

Cannibals in Space: The Coevolution of Cannibalism and Dispersal in Spatially Structured Populations

Volker H. W. Rudolf,^{1,*} Masashi Kamo,² and Mike Boots³

1. Department of Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005; 2. Advanced Industrial Science and Technology, Research Center for Chemical Risk Management, Onogawa 16-1, Tsukuba 305-8569, Japan; and 3. Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2DR, United Kingdom

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ABSTRACT: The propensity for cannibalism varies considerably both within and between species. Currently we have little understanding of both the causes of this variation and its evolutionary consequences for other life-history traits. We examine how different levels of spatial structure affect the evolution of cannibalism and how cannibalism in turn drives the evolution of dispersal. Using pair approximations and simulations, we show that cannibalism can easily evolve in spatially structured populations as long as some dispersal exists. Furthermore, for a wide range of intermediate levels of spatial structure, we find the possibility of evolutionary branching leading to polymorphism in cannibalism. We also show that cannibalism itself can have important evolutionary consequences and select for increased dispersal rates, thus helping to determine the spatial structure of populations. The coevolution of cannibalism and dispersal results in the evolution of various alternative life-history strategies with different dispersal and cannibalism regimes. Which strategy evolves depends on the environmental conditions that determine initial cannibalism rates. Our results therefore suggest that differences in spatial structure could explain variation in the propensity for cannibalism and cannibalistic polyphenism. Furthermore, results emphasize that cannibalism can drive the evolution of other life-history traits and determine the spatial structure of natural populations.

Keywords: stage structure, kin selection, intraspecific predation, polyphenism, evolutionary branching, spatial self-structuring.

Introduction

Cannibalism, the killing and at least partial consumption of conspecifics, is ubiquitous in natural communities. It has been recorded for more than 1,300 animal taxa ranging from protists and rotifers, through invertebrates, to vertebrates (Fox 1975a; Polis 1981; Elgar and Crespi 1992; Woodward et al. 2005). Cannibalism is known to impact community dynamics (Persson et al. 2003; Rudolf 2007a,

2007b), but the strengths of these effects depend critically on cannibalism rates, which are known to vary both within and between species. Some of this variation can be explained by ecological factors, including the availability of alternative resources (Fox 1975b; Leonardsson 1991; Loeb et al. 1994; Rudolf 2008b), the presence of predators (Rudolf 2008a), and population structure (Polis 1981; Hopper et al. 1996; Persson et al. 2003), but it is clear that the propensity for cannibalism has an important genetic component. Substantial genetic variation and inheritance for the propensity of cannibalism has been shown in flour beetles (Wade 1980; Stevens 1989), ladybird beetles (Wagner et al. 1999), salamanders (Cohen et al. 2005), mice, and a number of other species (reviewed in Polis 1981). Differences also occur across populations from different geographic locations (Baur 1994). Importantly, the propensity for cannibalism also varies considerably among closely related species (Gerber and Echternacht 2000; Yasuda et al. 2004; Rudolf 2008b). However, we still have very little understanding of what drives the variation in the evolution of cannibalism across and within species. Even less is known about the evolutionary consequences of this variation for the evolution of other life-history traits.

Cannibalism has several clear benefits for an individual. Conspecifics represent a high-quality resource (in the correct stoichiometric ratios) for cannibals (Mayntz and Toft 2006) and may thus be favored if species experience strong resource limitation (Polis 1981; Gabriel 1985). Theoretical work, however, indicates that although food limitation can facilitate cannibalism (Nishimura and Isoda 2004), it is not a requirement for cannibalism to evolve (Reed and Stenseth 1984) and it is only important if resource limitation solely affects the cannibalistic stage (Getto et al. 2005). That said, the net energy gain for the cannibal is a crucial component for the evolution of cannibalism (Stephan and Wissel 1989; Dercole and Rinaldi 2002; Getto et al. 2005). Cannibalism also has the additional advantage

* Corresponding author; e-mail: volker.rudolf@rice.edu.

of removing potential competitors, and selective filial cannibalism may also decrease density-dependent mortality in offspring (Klug and Bonsall 2007).

Given all these benefits, it is not surprising that cannibalism is so frequent. Yet, cannibalism rates vary considerably across and within species, and obviously not all species are cannibalistic. This may partially be explained by the direct and indirect costs of cannibalism. When attacking similarly sized conspecifics, cannibals may be injured or killed. However, this does not explain why species in which the risk of injury or mortality is small or negligible (e.g., adults cannibalizing smaller juveniles or eggs) do not exhibit cannibalism. Another cost that may select against cannibalism is the increased risk of infection when consuming conspecifics versus heterospecifics (Pfennig et al. 1991, 1998; Pfennig 2000). There is, however, little theoretical or empirical evidence that this actually drives the evolution of cannibalism in the long term, and theoretical studies suggest that this would require a very high force of infection (Bolker et al. 2008). Indeed, in most natural systems, cannibalism will typically reduce the prevalence of a disease or completely prevent its invasion into the host population, thereby strongly limiting the selective potential of disease (Rudolf and Antonovics 2007). The reason for this is that cannibals actively remove one or more infected individuals from the population but only result, on average, in less than one new infection.

It is therefore probable that the evolution of cannibalism could largely be limited by kin selection (Hamilton 1964). If cannibals are likely to consume their siblings or their offspring, cannibalistic behavior will result in a substantial loss in inclusive fitness. The main factor that determines the encounter between close relatives—and thus, the probability of consuming kin—is the spatial distribution of genotypes within populations. If cannibals are surrounded by their offspring, then indiscriminate cannibalism, which is observed in a variety of species (Polis 1981; Boots 2000; Schausberger 2003), would result in a high loss of inclusive fitness that could easily outweigh the benefits of cannibalism. On the other hand, if neighbors are mostly unrelated, then cannibals are unlikely to consume kin and the benefits of cannibalism might outweigh the costs. Spatial structure is an important driver that determines the interaction between ecological and evolutionary dynamics and thus the selection pressure on life-history traits. For example, depending on the cost of altruism, increased mobility can decrease the level of altruism (Le Galliard et al. 2009). Thus, the spatial structure of populations may also strongly influence the evolution of cannibalism.

