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Switching strategies, population dynamics, and mechanisms of co-existence in food webs with Jekyll-and-Hyde species

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ABSTRACT

Definition: Intra-guild predators prey on members of other species that belong to the same guild.

Question: What are the effects of polymorphic intra-guild predators on population dynamics and diversity?

Mathematical method: We use differential equations to model a specific form of trophic polymorphism where the polymorphic species is an intra-guild predator. This species can switch between two morphs – Jekyll, which competes with the intra-guild prey for a shared resource, and Hyde, which preys on the intra-guild prey. For generality, we explore two different food web arrangements (with and without cannibalism of Hyde on Jekyll) and two different switching strategies (constant and variable).

Key assumptions: We assume that switching between the morphs occurs continuously and in both directions. We also assume that switching is cost-free.

Conclusions: Switching in general stabilizes population dynamics, except in the case of the cannibalistic food web with variable switching. Population subsidies from one morph to the other create ecological opportunity for a specialist species with identical ecology as the subsidizing morph. Switching enhances opportunities for co-existence with the intra-guild prey when Hyde subsidizes Jekyll. However, when Jekyll subsidizes Hyde, opportunities for co-existence with the intra-guild prey are diminished.

Keywords: intra-guild predation, mechanism of co-existence, phenotypic switching,
trophic polymorphism.

INTRODUCTION

Predation can promote the co-existence of two consumer species competing for a common resource. This can occur in one of two ways. First, a distinct predator species preys more successfully or heavily on the consumer species that is itself the better competitor in the

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absence of predation (Paine, 1966; Leibold, 1996; Viola *et al.*, 2010). Or second, via intra-guild predation, the poorer resource competitor is able to prey upon the other consumer species (Rosenzweig, 1966; Holt and Polis, 1997; Borer *et al.*, 2003). With intra-guild predation, one of the consumers incidentally or intentionally preys upon the other consumer. Intra-guild predation becomes common in nature when the consumer's adaptations for its resource also make it reasonably apt at capturing the other consumer. For instance, the adaptations that permit a large spider species to capture herbivorous insects also allow it to capture smaller species of spiders. In fact, 'mesopredators' often find themselves both competing with and being preyed upon by larger predators.

An important, but less appreciated form of intra-guild predation occurs when the intra-guild predator species has two morphs: one competes with another consumer species, and the other preys upon it. We call the first morph Dr. Jekyll and the second Mr. Hyde after the story of the benign scientist who finds himself morphing into the malignant Mr. Hyde. Unlike the story, most ecological Jekyll-and-Hyde species possess a morph that cannot convert back within the lifetime of the individual. At some point in its development or ecology, the individual irreversibly becomes the predatory morph. Only through offspring can the original morph or a mixture of morphs be recovered.

The single-cell ciliate, *Tetrahymena vorax*, represents a Jekyll-and-Hyde species. As a microstome, *T. vorax* feeds on bacteria, ingesting numerous individuals to form a food vacuole eventually. As a macrostome, *T. vorax* feeds on other ciliates in its guild (such as *T. pyriformis*), engorging itself through the capture of just a single prey item. An individual microstome metamorphoses into a macrostome by changing its morphology and the structure of its intake orifice. But it need not do so; a microstome can simply divide into a pair of macrostomes. The macrostome cannot morph back into a microstome. The microstome is an obligatory bacteria feeder, and the macrostome is an obligatory predator of other ciliates. They are Dr. Jekyll and Mr. Hyde, respectively. Morin (1999) examined competition between morphing and non-morphing ciliates and found that the non-morphing *Colpidium* outcompeted the morphing *Blepharisma* at low productivity. But at higher productivity, the two largely co-existed. Theory had predicted these outcomes.

Jekyll and Hyde morphs are present in other ciliates (e.g. *Lembadion bullinum*). They also occur, albeit infrequently, across the animal kingdom. The tiger salamander, *Ambystoma tigrinum nebulosum*, develops into a cannibalistic morph when macro-invertebrates are available to its larvae (Maret and Collins, 1997; Whiteman *et al.*, 2003). Both field and laboratory experiments show that cannibals prefer conspecifics over macro-invertebrates. On the other hand, typical morphs consume only macro-invertebrates and other prey and apparently never cannibalize conspecifics. Other trophic-induced polymorphisms, though not of a Jeckyll-and-Hyde nature, are common among fish [e.g. many cichlid species (Meyer, 1990), perch (Hjelm *et al.*, 2001), and charr (Garduño-Paz and Adams, 2010)]. Wimberger (1994) and Skulason and Smith (1995) review trophic-induced polymorphisms among vertebrates.

Here we model the dynamics, switching strategies, and opportunities for species co-existence when the community contains a Jekyll-and-Hyde species, such as *T. vorax*. We consider both a constant and a variable switching strategy. We seek to answer three questions: (1) What is the effect of different switching strategies on population dynamics? (2) What is the effect of different switching strategies on co-existence with the intra-guild prey? (3) What is the relationship between switching species and their specialist counterparts? Jekyll-and-Hyde morphs represent an extreme form of prey switching that is more generally associated with specialist species rather than specialist morphs within a species.

Therefore, we introduce non-switching specialists (that correspond to each morph) into the community to understand the relationship between a switching species and their specialist counterparts.

Tetrahymena as a Jekyll-and-Hyde system

The two main cell types of the polymorphic *T. vorax* are the microstomal form (77×29 μm) with a characteristically small oral apparatus (10.5×5.5 μm) and the macrostomal form (110×75 μm) with a large oral apparatus (29×23 μm). In the microstome, a food vacuole forms as an individual continuously traps small particles including bacteria. In the macrostome, the large oral apparatus opens into a large, semi-permanent pouch (surface area = 5715 μm^2). The pouch acts as a prey receptacle prior to its pinching off from the cytostome.

