstable. Parameter values were set to: $k_{11}=0.68$, $k_{12}=0.39$, $r_1=0.05$, $r_2=0.99$, $a_1=0.72$, $d_n=0.04$, $d_1=0.03$. In this example, $q'=0.197$ and the system is unstable in the interval $L=[0.197,0.5]$ and stable elsewhere

Appendix 2: existence and stability of the internal equilibrium for the 4D system Eq. 1 (cases II and III)

Existence of internal equilibrium of Eq. 1 with nonidentical predators—case III

When nonidentical predators are involved (i.e., Eq. 3 does not hold true), we have the following expressions for the internal equilibrium values of N_1 and N_2:

$$N_1^* = \frac{qd_1k_{22}a_2 - (1-q)d_2k_{12}a_1}{a_1a_2\left[k_{22}k_{11}q^2 - k_{12}k_{21}(1-q)^2\right]},$$

$$N_2^* = \frac{qd_2k_{11}a_1 - (1-q)d_1k_{21}a_2}{a_1a_2\left[k_{22}k_{11}q^2 - k_{12}k_{21}(1-q)^2\right]},$$

(9)

It can be shown that the conditions for $N_1^* > 0$ and $N_2^* > 0$ (and, therefore, necessary conditions for the internal equilibrium for Eq. 1) are:

$$q \leq \min(X_1, X_2, X_3) \text{ or } q \geq \max(X_1, X_2, X_3),$$

(10)

Where:

$$X_1 = \frac{d_1k_{21}a_2}{d_2k_{11}a_1 + d_1k_{21}a_2}, \quad X_2 = \frac{\sqrt{k_{12}k_{21}}}{\sqrt{k_{11}k_{22}} + \sqrt{k_{12}k_{21}}},$$

$$X_3 = \frac{d_2k_{12}a_1}{d_2k_{12}a_1 + d_1k_{22}a_2},$$

By adding the first two equations in Eq. 1, another necessity condition can be yielded, namely, $r_2>d_n$. To summarize, necessary conditions for the existence of the internal equilibrium for the nonidentical predator's case of Eq. 1 are:

$$r_2 > d_n,$$

(11a)

$$q \leq \min(X_1, X_2, X_3) \text{ or } q \geq \max(X_1, X_2, X_3),$$

(11b)

We see from Eq. 10 that X_1, X_2, X_3 are all positive fractions (i.e., all lie in the closed interval [0,1]), provided all the model's parameters are positive (which they obviously are). Therefore, if equilibrium exists at all, it must be in certain neighborhoods of $q=0$ or $q=1$ which are usually not equal (unless Eq. 3 holds true). Alternatively, if there is a region of q where equilibrium is not possible, then it is an interior interval in the closed interval [0,1] which is usually not centered at $q=0.5$. The size of this interval depends on the model's parameters. For example, when symmetrical predators are involved (case II), by setting Eq. 3 into Eq. 10, we see that $X_1=X_2=$, $X_3=0.5$, and equilibrium is possible for every q, so the impossible interval length is 0 insofar as it concerns the prey population (predators population set another limitation on the q's range where equilibrium is impossible).

Stability of the internal equilibrium of the 4D system Eq. 1 (cases II and III)

Again, by looking at the Jacobian matrix of Eq. 1 at the internal equilibrium, we can formulate the Routh–Hurwitz criteria for the characteristic polynomial that must be satisfied in order to be locally stable. If the characteristic polynomial of a 4D system has the form:

$$\lambda^4 + A_3\lambda^3 + A_2\lambda^2 + A_1\lambda + A_0 = 0,$$

Than Routh–Hurwitz criteria are:

$$A_0 > 0, \ A_1 > 0 \ A_3 > 0,$$

(12a)

$$f_1 = A_3A_2 - A_1 > 0,$$

(12b)

$$f_2 = A_1f_1 - A_3^2A_0 > 0,$$

(12c)

Writing those conditions for Eq. 1 for an arbitrary q yields very complicated expressions. However, when $q=0$ or $q=1$, they have simpler forms. We begin by defining the following variables: *For $q=0$*

$$X_0 = k_{21}a_2d_1r_2 - k_{12}a_1r_1d_2,$$

(13a)

$$Y_0 = k_{12}a_1d_2r_1 - k_{21}a_2d_nd_1, \tag{13b}$$

For $q=1$

$$X_1 = k_{11}a_1d_2r_2 - k_{22}a_2r_1d_1, \tag{13c}$$

$$Y_1 = k_{22}a_2r_1d_1 - k_{11}a_1d_nd_2, \tag{13d}$$

Again, Eq. 12a is always satisfied for $q=1$ or $q=0$. This can be verified by looking at the signs of the polynomial coefficients. Condition Eqs. 12b and 12c have the following expressions for $q=0$ and $q=1$: For $q=0$

$$f_1 = \frac{k_{12}^3a_1^3r_1d_2^2Y_0 + k_{21}^3a_2^3d_1^2r_2X_0}{k_{12}^2k_{21}^2a_1^2a_2^2d_1d_2}, \tag{14a}$$

$$f_2 = \frac{r_1r_2\left(a_1^2k_{12}^2d_2r_1 - a_1a_2k_{12}k_{21}d_1d_n + a_1a_2k_{12}d_2k_{21}r_1 - r_2a_2^2k_{21}^2d_1\right)^2}{k_{21}^2a_2^2k_{12}^2a_1^2}, \tag{14b}$$

For $q=1$

$$f_1 = \frac{k_{11}^3a_1^3d_2^2r_2X_1 + k_{22}^3a_2^3d_1^2r_1Y_1}{k_{11}^2k_{22}^2a_2^2a_1^2d_1d_2}, \tag{14c}$$

$$f_2 = \frac{r_1r_2\left(-d_2k_{11}^2a_1^2r_2 + r_1d_1k_{11}a_1k_{22}a_2 - d_nd_2k_{11}a_1k_{22}a_2 + k_{22}^2a_2^2r_1d_1\right)^2}{k_{22}^2k_{11}^2a_1^2a_2^2}, \tag{14d}$$

We see that $f_2>0$ for both $q=0$ and $q=1$. $f_1>0$ for $q=0$ if $X_0>0$ and $Y_0>0$, which are equivalent to condition Eq. 8b, and $f_1>0$ for $q=1$ if $X_1>0$ and $Y_1>0$, which are equivalent to condition Eq. 8a. We conclude (from Eqs. 8a, 8b, 12a–12c, and 14a–14d) that if an internal equilibrium exists for $q=0$ or $q=1$, then it is stable.

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