Despite the potential importance of the spatial structure of populations, it has largely been ignored in previous studies on the evolution of cannibalism. Only recently did Lion and van Baalen (2007) suggest that cannibalism is

likely to evolve with global interactions (i.e., in completely randomly mixed populations) but not in populations where cannibals and their offspring are direct neighbors (i.e., interactions are only local), where parental care should evolve. While this strongly emphasizes the importance of spatial structure for the evolution of cannibalism, the study focused on two extreme situations and not on the continuum and diversity of different dispersal strategies and interaction types that we see in natural populations. It is unclear, however, how differences in the degree of spatial clumping or differences in dispersal strategy among stages alter the evolution of cannibalism.

There has also been relatively little work on the evolutionary consequences of cannibalism on other life-history traits. The only exception is body size, which typically serves as a surrogate for the ability to cannibalize (Dercole and Rinaldi 2002; Wakano et al. 2002). There is, however, no *a priori* reason to assume that cannibalism is the trait under selection and not the selection pressure itself that is driving the evolution of other life-history traits. Indeed, there are several alternative strategies that could reduce the risk of being cannibalized without changing the propensity for cannibalism. For example, in many species including chameleons, salamander, fish, insects, and crustaceans, small individuals alter their habitat use in response to cannibalistic conspecifics (Sih 1982; Leonardsson 1991; Persson and Eklov 1995; Bystrom et al. 2003; Keren-Rotem et al. 2006; Rudolf 2006, 2008b). If offspring disperse away from their cannibalistic parents, this would reduce the indirect cost of cannibalism (i.e., loss of inclusive fitness) without losing its benefits (i.e., energy gain and removal of competitors). Thus, instead of selecting against or for the propensity for cannibalism in adults, selection could favor different dispersal strategies in the noncannibalistic stage (e.g., offspring) that provide alternative but similar or even more efficient strategies. If the risk of cannibalism alters the propensity for dispersal, this could have important consequences for the structure of populations. However, the conditions that favor such alternative strategies over cannibalism and how they coevolve with cannibalism are largely unknown.

Here we present a theoretical study that examines how variation in spatial structure affects the evolution of cannibalism and how cannibalism in turn drives the evolution of dispersal and thereby determines the spatial pattern of populations. In particular, we first ask how different degrees of dispersal alter the evolution of cannibalism. Then we examine how different cannibalism rates can drive the evolution of dispersal. Finally, we examine which life-history strategy is favored when both cannibalism and dispersal are allowed to coevolve. Using these pair approximations and simulations, we find that spatial structure determines the evolution of cannibalism rates and that it

can result in cannibalistic polymorphisms. We also find that cannibalism itself can drive the evolution of dispersal rates, thus helping to shape the spatial structure of populations.

Modeling

To examine the evolutionary consequences of the interaction of cannibalism and spatial structure, we build on previous theory that considers a stage-structured population in an explicit spatial context. To account for the naturally size-structured and asymmetric interactions between cannibals and conspecific victims that are observed in empirical systems, we assume a stage-structured population that consists of cannibalistic adults (A) and non-cannibalistic juveniles (J). We build a spatially explicit model where the adults and juveniles can interact locally and globally. Our approach is to capture the spatial interactions by keeping track of how pairs of individuals and empty space change through time, and we apply modern evolutionary game theory to calculate the long-term evolutionary outcomes.

Juveniles mature into adults at the rate μ . Adults reproduce into an empty site at rate b_A , thereby resulting in density-dependent reproduction. Adults and juveniles die at a constant background death rate of d_A and d_J , respectively. In addition, the mortality rates of juveniles and adults are functions of cannibalism rates that depend on the spatial structure of the population. Population structure is modeled on a regular lattice, where each location is empty or occupied by either an adult or a juvenile and interacts with the same number of other locations.

Following Lion and van Baalen (2007), let us denote the densities of adults (A) and juveniles (J) by p_A and p_J , respectively. The density of empty sites (O) is then described by $p_O = 1 - p_A - p_J$. We assume that cannibalism always occurs locally but that reproduction occurs both locally and globally, with a probability R that ranges from 0 to unity (e.g., if $R = 1.0$, adults give birth in a randomly chosen empty site, and if $R = 0$, reproduction occurs locally). This assumption represents most natural systems where the offspring have the ability to disperse away from their cannibalistic parents but where cannibalistic interactions occur among individuals that are most likely to encounter each other (i.e., close neighbors). The average death rate of juveniles (δ_J) increases with the level of cannibalism and is thus

$$\delta_J = d_J + cq_{A/J}, \quad (1)$$

where d_J is a background death rate of juveniles and c represents the level of cannibalism. Note that larger c values represent higher levels of cannibalism. $q_{A/J}$ is the prob-

ability that a randomly chosen juvenile (J) has an adult (A) at the nearest site. We assume that the reproduction rate of adults (b_A) increases with cannibalism in the form

$$b_A = b_0 + \gamma c(1 - \theta)q_{J/AO}, \quad (2)$$

where b_0 is the background birth rate, θ is $1/z$, z is the number of nearest neighbors (it has a value of 4 throughout this article), and λ is a scaling constant (with a value of 0.4 throughout this article, i.e., the intensity of cannibalism to birth rate is 60% smaller than the intensity of cannibalism to juvenile death rate). $q_{J/AO}$ is the probability that a randomly chosen AO pair has a J at the nearest sites, where AO simply represents the condition that successful reproduction can only occur at an empty site. Note that cannibalism increases the host reproductive rate, and thus it accounts for the energy gain resulting from cannibalism.