The feeding strategies of the microstome and macrostome cells differ radically, reflecting their prey. In the filter-feeding microstome, ciliary membranelles produce a current that sweeps bacteria and other small particles across the oral apparatus in which they are trapped by the cilia of the undulatory membrane (which acts as baleen allowing water to pass through). The trapped particles then fall down the oral ribs into the cytostome where phagosomes form.

In contrast, the macrostome ingests small ciliates whole as it moves through a liquid medium with its cytostomal opening partially agape. When a prey item passes through the cytostome, the macrostome accelerates, forcing the prey into the pouch. The pouch then seals off from the cytostome forming a large phagosome in which digestion occurs. Following phagosome formation, a new pouch forms.

The two feeding strategies are cell type specific because of the relative sizes and morphologies of their respective feeding structures. The microstomal form cannot feed on large prey and the macrostomal form cannot feed on small prey.

A potential prey ciliate also produces the trigger for microstomal to macrostomal differentiation. Buhse (1966a, 1966b, 1967) isolated a mixture of cell exudates as the triggering factor and named it 'stomatin' because it initiated the differentiation of the macrostome from the microstome. More recently, Ryals *et al.* (2002) identified the active principle as an iron chelate of hypoxanthine and uracil. The chelate apparently forms as part of an elimination process of purine and pyrimidine catabolites. The chelate may bind to a receptor, which activates genes that initiate the differentiation process.

Differentiation of the macrostome occurs by replacement of the microstomal oral apparatus. The apparatus is resorbed and replaced with a larger one typical of the macrostomal form. The process ends with formation of a prey receptacle called the cytopharyngeal pouch (Buhse, 1966b). The differentiation process occurs within 6–8 h following treatment with stomatin or the chelate. Maximal differentiation occurs when populations of microstomal cells are in the early, stationary phase of population growth (Buhse, 1966a), and most cells appear in the late S or G2 stage of the cell cycle.

The macrostome is a transient condition contingent upon prey availability and apparently correlated with cell division. If ciliate prey are abundant, macrostome cell division produces macrostomes. If ciliate prey are scarce, macrostome cell division produces microstomes (Buhse, 1966a). Switching may be adaptively modulated in response to feeding opportunities provided by bacteria (to the microstome) and other ciliates (to the macrostome).

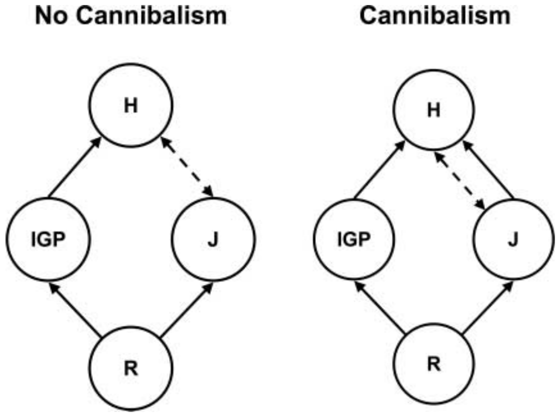

Fig. 1. Graphical depiction of the food webs we model. The solid arrows indicate trophic transfers. The dotted arrows indicate switching between the morphs of the polymorphic species. H, J, IGP, and R stand for Hyde, Jekyll, intra-guild prey, and a resource species, respectively.

MODEL DESCRIPTION

We consider two different food webs: (1) a web without cannibalism, where the Hyde morph feeds solely on the intra-guild prey species, and (2) a web with cannibalism, where the Hyde morph feeds on both the intra-guild prey and the Jekyll morph (Fig. 1). In our analysis of these models, we consider a resource species, intra-guild prey, and a switching species with two distinct morphs. Furthermore, to understand the effect of switching on population dynamics, opportunities for co-existence, and the adaptive value of switching, we also consider two specialist species corresponding to each of the morphs. While ecologically identical to the switching morphs, they are distinct species that do not switch.

We build upon MacArthur's (1972) consumer–resource model (Table 1). At the base of each web is a resource species, which is self-limited by logistic growth. Consumers have type-II functional responses (Holling, 1959) and suffer constant density-independent mortality. Intra-guild predation is introduced through the linkage of Jekyll and Hyde morphs as a single switching species. The variables c_j and c_h are the per capita switching rates of Jekyll to Hyde and Hyde to Jekyll, respectively. We model two different switching strategies – a constant per capita switching rate, and a variable switching rate. When the switching rate is variable, we let the rate of switching increase with the fitness difference between the potential morph and the individual's current morph. This is analogous to switching models from habitat selection. Throughout, we assume for simplicity that switching is cost-free.

To model variable switching we use a β-function (e.g. Fryxell and Lundberg, 1998) (equation 1). We let our model organism estimate the fitness of each morph from environmental information. Fitness of a morph is defined as its per capita growth rate in the absence of those switching into and out of the morph. The switching function is parameterized by the switch point (δ) and the sensitivity of switching to changes in the environment (z). By setting the switch point δ to 0, the morphs are equally likely to switch when there is no fitness difference between the morphs. Individuals using this strategy become more likely to switch morphs

Table 1. Equations governing the dynamics of the food webs

Description	*Food web without cannibalism*	*Food web with cannibalism*
Resource growth rate	$\frac{\mathrm{d}R}{\mathrm{d}t} = R\left[r\left(1 - \frac{R}{K}\right) - \frac{a_{rp}P}{1 + a_{rp}h_{rp}R} - \frac{a_{rj}\sum_{t=1}^{2} J_i}{1 + a_{rj}h_{rj}R}\right]$	$\frac{\mathrm{d}R}{\mathrm{d}t} = R\left[r\left(1 - \frac{R}{K}\right) - \frac{a_{rp}P}{1 + a_{rp}h_{rp}R} - \frac{a_{rj}\sum_{t=1}^{2} J_i}{1 + a_{rj}h_{rj}R}\right]$
Intra-guild prey growth rate	$\frac{\mathrm{d}P}{\mathrm{d}t} = P\left[\frac{b_{rp}a_{rp}R}{1 + a_{rp}h_{rp}R} - m_p - \frac{a_{ph}\sum_{i=1}^{2} H_i}{1 + a_{ph}h_{ph}P}\right]$	$\frac{\mathrm{d}P}{\mathrm{d}t} = P\left[\frac{b_{rp}a_{rp}R}{1 + a_{rp}h_{rp}R} - m_p - \frac{a_{ph}\sum_{i=1}^{2} H_i}{1 + a_{ph}h_{ph}P + a_{jh}h_{jh}\sum_{i=1}^{2} J_i}\right]$
Jekyll growth rate	$\frac{\mathrm{d}J_i}{\mathrm{d}t} = J_i\left[\frac{b_{rj}a_{rj}R}{1 + a_{rj}h_{rj}R} - m_j - c_{ji}\right] + c_{hi}H_i$	$\frac{\mathrm{d}J_i}{\mathrm{d}t} = J_i\left[\frac{b_{rj}a_{rj}R}{1 + a_{rj}h_{rj}R} - m_j - c_{ji} - \frac{a_{jh}\sum_{i=1}^{2} H_i}{1 + a_{ph}h_{ph}P + a_{jh}h_{jh}\sum_{i=1}^{2} J_i}\right] + c_{hi}H_i$
Hyde growth rate	$\frac{\mathrm{d}H_i}{\mathrm{d}t} = H_i\left[\frac{b_{ph}a_{ph}P}{1 + a_{ph}h_{ph}P} - m_h - c_{hi}\right] + c_{ji}J_i$	$\frac{\mathrm{d}H_i}{\mathrm{d}t} = H_i\left[\frac{b_{ph}a_{ph}P + b_{jh}a_{jh}\sum_{i=1}^{2} J_i}{1 + a_{ph}h_{ph}P + a_{jh}h_{jh}\sum_{i=1}^{2} J_i} - m_h - c_{hi}\right] + c_{ji}J_i$

Notes: The i subscripts on both Jekyll and Hyde and their switching rates indicate either a single morph of the switching species or a separate specialist species. The sums then represent the abundance of both the morph and the specialist species, since they are ecologically equivalent in all respects besides switching strategy.

when the alternate morph has higher fitness than the morph they currently occupy. Perfectly adaptive behaviour occurs when z approaches infinity in the model.

$$c_k = \frac{e^{z\delta}}{e^{z\delta} + e^{zx}}. \tag{1}$$

In the following sections, we first investigate the effects of the switching strategies on population dynamics and co-existence with intra-guild prey. Then we consider the relationship of switching species and their specialist counterparts. We address these questions mainly through numerical simulation of the model. We begin by choosing parameters that allow the two specialist species to co-exist with the intra-guild prey within a range of environmental productivities (K, Table 2). Following Holt and Polis (1997), we assume a predation risk–foraging trade-off between Jekyll and the intra-guild prey species, such that Jekyll is better at managing predation risk and the intra-guild prey is a superior resource exploiter. Then we vary select model parameters to explore the generality of our conclusions. Throughout we compare and contrast the two food webs and the two switching behaviours.

Table 2. Parameter meanings and values used in simulations

Parameter	Meaning	Value (units)
K	Resource carrying capacity	Variable (resource biomass)
r	Resource intrinsic growth rate	1 (time^{-1})
a_{rj}	Encounter rate of Jekyll on resource	0.075 (time^{-1})
a_{rp}	Encounter rate of intra-guild prey on resource	0.1 (time^{-1})
a_{ph}	Encounter rate of Hyde on intra-guild prey	0.01 (time^{-1})
a_{jh}*	Encounter rate of Hyde on Jekyll	0.005 (time^{-1})
h_{rj}	Handling time of Jekyll on resource	0.1 (time/resource)
h_{rp}	Handling time of intra-guild prey on resource	0.1 (time/resource)
h_{ph}	Handling time of Hyde on intra-guild prey	2 (time/intra-guild prey)
h_{jh}*	Handling time of Hyde on Jekyll	2 (time/Jekyll)
b_{rj}	Conversion efficiency of captured resources into Jekyll	0.05 (biomass of Jekyll/unit resource consumed)
b_{rp}	Conversion efficiency of captured resources into intra-guild prey	0.05 (biomass of intra-guild prey/unit resource consumed)
b_{ph}	Conversion efficiency of captured intra-guild prey into Hyde	0.15 (biomass of Hyde/unit intra-guild prey consumed)
b_{jh}*	Conversion efficiency of captured Jekyll into Hyde	0.05 (biomass of Hyde/unit Jekyll consumed)
m_p	Per capita mortality rate of intra-guild prey	0.05 (time^{-1})
m_j	Per capita mortality rate of Jekyll	0.05 (time^{-1})
m_h	Per capita mortality rate of Hyde	Variable (time^{-1})
z	Switching sensitivity	Variable (unitless)

*Parameters exclusive to the cannibal food web.

RESULTS

Switching strategies and population dynamics

We begin by considering the different food webs and switching behaviours along a gradient of productivity (K). The top panel of Fig. 2 shows the two food webs without switching. Here Jekyll and Hyde are two distinct specialist species. In these food webs, there are three types of dynamical behaviour. At low productivity, the population dynamics are stable. At intermediate productivities, the dynamics exhibit limit cycles. While at higher productivities, the limit cycles have higher frequencies and amplitudes. Increasing K causes the paradox of enrichment (Rosenzweig, 1971), i.e. increasing productivity destabilizes the dynamics.