The dynamics of the global densities of juveniles and adults are given by

$$\begin{aligned} \dot{p}_J &= R[b_0 + \gamma c(1 - \theta)q_{J/A}]p_A p_O \\ &\quad + (1 - R)b_A p_{OA} - (\mu + \delta_J)p_J, \\ \dot{p}_A &= \mu p_J - d_A p_A, \end{aligned} \quad (3)$$

where \dot{p}_J and \dot{p}_A are the time derivatives of p_J and p_A , respectively; δ_J and b_A are given by equations (1) and (2); and R ($0 \leq R \leq 1$) is the probability of global reproduction. If $R = 1.0$, adults give birth at a randomly chosen empty site, and if $R = 0$, reproduction occurs locally. Here p_{AO} denotes the density of AO pairs. A full description of the pair dynamic is given in the appendix in the online edition of the *American Naturalist*. Note that the proportion of local and global reproduction (i.e., juvenile dispersal) can be manipulated independently from the spatial (i.e., local) scale at which cannibalism occurs by altering R . Thus, we are able to represent different and more realistic life-history strategies and examine the evolution of cannibalism and reproduction separately without confounding both of them.

To examine the effect of the spatial population structure, we vary the proportion of global and local reproduction (i.e., R). This approach has been used successfully to capture key features of the complex variation in spatial structure in natural populations (Boots and Sasaki 1999, 2002; Kamo et al. 2007). We use a combination of pair approximations of the full spatial system and spatially explicit simulations to analyze the evolutionary dynamics of the system. The approximations allow us to quickly explore the outcomes of the approximate model, the results of which are then compared with the full spatially explicit

simulations. The qualitative predictions of the approximations match those of the spatial models very well.

First, we examine how the rate of cannibalism (c) evolves depending on the probability of global reproduction and therefore on the propensity of juveniles to disperse. Lion and van Baalen (2007) have shown that the lowest level of cannibalism evolves when the system is completely local. We are interested in how c evolves when cannibalism occurs locally but when the reproduction is partially global. Second, the evolution of the probability of global reproduction and therefore the propensity to disperse (R) is examined for any particular and fixed level of cannibalism c . Finally, the coevolution of both cannibalism c and a propensity to disperse R are examined. For clarity, the values of the other parameters are the same as they are in the article by Lion and van Baalen (2007), and they are summarized in table 1. We also conduct invasion analyses using global (eq. [1]) and pair densities of sites with the techniques of adaptive dynamics. Details of these analyses are given in the appendix.

Results

Evolution of Cannibalism

We begin by examining the situation in which we allow the propensity for cannibalism to evolve in populations that differ in their spatial structure and mixing. In all cases, cannibalism events are assumed to occur between neighbors but reproduction can happen either locally or at a distance (i.e., juveniles stay close by or migrate away from adult sites). Our aim is to determine how different degrees of spatial mixing—in this case, long-distance reproduction—influence the evolutionarily stable (ES) cannibalism rates. Pair approximations are used to produce pairwise invasion plots (PIPs) of the system, while numerical simulation of a fully spatial lattice is used to produce the evolutionary dynamics over time and a final ES strategy (ESS). The corresponding equations for the invasion plots are given in the appendix.

Figure 1 shows PIPs from the approximate analysis and

figure 2 shows the evolutionary trajectories from the full spatial models. In a result consistent with those of previous studies (Lion and van Baalen 2007), we find that cannibalism will not evolve in the extreme case where reproduction is completely local, resulting in highly clustered populations (figs. 1A, 2A). We show, however, that even if cannibalistic interactions are completely local, cannibalism rates will still be maximized if reproduction is completely global, resulting in randomly mixed populations (figs. 1C, 2C). Furthermore, by modeling spatial structures between the two extremes, we find the possibility of evolutionary branching leading to the evolution of a dimorphism between highly cannibalistic individuals and individuals that never cannibalize (figs. 1B, 2B). Spatial structure therefore provides a mechanism that could lead to cannibalistic polyphenism. In summary, we would therefore expect the evolution of very high cannibalism, no cannibalism, or a dimorphism depending on the spatial structure of populations. Species with generally local dispersal are less likely to be cannibalistic, while highly dispersing species are more likely to be monomorphic with highly cannibalistic individuals. Furthermore, we predict the evolution of a dimorphism between cannibals and noncannibals in populations over a range of intermediate spatial mixing patterns from the local to the global. How wide the range of spatial mixing is for dimorphism depends on demographic parameters, but at the extreme of dispersal it becomes less likely. Overall, it is clear that the degree of dispersal has a threshold effect on whether full, partial, or no cannibalism evolves within a population.

Evolution of Dispersal

Next we address the question of what rate of dispersal will evolve in the face of different rates of cannibalism. It is easy to show that if there is no cost to dispersal, then dispersal is always beneficial, since it reduces the effect of local density dependence and kin competition. Consequently, the system always evolves to completely global, maximum dispersal irrespective of the presence or absence of cannibalism (Hamilton and May 1977). We follow pre-

Table 1: Descriptions and values of parameters

Parameter	Description	Value
d_j	Background death rate of juveniles	1.5
d_A	Background death rate of adults	1.0
μ	Maturation rate of juveniles	2.0
b_0	Background reproduction rate of adults	4.0
γ	Scaling constant for adult reproduction	.4
z	Number of the nearest neighbors	4
θ	$1/z$.25
c	Level of cannibalism	Subject to evolution; $0 \leq c \leq 2$
R	Probability of global reproduction	Subject to evolution; $0 \leq R \leq 1$