The middle panels of Fig. 2 show the two food webs with a fixed and a low rate of switching ($c = 0.001$). The constant switching behaviour stabilizes the population dynamics. In both models, the limit cycles do not occur until very high productivities. The stabilizing effect of switching comes about through increased negative density dependence. To demonstrate this, we let γ equal the net per capita rate of transfer from Hyde to Jekyll:

$$\gamma = -c + c\frac{J}{H}.$$

Taking the derivative of γ with respect to H gives the direct per capita density dependence due to switching,

$$\frac{\partial \gamma}{\partial H} = -\frac{cJ}{H^2}.$$

Thus switching adds negative density dependence, which shortens time lags and stabilizes the dynamics. The effect is strongest when H (Hyde abundance) is small. This happens because the per capita outflow from a particular morph is constant, but the per capita inflow decreases with morph population size.

Figure 3 shows the effects of increased per capita rate of constant switching (c). These results confirm and reinforce the conjectures that switching is stabilizing. Under low productivity, increasing the switching rate quickly stabilizes the dynamics. Under high productivity, the dynamics are not stabilized for the range of switching rates shown. We note that the dynamics do stabilize by $c = 0.1$ in both food webs.

The variable switching strategy has different consequences for stability depending upon food web structure. In the non-cannibal food web, variable switching (bottom panel of Fig. 2) is more stabilizing than the constant switching strategy. Large increases in a morph's population result in negative fitness (per capita growth rate excluding switching), which results in increased per capita switching outflows from the morph. In the non-cannibal web, the dynamics are stabilized over a wider range of productivities. In the cannibal web, however, variable switching is actually less stabilizing than constant switching. Since Hyde feeds on Jekyll, predator–prey dynamics coupled with the variable switching result in cannibalistic population cycles. The positive feedback in Hyde abundance drives this instability. Increases in Hyde abundance immediately decreases Jekyll's fitness, which in turn causes Jekyll to switch to Hyde, further inflating Hyde abundance.

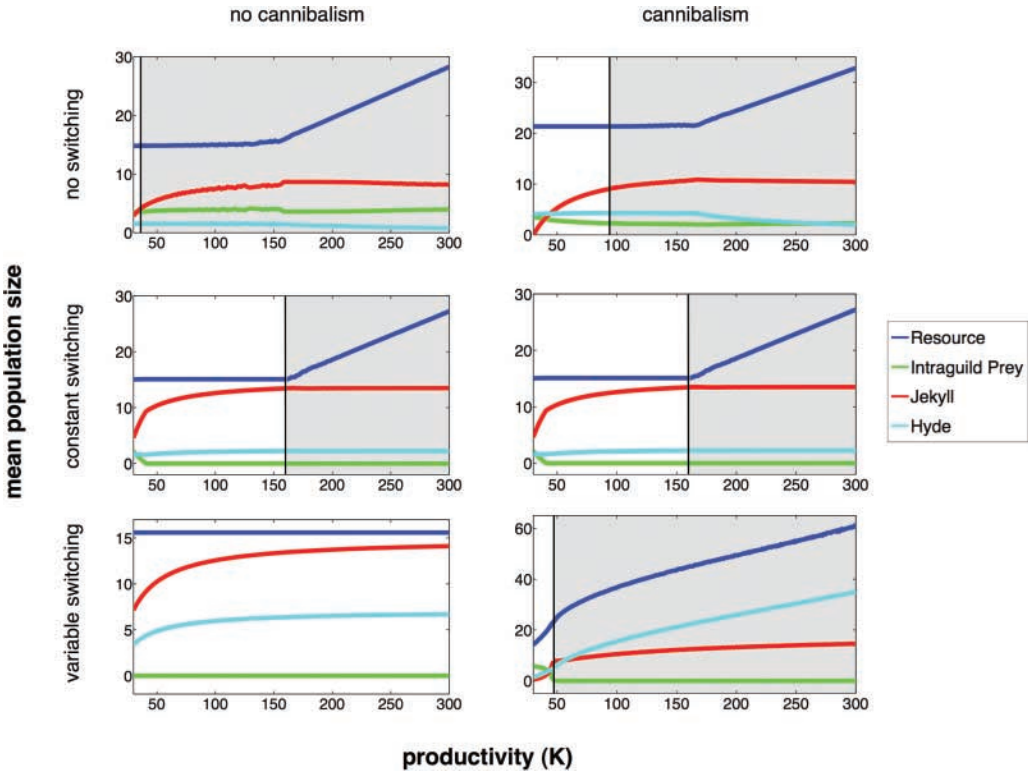
no cannibalism
cannibalism
mean population size
no switching
constant switching
variable switching
0
5
10
15
20
30
40
60
50
100
150
200
250
300
Resource
Intraguild Prey
Jekyll
Hyde
productivity (K)