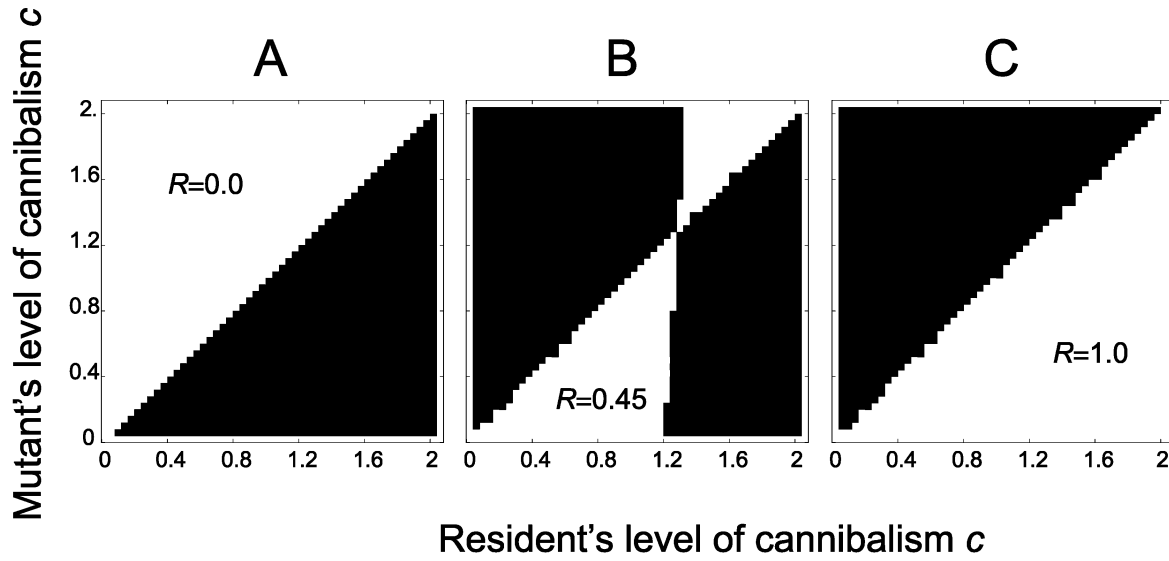


Figure 1: Pairwise invasion plots from the approximate pairwise analysis of the evolution of cannibalism levels at different levels of dispersal (proportions of global reproduction, R): dispersal is completely local ($R = 0$) in A, intermediate ($R = 0.45$) in B, and completely global ($R = 1$) in C. In the shaded areas, the mutant is able to invade the resident population, while in the blank areas, the mutant has a negative growth rate and therefore cannot invade. In A, with local dispersal, cannibalism is minimized, as lower resident types can always invade, while in C (with global dispersal) it is maximized, as mutants with higher levels of cannibalism can always invade. Evolutionary branching is predicted in B since there is convergence stability (mutants nearer to the evolutionary singularity can invade), but the singular strategy, when reached, can be invaded. Details of the analysis are given in the appendix in the online edition of the *American Naturalist*.

vious models (Johnson and Gaines 1990) in assuming that there is a cost to dispersal such that more global reproduction leads to a higher death rate, and we examine the role that cannibalism may play in determining the propensity of organisms to disperse. We therefore invoke a trade-off with dispersal, where the death rate of juveniles (δ_j) is described by

$$\delta_j = d_j + cq_{A/j} + k\sqrt{R}, \quad (4)$$

where k is a constant.

Given this cost, we find that once cannibalism occurs, there is always a locally ES level of dispersal that increases with higher rates of cannibalism (fig. 3; fig. A1 in the online edition of the *American Naturalist*). This indicates that cannibalism does generally select for more dispersal. However, there is always a bistability for this trade-off relationship such that zero dispersal is also always an ESS (fig. 3; fig. A1). The likelihood of evolving no dispersal, however, falls as the degree of cannibalism increases in stochastic simulations, because the attractor basin for $R = 0$ decreases as the level of cannibalism (c) increases (fig. 3). Increasing or decreasing k results in lower or higher dispersal rates, respectively, but it does not alter the overall

pattern. The general insight that cannibalism favors dispersal therefore always holds.

Coevolution of Cannibalism and Dispersal Rates

Finally, we allow both dispersal and cannibalism to co-evolve together. If global reproduction is not costly (i.e., $k = 0$), we first observe evolution to completely global reproduction ($R = 1.0$), which is followed by the evolution of maximum cannibalism (c evolving to its maximum value, 2.0). Figure 4 shows examples of evolutionary trajectories when global reproduction is costly (i.e., $k > 0$), assuming a trade-off (eq. [4]) between juvenile death and the probability of global reproduction. If we begin at relatively high rates of cannibalism, then intermediate dispersal and maximum cannibalism evolve. In contrast, if we start from a situation when cannibalism rates are low, the system evolves to zero cannibalism but, once again, intermediate levels of dispersal. Note that the system would evolve to no dispersal ($R = 0$) if cannibalism was fixed at 0 and not allowed to evolve, with the cost of dispersal (eq. [4]) being sufficient to restrain the evolution of dispersal. Therefore, even in the apparent absence of cannibalism, the potential for evolving cannibalism still alters the spatial structure of the population.

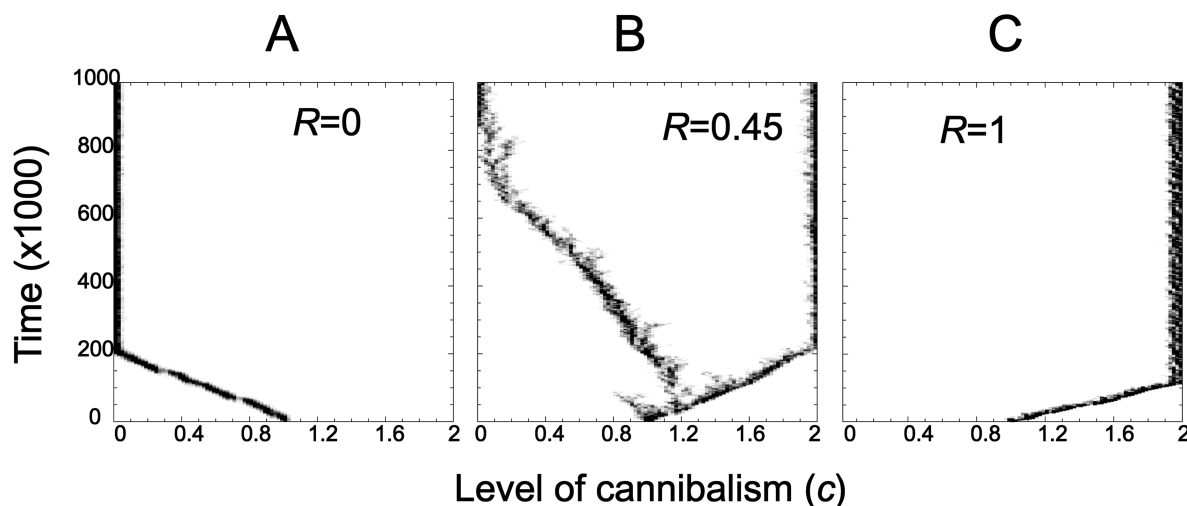


Figure 2: Results of simulations of the evolution of cannibalism in the full spatial model at the parameters used in the approximate analysis in the pairwise invasion plots (PIPs) in figure 1. The simulations confirm the predictions of the PIPs: no cannibalism evolves without dispersal ($R = 0$), maximum cannibalism evolves with global dispersal ($R = 1$), and branching leading to a dimorphism at maximum and minimum cannibalism occurs at intermediate dispersal ($R = 0.45$). Darker areas (black indicates greater than 50,000 individuals) on the simulation represent a higher number of adults. The size of the lattice is 600×600 .

When examining the evolutionary trajectory over time, we find that when simulations start with intermediate levels of cannibalism, intermediate levels of global reproduction evolve and the rates of cannibalism split for a while until cannibalism eventually goes to 0. The numbers of individuals in each morph change through time such that the mean rate of cannibalism in the population moves up and down. Finally, evolution stops at the smallest value of c and intermediate R . We can therefore find dimorphism in cannibalism rates when there is coevolution between cannibalism and reproduction, but only in the transient evolutionary dynamics. More examples of evolutionary trajectories are available at the Web site listed in the legend of figure 4. Given some dispersal ($R > 0$), evolution first moves the population to the ESS level (i.e., intermediate rates) of global reproduction, and then the cannibalism rates move to either maximum or minimum values. An analysis of the adult densities (no. adults/size of lattice) at the end of simulations in figure 4 showed that the densities are higher at $c = 0$ than at $c = 2$. This suggests that the costs of both cannibalism and dispersal offset the cost of localizing.

Discussion

The spatial self-structuring of populations can have important consequences to both inter- and intraspecific interactions and the evolution of life-history traits (Boots and Sasaki 1999, 2002; Murrell et al. 2002; Murrell and

Law 2003; Boots and Meador 2007; Kamo et al. 2007). Here we emphasize that spatial structure can alter the evolution of intraspecific interactions but also that intraspecific interactions can alter life-history traits that determine the spatial structure itself. First we show that the spatial structure of populations can determine the presence and absence of cannibalistic behavior. Importantly, we also found evolutionary branching at intermediate levels of spatial structures leading to cannibalistic dimorphism. Second, we provide insights into the evolutionary consequences of cannibalism by demonstrating that cannibalism rates can determine dispersal rates and thus the spatial self-structuring of populations. Finally, we demonstrate that the coevolutionary dynamics of cannibalism and dispersal can result in alternative life-history strategies that have different dispersal and cannibalism regimes. Below we will address each of these points separately.

Spatial Structure and the Evolution of Cannibalism

We found that higher dispersal rates increased the probability of cannibalism. This makes intuitive sense, since as populations become more local there is an increased risk of cannibalizing kin. Cannibals in local populations therefore pay a higher inclusive fitness cost that outweighs the benefits of cannibalism (e.g., reduced competition and increased reproduction). Thus, our results are consistent with previous theoretical (e.g., Hamilton 1964; Bobisud and Potratz 1984; Stephan and Wissel 1989; Lion and van