Fig. 2

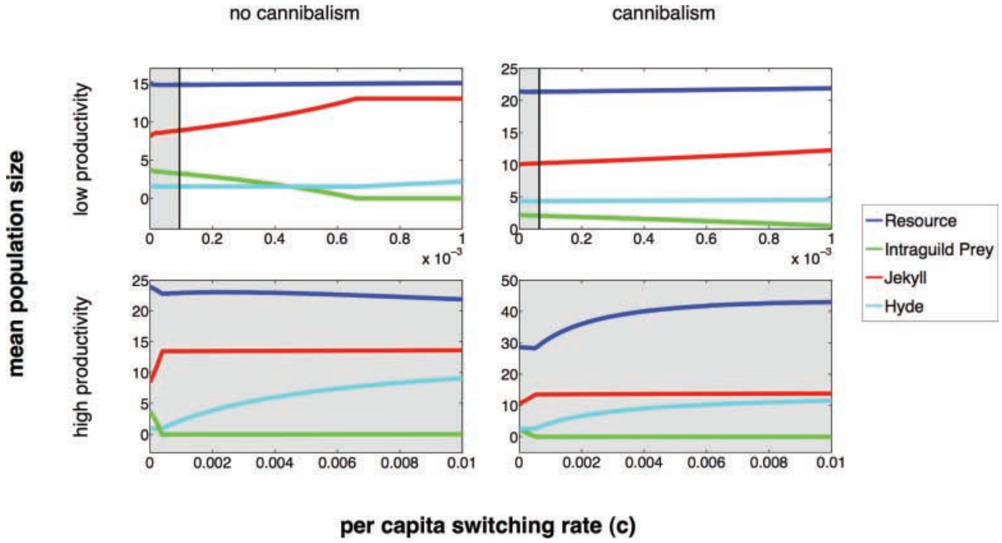
no cannibalism
cannibalism
mean population size
low productivity
high productivity
0
5
10
15
20
25
30
40
50
0.2
0.4
0.6
0.8
1
x 10^{-3}
0.002
0.004
0.006
0.008
0.01
Resource
Intraguild Prey
Jekyll
Hyde
per capita switching rate (c)

Fig. 3

Switching strategies and co-existence with intra-guild prey

For the parameters used in Fig. 2, constant switching restricts the conditions under which Jekyll, Hyde, and the intra-guild prey co-exist. To understand why, consider the effects of productivity on the two food webs. In the non-cannibalistic food web, increasing K allows the resource to support more consumers. Since Hyde fixes the abundance of intra-guild prey, and Jekyll fixes the abundance of the resource, increasing K translates into more Jekyll. When the two morphs are linked through switching, the increase in Jekyll increases Hyde to an artificially high level. As a result, Hyde depletes the intra-guild prey. Therefore, increasing productivity combined with switching increases the per capita mortality rates on the intra-guild prey, and decreases opportunities for co-existence.

In the cannibalistic food web, Hyde feeds on both Jekyll and the intra-guild prey as substitutable resources. The negative effect of subsidized Hyde abundance still occurs. However, since the intra-guild prey and Jekyll are both part of Hyde's functional response, there is also an indirect mutualistic effect between the intra-guild prey and Jekyll. Increasing Jekyll causes Hyde individuals to spend more time handling them, which then decreases predation pressure on the intra-guild prey. This counteracts the effects of subsidies to Hyde. This short-term mutualistic effect between Jekyll and intra-guild prey in the cannibalistic web enhances co-existence of the intra-guild prey relative to the non-cannibalistic web. But co-existence is still limited relative to the cannibal web with no switching.

Figure 3 shows how increased switching rates drive the intra-guild prey extinct. This is because Jekyll subsidizes the abundance of Hyde. This subsidy grows as the switching rate increases, thus amplifying this effect. In addition, the effect is also enhanced by productivity. Under high productivities, the intra-guild prey goes extinct at comparatively lower switching rates. At higher productivities, the system fluctuates at high frequency and greater amplitude. These types of fluctuations increase the benefit of higher switching rates. As the switching rates increase, the switching species becomes more efficient and both bacteria and intra-guild prey abundances are decreased. This increased efficiency drives the intra-guild prey extinct in both food webs.

Interestingly, we found that intra-guild prey co-existence depends upon the relative efficiencies of Jekyll and Hyde (i.e. which morph is subsidized and which is subsidizing). The morph with the higher average abundance is the morph that acts as a subsidy, since the per capita rate of switching is equal in both directions between the morphs. When Jekyll subsidizes Hyde abundance (as is generally the case in Fig. 2), co-existence becomes restricted relative to the food web with no switching. Alternatively, when Hyde subsidizes Jekyll abundance, co-existence is enhanced. This occurs because the intra-guild prey is more

Fig. 2. Population stability and species co-existence as a function of productivity (K) for the two food webs, with no ($c = 0$), constant ($c = 0.001$), and variable ($z = 100$) switching strategies. Population values shown are means of simulated time series after the dynamics have reached equilibrium. Shaded and unshaded areas indicate population dynamics characterized by limit cycles and stability, respectively.

Fig. 3. Population stability and species co-existence as a function of the per capita switching rate (c) of constant switchers in the two food webs under low ($K = 125$) and high ($K = 250$) productivity. Population values shown are means of simulated time series after the dynamics have reached equilibrium. Shaded and unshaded regions indicate population dynamics characterized by limit cycles and stability, respectively.

limited by predation than food. If Hyde subsidizes Jekyll abundance, predation pressure on the intra-guild prey decreases and the shared resource is depressed. Since the intra-guild prey is more limited by predation, an increased switching rate will temporarily increase the fitness of the intra-guild prey.

The variable switching strategy greatly reduces the possibility of co-existence with the intra-guild prey. The intra-guild prey co-exists only at very low productivity (bottom panel of Fig. 2). In the specialist web, the variable switching is stabilizing, and at equilibrium, switching rates are high. This increases subsidies between morphs and drives the intra-guild prey extinct. In the cannibal web, switching-driven cannibalistic cycles inflate the average abundance of Hyde and drive the intra-guild prey extinct.

Switching versus specialization

In this section, we investigate the relationship between a switching species and its specialist counterparts. When do they co-exist and when does one outcompete the other? To answer these questions, we expand the food webs to include both the switching species and its specialist counterparts.