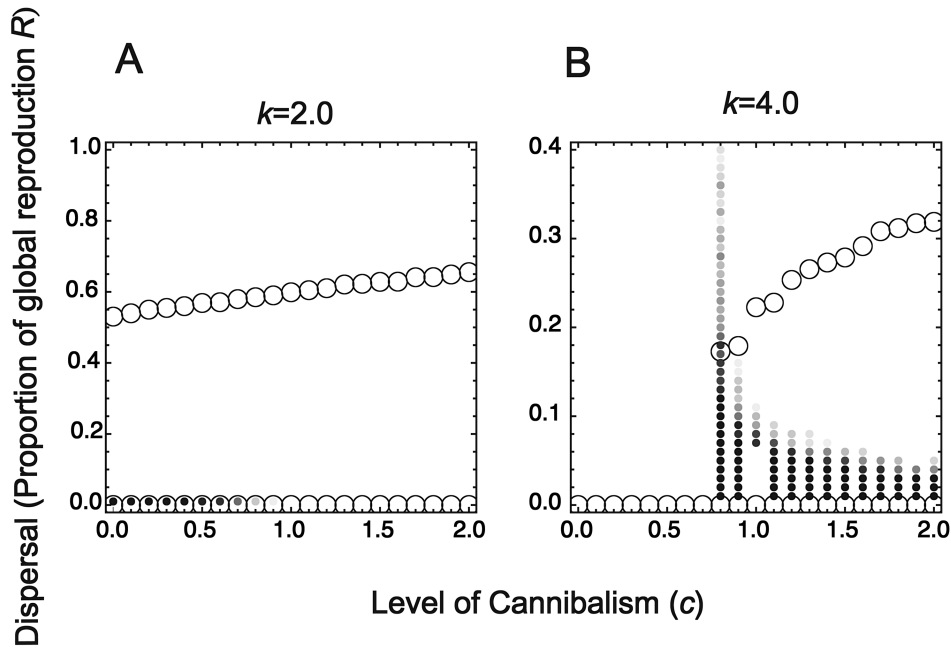


Figure 3: Evolutionarily stable (ES) propensity to disperse (R), showing regions of bistability that are dependent on the cost of dispersal: $k = 2.0$ (A) and $k = 4.0$ (B). Open circles show the ES dispersal rate (R) as a mean of 20 replicates. In regions where there is a bistability (all of A and cannibal level $c > 0.7$ in B), we examine the dependency of starting conditions on the final outcome. Twenty simulations were started over the range of dispersals from 0 to 1. If $R = 0$ evolves 20 times out of 20 runs, then the dots are black. A gray scale represents lower proportions of the simulations that lead to $R = 0$, with no dot (completely white area) when a nonzero ES dispersal always evolved. Notice that in some cases when $k = 4.0$ and $c = 0.8$, $R = 0$ evolves even if the initial starting points of the simulations are larger than the ES R value. This is because the bistability region at $c = 0.8$ is very small and mutants that enter an the attractor for $R = 0$ take over the population by chance (the size of the lattice is 200×200).

Baalen 2007) and empirical (Wade 1980) work that indicate that kin selection can determine the evolution of cannibalism. It is important to emphasize that our models include explicit ecology, with births into empty space and deaths creating the empty space. This dynamic demography creates ecological structure and also influences the genetic structure and therefore the relatedness of the interacting individuals, and it is crucial to our results (van Baalen and Rand 1998; Lion and van Baalen 2007). We provide an important extension of previous studies by showing that cannibalism can evolve over a large range of spatial structures (i.e., dispersal rates) as long as neither cannibalism nor reproduction is completely local. This shows that cannibalism is not restricted to systems with completely mixed populations (i.e., random interactions between individuals) but that it can easily persist as long as there is some level of dispersal in adults or juveniles. While there is very little information on the correlation between spatial structure and cannibalism rates in natural systems, our results are consistent with the few data that exist. Ascidian species that exhibit highly gregarious settlements reject conspecific eggs and larvae, while nongre-

garious species readily consume both. The noncannibalistic species also show morphological modifications that reduce the risk of accidental cannibalism, suggesting that the spatial clumping of individuals may indeed have selected against cannibalism (Young 1988). While this lends some support for our results, more empirical studies are needed to examine the relation between population structure, dispersal rates, and cannibalistic behavior. In addition, the level of cannibalism that occurs will depend on the demographics of the species. High reproductive rates lead to less empty space and will tend to lead to higher cannibalism rates. It is possible that with very low reproduction rates and therefore very sparse populations, no cannibalism evolves, no matter the level of dispersal.

Most natural populations fall somewhere between the extremes of completely local interactions and random mixing. Here we show that there is a wide range of dispersal rates over which there is an evolutionary branching point leading to dimorphic populations with highly cannibalistic individuals and noncannibals. As such, we are proposing spatial structure as a mechanism for the maintenance of variation in cannibalism in a wide range of systems. The

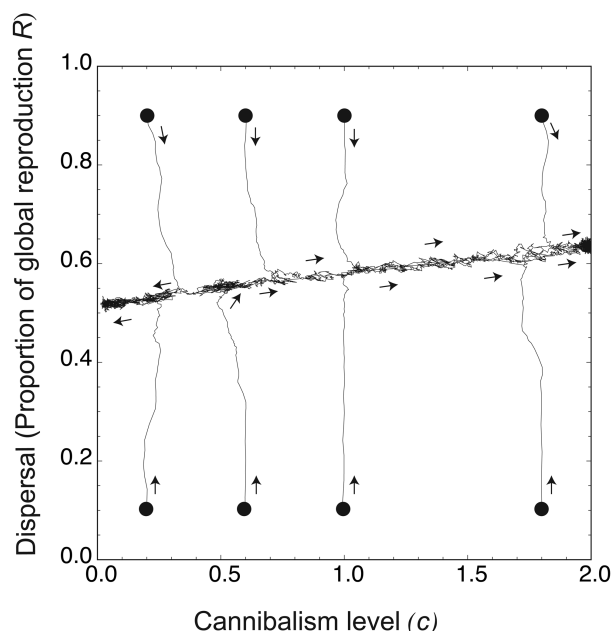


Figure 4: Coevolutionary trajectories of both the propensity to disperse (R) and the level of cannibalism (c) starting from different initial conditions. Both R and c are allowed to evolve at the same rate. When the simulation starts with low rates of cannibalism (small c ; left two circles), zero cannibalism always evolves ($c \rightarrow 0$). When the simulation starts at higher rates of cannibalism, maximum cannibalism always evolves. Evolution moves at first to the evolutionarily stable dispersal rate (ES R) and then gradually moves to either $c = 0$ or $c = 1$. The size of the lattice is 600×600 . A GIF animation of the coevolutionary trajectories can be seen at <http://bio-math10.biology.kyushu-u.ac.jp/~kamo/Appendices.html>.