Figure 4 shows the zero net growth isoclines (ZNGIs) of the specialist species and the switching species (the Appendix derives the ZNGIs) with constant switching in the

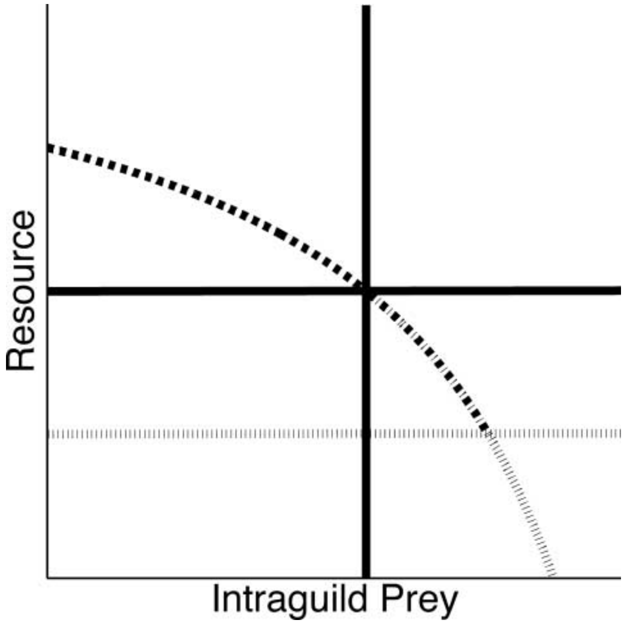

Fig. 4. Zero net growth isoclines of the two specialist species (solid lines) and a constant switching species (dashed line) in the non-cannibalistic food web. The solid vertical line is the ZNGI of the Hyde specialist. The solid horizontal line is the ZNGI of the Jekyll specialist. The dotted horizontal line is the ZNGI of the intra-guild prey when it suffers no mortality from predation. The switcher's ZNGI is broken into three regions. Equilibrium points on the dashed region ensure that Jekyll subsidizes Hyde. Equilibrium points on the dash-dot portions of the ZNGI ensure that Hyde subsidizes Jekyll. The dotted portion of the switcher's ZNGI represents a region where no equilibrium points can occur, since the intra-guild prey will be driven extinct.

non-cannibalistic food web. The ZNGIs represent all combinations of resource abundance and intra-guild prey required for a given species to subsist (Tilman, 1980). The relative simplicity of the non-cannibalistic food web allows us to derive this graphical description of the model. On the other hand, the multidimensionality of the switcher's growth function in the cannibalistic web requires a four-dimensional ZNGI. However, the general results illustrated by the ZNGIs of the non-cannibalistic web also apply to the cannibalistic web.

In simple communities including the resource, intra-guild prey, and the switching species, equilibrium points could occur at any point on the switcher's ZNGI (excluding the dotted portion of the switcher's ZNGI). Under these circumstances, one morph will subsidize the other. For instance, if the equilibrium point occurs on the dashed portion of the switcher's ZNGI, resource abundance is higher than the requirements of the Jekyll specialist, and intra-guild prey abundances are lower than the requirements of the Hyde specialist. Therefore, the Jekyll morph subsidizes Hyde. Alternatively, equilibrium points on the dash-dot portion of the switcher's ZNGI result in Hyde subsidizing Jekyll. Note that equilibrium points cannot occur on the dotted portion of the switcher's ZNGI because such points will drive the intra-guild prey extinct. As a consequence of these inherent subsidies, the specialist species corresponding to the subsidizing morph can always invade. In fact, there is an equilibrium point where the switcher and the two specialist species can all co-exist. This is a consequence of having no cost to switching.

To study competition and co-existence between the switching species and its specialist counterparts, we varied the efficiencies of both Jekyll and Hyde by varying their per capita mortality rates. We then determined stable community outcomes. The different food web structures and switching strategies interact to produce different regions of community outcomes (Fig. 5). Outcomes depend upon both the stability and direction of subsidies between the morphs. Limit cycles produced by the specialist species can be sustained when a switching species is present. Given limit cycles, the switcher may co-exist with the specialist corresponding to the subsidizing morph (regions C and D). Limit cycles can also create a situation where the switching species outcompetes both specialists (region B). However, this occurs only in very narrow regions of parameter space where the relative efficiencies of Jekyll and Hyde are nearly equal, such that subsidies from one morph to the other are effectively absent. Stable dynamics can result in the co-existence of the switching species with both specialist species (region E).

Figure 5 shows that when the Jekyll morph is relatively more efficient, it subsidizes Hyde, and the Jekyll specialist can co-exist with the switcher (region C). The co-existence of the Hyde specialist (region D), however, depends on the type of food web. In the non-cannibalistic food web, the Hyde specialist co-exists over a broader range of Jekyll efficiencies when Hyde efficiency is lower. This counterintuitive result occurs because in the non-cannibal web, increases in Hyde mortality indirectly decrease equilibrium abundances of Jekyll. For constant switchers, as long as Hyde abundances are on average greater than those of Jekyll, Hyde will be subsidizing Jekyll. In the cannibalistic food web, the Hyde specialist co-exists over a broad range of Jekyll efficiencies when Hyde efficiency is higher. In both the non-cannibalistic web with variable switching and the cannibal web with constant switching, there is a region where the dynamics are stabilized and all species co-exist (region E). In the cannibal webs, there is a region where the switching species is driven extinct (A). When Jekyll has low enough efficiency, the Jekyll specialist goes extinct and the Jekyll morph is strongly subsidized by the Hyde morph. Under these conditions, the Hyde specialist outcompetes the switcher and co-exists with the intra-guild prey.

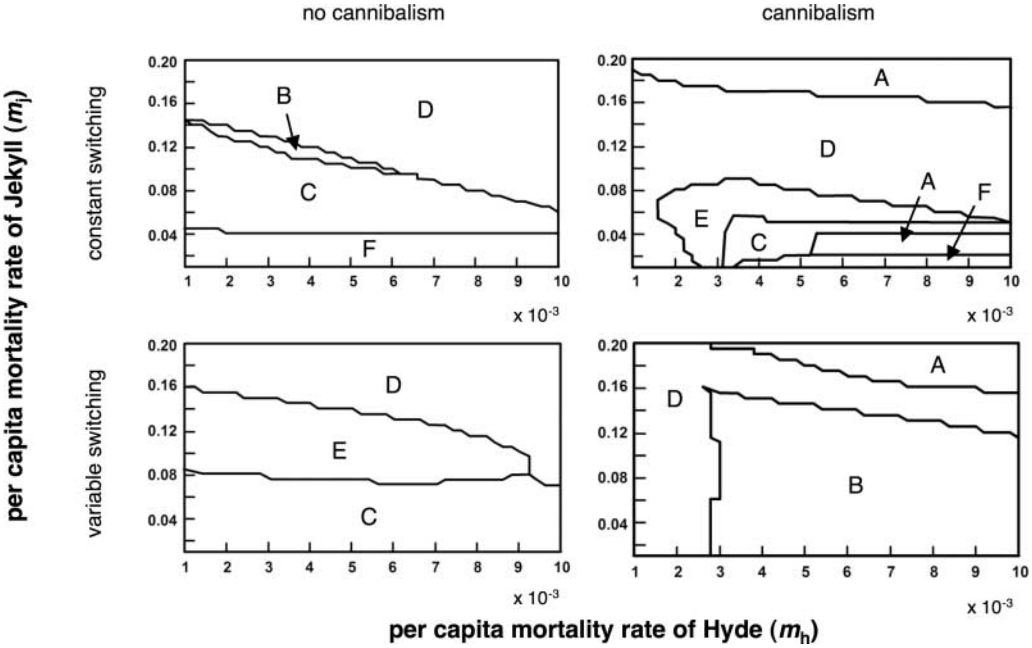

Fig. 5. Species co-existence as a function of the per capita mortality rates of Jekyll (m_j) and Hyde (m_h) in the two food webs with constant ($c = 0.001$) and variable ($z = 100$) switching strategies. Letters differentiate community outcomes. A = the switching species is driven extinct. B = the switching species is present and both specialists are driven extinct. C = the switching species and the Jekyll specialist co-exist. D = the switching species and the Hyde specialist co-exist. E = all species co-exist. F = no numerical solution found. For these simulations, $K = 250$.

The cannibal web with variable switching is distinct. For most of the parameter space, the switching species drives both specialists extinct (region B). In this region, the switching species displays switching-driven cannibalistic population cycles. Both Jekyll and Hyde have negative fitnesses over the long-term course of these cycles. As a result, when rare, neither specialist species can invade the system. The variable switching strategy permits the Jekyll and Hyde morphs of the switching species to exploit favourable times and avoid unfavourable times.

DISCUSSION

This investigation of the ecological behaviour of communities with polymorphic intra-guild predators complements a body of empirical work regarding trophic polymorphisms (e.g. Skulason and Smith, 1995; Banjeri and Morin, 2009). We report three key results: (1) switching stabilizes population dynamics; (2) switching can either enhance or restrict opportunities for co-existence with intra-guild prey species depending on which morph is subsidizing; and (3) subsidies between the two morphs of the switching species promote co-existence with a specialist species.

A species that can switch between trophic levels stabilizes population dynamics by increasing negative density dependence within each morph. However, our model assumes instantaneous switching. Time lags in the switching process might be destabilizing. In *T. vorax*, switching takes an average of 4.5 h (Buhse, 1966a), approximately half that of their generation time of 8 h (Williams, 1961). Moreover, predatory Hyde morphs are generally larger than their Jekyll counterparts, and switching may require cell division or lengthy developmental changes (e.g. Whiteman *et al.*, 2003; Banerji and Morin, 2009). These details of phenotypic switching will ultimately influence stability. Our model also shows how the feeding behaviour of the switching species influences stability. In the generalist food web with variable switching, cannibalism from the Hyde morph feeding on the Jekyll morph can induce cyclic population dynamics.

The question of stability is important because it has a direct bearing on selection pressures favouring switching species. If there are costs to switching, in a stable system a switching species will not be selected for. More efficient specialist species can depress resource levels lower than that required by a switching species. A fluctuating system can select for switching species. Figure 3 shows how increased switching depresses resource abundances, demonstrating that switching can be evolutionarily advantageous in fluctuating environments. It also shows how increased rates of switching stabilize the system. Thus, initially, mutant switchers may increase in abundance and even outcompete specialist phenotypes. However, the evolution of switching can stabilize the system and hence destroy the ecological conditions that selected for it. Therefore, switching may need to evolve in systems where fluctuations are either driven by abiotic elements or other species in the system. Alternatively, cannibalism could drive the evolution of switching species. Interestingly, Loeb *et al.* (1994) found that tiger salamanders (*Ambystoma tigrinum nebulosum*) were induced to their cannibalistic morph only in the presence of conspecifics. However, their study did not include population dynamics.

In our model, switching can either enhance or restrict opportunities for co-existence with the intra-guild prey. For the intra-guild prey to co-exist, it must be relatively more limited by predation than food. If Jekyll subsidizes Hyde, then switching Jekylls inflate Hyde abundances, thus increasing predation pressure on the intra-guild prey and even further restricting opportunities for co-existence. The intra-guild prey co-exists only under low productivity. On the other hand, if Hyde subsidizes Jekyll, Hyde abundances will be depressed and predation pressure relieved. This in turn will enhance opportunities for co-existence, which can occur over a broad range of productivities. In traditional models of intra-guild predation, the intra-guild prey co-exists if the intra-guild predator is an efficient predator and poor competitor (Holt and Polis, 1997). Alternatively, when predation acts more as a form of interference competition, intra-guild predation can lead to alternate stable states. Moreover, Holt and Polis (1997) found that the intra-guild prey tends to co-exist under intermediate productivity levels.