existence of this dimorphism implies that there are negative frequency-dependent processes such that both cannibals and noncannibals have an advantage when they are rare. It is intuitive that when populations are completely mixed (i.e., interactions are global), rare highly cannibalistic individuals mostly eat noncannibals, and therefore cannibalism increases. As cannibals become more common, they are more likely to eat other cannibals as the local density of cannibals next to cannibals rises: the local spatial structuring leads to genetic structuring within the population. This is also the case in local populations, although less markedly so, and therefore cannibals always have an advantage when they are rare across the range of spatial mixing that can occur. For noncannibals, the situation is more complex: since they are clearly at a disadvantage when interacting with cannibals, this means that at first sight noncannibals would always be at a disadvantage when rare. We find dimorphism only at intermediate levels of dispersal, suggesting that this negative frequency dependence for noncannibals does not occur in very local

and global populations. In global populations, all individuals can be reached by a cannibal. In very local populations, most interactions occur within patches, and therefore, noncannibals will interact with each other. As noncannibals become more common, there is therefore little difference in the risk that a cannibal is next to them in the local and global populations compared with when they were rare. In intermediate-structured populations, cannibals may reach some but not all of the patches of individuals. As noncannibals become more common, more of the patches are noncannibals. Therefore, relatively rare cannibals arriving at a patch are very likely to find it lacking in cannibals. In contrast, when noncannibals are rare, only a few of the patches will consist of noncannibals, and therefore, at intermediate dispersals, there is a good chance that a cannibal will not reach the patch itself. As such, there is a negative frequency dependence that does not occur at either local or global dispersal. This emphasizes that, in spatial populations, selection can act within and between patches.

Cannibalistic dimorphism has been observed in a variety of species ranging from protists to flagellates and across amphibians and fish (Polis 1981). For example, in natural populations of *Asplanchna* rotifers (Gilbert 1975), spadefoot toad tadpoles (Pfennig 1992), and salamander larvae (Collins and Cheek 1983; Nishihara 1996; Chivers et al. 1997), “typical” noncannibalistic phenotypes commonly coexist with cannibalistic phenotypes that differ in their morphology (e.g., size, mouth parts, head shape) and that prey heavily on their conspecifics. While the proximate mechanisms that induce such polymorphisms have been examined (e.g., Loeb et al. 1994; Hoffman and Pfennig 1999), it is still unclear what ultimately leads to the evolution of the polymorphisms. Our results suggest that the spatial structures within populations could at least partly be responsible for the evolution of cannibalistic dimorphism. Although dispersal rates have not been measured in these examples, the polymorphic species show neither completely local nor completely global interactions. While this is consistent with our results, experimental studies are needed to explicitly test the impact of spatial structure on the presence of cannibalistic polymorphism and cannibalism in general in natural populations.

The Evolutionary Consequences of Cannibalism for Dispersal and Population Structure

It is typically assumed that cannibalism is a trait under selection (e.g., Bobisud 1976; Stenseth 1985; Nishimura and Hoshino 1999; Dercole and Rinaldi 2002; Lion and van Baalen 2007). However, cannibalism itself is equally likely to be the selective force that drives the evolution of other life-history traits. Yet, the evolutionary consequences

of cannibalism for other life-history traits are virtually unknown. Our study clearly shows that cannibalism can drive the evolution of dispersal and thus strongly alter the spatial structure of populations. We found that increased cannibalism rates generally lead to populations in which there is an overall higher dispersal rate. This is consistent with dispersal behavior observed in natural populations. For example, in flour beetles, populations of cannibalistic strains showed significantly higher dispersal rates than did less cannibalistic strains (Mayes and Englert 1984). Studies of natural populations of the beetle *Zophobas atratus* also suggest that increased dispersal rates in the larval stage evolved as a response to cannibalism by adults (Tschinkel 1981). In addition, in many species, small individuals disperse away from large cannibalistic conspecifics (Persson and Greenberg 1990; Biro et al. 2003; Keren-Rotem et al. 2006; Rudolf 2006, 2008b). Although it is difficult to separate the direction of causality in these studies, this finding suggests that cannibalism can increase dispersal rates of vulnerable individuals and alter the spatial structure of natural populations as predicted by our model.

As well as in the evolution of cannibalism, we also found a clear bistability in the evolution of the optimal dispersal range in the face of cannibalism. Bistabilities often emerge in spatial models when a particular strategy leads to spatial structures within the population that in turn favor individuals that adopt the strategy (Boots et al. 2004). Thus, certain spatial structures promote positive frequency dependence. Here we find bistability between no dispersal and intermediate levels of dispersal when there is cannibalism. With low dispersal, siblings clump; in this situation, dispersing offspring may tend to increase their risk of being cannibalized. In contrast, when the population is less clumpy, remaining local is likely to increase the risk of being eaten by one's kin without reducing the chance of being eaten by other individuals. This process leads to a form of positive frequency dependence, keeping dispersal local when the population is in similarly aged clumps but not when the population is less clumpy. These feedbacks generate bistabilities that may result in sudden shifts in either dispersal or cannibalism.

Coevolutionary Dynamics of Cannibalism and Dispersal

The spatial structure impacts the evolution of cannibalism because it determines the probability of encounters with kin. However, if the spatial structure is fixed, then this predetermines the probability of encountering kin and the costs of cannibalism (i.e., consuming kin) can therefore be changed only by reducing cannibalism rates. While this approach has typically been used to examine the evolution of cannibalism, it does not account for alternative mechanisms to ameliorate the cost of cannibalism. By allowing

both dispersal and cannibalism to evolve, we show selection either against cannibalism or, alternatively, for dispersal away from conspecifics while maximum cannibalism rates are maintained.