Subsidies between the Jekyll and Hyde morphs decrease the average fitness of individuals of the switching species. This creates selective pressure for smarter switching strategies that use environmental cues to inform switching decisions. Variable switching rules are ubiquitous among known species exhibiting trophic polymorphism [e.g. protists (Kusch and Heckmann, 1992), fish (Garduño-Paz and Adams, 2010), and salamanders (Loeb *et al.*, 1994)]. For instance, *T. vorax* can be induced to switch from Jekyll to Hyde based on concentrations of an iron chelate released by ciliate prey (Ryals *et al.*, 2002). Banerji and Morin (2009) have recently shown that switching in *T. vorax* is a coordinated adaptive response to environmental conditions. In our model, variable switching in the specialist food web is even more stabilizing than the constant switching strategy. The cannibalistic food web combined with switching caused population cycles. We also found that if switching is not perfect, then subsidies are reduced but still present.

Subsidies between the morphs create an ecological opportunity for the specialist species corresponding to the subsidizing morph. In general, a single specialist species can co-exist with the switching species. The exception occurs in the cannibalistic web with variable switching. In this case, over most of the parameter space, the switching species drove both of the specialists and the intra-guild prey extinct. This was due to cannibalism-driven population cycles. The switching species and both specialists co-existed only when the system exhibited stable population dynamics. However, given a cost to switching, the specialists should outcompete the switching species. Only under stable conditions are specialist species favoured over switching species. Fluctuating conditions, with imperfect switching, allow a single specialist to co-exist with the switching species. The realized niche of a switching species requires population fluctuations resulting from unstable dynamics or stochastic environments.

Skulason and Smith (1995) hypothesize that polymorphic species may be stepping-stones on the path to speciation. From this perspective, a switching Jekyll and Hyde could be a transient species on its way to splitting into separate Jekyll and Hyde specialists. However, as we point out, a polymorphic species can occupy its own evolutionarily stable niche. Switching morphs is advantageous only if the environment at times favours one morph and at other times favours the other morph. Therefore, a switching species may occupy a stable peak on an adaptive landscape in a fluctuating environment. In this situation, the polymorphic traits are not correlated with ecological isolation, a condition necessary for speciation as hypothesized by Skulason and Smith (1995). Our model, therefore, suggests that only certain resource polymorphisms may in fact be stepping-stones to speciation.

Tetrahymena vorax and other protist species provide opportunities to test the theory's predictions (Holyoak and Lawler, 2005). Peter Morin and his colleagues have studied *T. vorax* extensively (Price and Morin, 2004, 2009; Banjeri and Morin, 2009). Price and Morin (2004) found alternate stable states in systems with both *T. vorax* and another switching intra-guild predator *Blepharisma americanum.* When *B. americanum* was initially present, *T. vorax* failed to invade the community. However, when *T. vorax* was initially present, *B. americanum* was able to invade, and the two species generally co-existed. In a subsequent study, Price and Morin (2009) found that relative initial densities of the two species did not directly cause the alternate stable states. Rather, the effect appeared to be mediated through bacterial depletion. Our theory does not address competition between intra-guild predators, but could be modified to do so. However, our theory does highlight the importance of resource fluctuations to the success of a switching species. This could potentially play a role in determining the outcome of inter-specific interactions. In this case, how does each species influence stability and react to fluctuations in resources in terms of phenotypic switching? Moreover, under what conditions does either morph of a species act as a subsidy? And how do these configurations influence the outcomes of inter-specific interactions?

In conclusion, our theory uncovers some of the main theoretical attributes of the community ecology of switching species. Interestingly, we found that although species exhibiting trophic polymorphisms have a broad niche breadth, they do not necessarily decrease the diversity of a system. They may actually provide ecological opportunities for specialist species. As Peter Morin's work highlights, aspects of this theory may be testable through the use of protist species in laboratory settings.

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APPENDIX

Derivation of zero net growth isoclines for constant switchers in the food web without cannibalism

A zero net growth isocline (ZNGI) represents all combinations of resource abundances required for a consumer to subsist (Tilman, 1980). Solving for ZNGIs generally requires setting per capita growth rates equal to zero and solving in terms of a particular resource's abundance. Here we show how to derive a ZNGI in the special case of a polymorphic species with a constant switching strategy in our food web without cannibalism. We start by setting the per capita growth rate of Jekyll to 0:

$$\frac{\mathrm{d}J}{J\mathrm{d}t} = \frac{b_{rj}a_{rj}R}{1 + a_{rj}h_{rj}R} - m_j - c + cq = 0.$$

Let $q = H/J$ be the ratio of Hyde to Jekyll abundance. The equilibrium point of the system will be characterized by some value of q. Next, we solve for q in the above equation:

$$q^* = \frac{(m_j + c)(1 + a_{rj}h_{rj}R) - b_{rj}a_{rj}R}{c(1 + a_{rj}h_{rj}R)}.$$

Then we substitute q^* into the per capita growth rate of Hyde and set the equation to zero:

$$\frac{\mathrm{d}H}{H\mathrm{d}t} = \frac{b_{ph}a_{ph}P}{1 + a_{ph}h_{ph}P} - m_h - c + \frac{c}{q^*} = 0.$$

Finally, we solve the above equation for R to get the ZNGI in the state space of R vs. P:

$$R^* = \frac{(c+m_j)\left(c+m_h-\dfrac{b_{ph}a_{ph}P}{1+a_{ph}h_{ph}P}\right)-c^2}{c^2 a_{rj}h_{rj}+(a_{rj}b_{rj}-a_{rj}h_{rj}\,(c+m_j))\left(c+m_h-\dfrac{b_{ph}a_{ph}P}{1+a_{ph}h_{ph}P}\right)}.$$