Interestingly, the life-history strategy that evolved was dependent on the initial cannibalism rates; initially, high cannibalism rates lead to maximum cannibalism while lower initial cannibalism rates lead to zero cannibalism. The presence and strength of cannibalism varies substantially between closely related species (Gerber and Echternacht 2000; Yasuda et al. 2004; Rudolf 2008b) and even within species (Michimae and Wakahara 2002). Our results suggest that this variation could be driven by differences in the environmental conditions that determine initial cannibalism rates, such as the availability of alternative prey (e.g., Leonardsson 1991; Rudolf 2008b), the presence of predators (Rudolf 2008a), stage/size structure, or the density of conspecific prey (reviewed in Polis 1981). This prediction is consistent with observations on the presence and absence of cannibalistic morphs observed in nature. For example, in the tiger salamander *Ambystoma tigrinum*, typical morphs develop into cannibalistic morphs when densities of conspecifics are high (Hoffman and Pfennig 1999) or when the typical morphs are sufficiently larger than their conspecifics (Maret and Collins 1994). Both factors are directly associated with initially high cannibalism rates that should favor the evolution of cannibalism. These examples represent species that experience large environmental variation that favors phenotypic plasticity in cannibalistic behavior rather than developing a single phenotype for cannibalism. However, studies on the salamander *Hynobius retardatus* suggest that this phenotypic plasticity for cannibalism is lost if population densities are constantly low (Michimae and Wakahara 2002). Similarly, we expect that species or populations that show little variation in the initial conditions for cannibalism rates will evolve either a cannibalistic or a noncannibalistic behavior.

Perspectives

There are several different ways of modeling spatial relationships within and between populations. Here we assumed that individuals were in discrete spatial locations and that interactions were either completely local or at random. More complex dispersal kernels in continuous or discrete space, irregular interactions that represent social rather than spatial interactions, and explicit movement patterns can also be modeled and would provide important insights in the future. Overall, however, the general predictions of the model are unlikely to be dependent on the simplistic way in which we model space, since the processes that we highlight are general implications of spatial structuring. The key is that we explore populations with neither

completely local nor random interactions; it is at these intermediate and more realistic levels of mixing that we see important phenomena.

In this study, we did not assume that adult behavior is a continuum of cannibalism and parental care (Lion and van Baalen 2007). Several species show both parental care and cannibalism at the same time (Klug and Bonsall 2007), indicating that both behaviors can be independent and under different selection regimes. Integrating both of these independent behaviors into a common evolutionary framework is beyond the scope of our model, but it would be an interesting challenge for future evolutionary models. While we show that dispersal is one alternative strategy to cope with the cost of cannibalism, kin recognition could be yet another potential alternative to dispersal. The evolution of kin recognition is the next important extension of our model, and future work that examines the evolution of multiple alternative strategies including kin recognition will provide important new insight into the evolution of cannibalism and will help to further explain the natural variation in cannibalism in nature.

In conclusion, our results show that cannibalism can have important evolutionary consequences, resulting in the evolution of alternative life-history strategies and altering the structure of populations. Furthermore, the spatial structure of populations is crucial to the evolution of cannibalism. There has been more interest in how spatial structure affects the evolution of interspecific interactions such as host-parasite interactions, but here we emphasize that it is also crucial to intraspecific interactions. It may be difficult to get a full picture of the evolution of any trait without considering the implication of spatial structure and, in particular, examining populations that are intermediate between the random and the completely local. Our work also further emphasizes the importance of cannibalism in nature. Here we have shown that it is likely to be an important driver of the spatial structure of populations, and this has important implications for the evolution of species and the structuring of communities.

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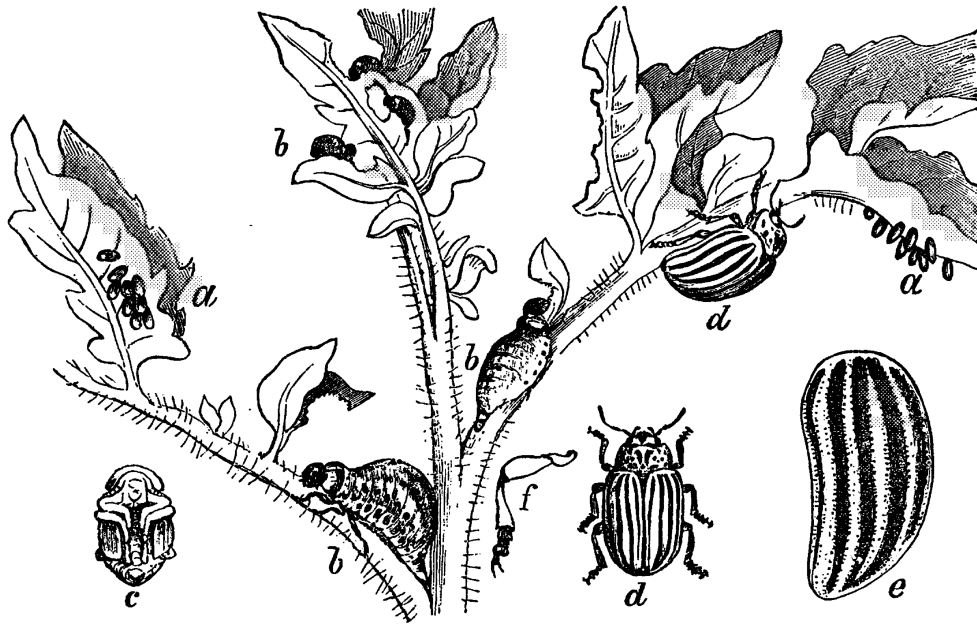
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"Of the several distinct species of potato bugs, the Colorado Beetle (*Doryphora 10-lineata* Say, ... *a*, eggs; *b*, young and fully grown larvae; *c*, pupa; *d*, beetle; *e*, left wing cover, magnified; *f*, leg, magnified) has chiefly attracted attention at the West during the few years past. It has been very destructive, hence anything bearing upon its habits is interesting to farmers. Last year they were more numerous in Illinois than at any other time. Whole acres were entirely destroyed by them. ... Entomological writers usually represent cannibal insects as the most efficient means in nature for extermination of injurious insects." From "Insects Injurious to the Potato" by Henry Shimer (*American Naturalist* 1869, 3:91–99).