Social Personality Polymorphism and the Spread of Invasive Species: A Model

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ABSTRACT: Ecological invasions are a major worldwide problem exacting tremendous economic and ecological costs. Efforts to explain variability in invasion speed and impact by searching for combinations of ecological conditions and species traits associated with invasions have met with mixed success. We use a simulation model that integrates insights from life-history theory, animal personalities, network theory, and spatial ecology to derive a new mechanism for explaining variation in animal invasion success. We show that spread occurs most rapidly when (1) a species includes a mix of life-history or personality types that differ in density-dependent performance and dispersal tendencies, (2) the differences between types are of intermediate magnitude, and (3) patch connections are intermediate in number and widely spread. Within-species polymorphism in phenotype (e.g., life-history strategies or personality), a feature not included in previous models, is important for overcoming the fact that different traits are associated with success in different stages of the invasion process. Polymorphism in sociability (a personality type) increases the speed of the invasion front, since asocial individuals colonize empty patches and facilitate the local growth of social types that, in turn, induce faster dispersal by asocials at the invasion edge. The results hold implications for the prediction of invasion impacts and the classification of traits associated with invasiveness.

Keywords: behavioral syndromes, invasion, dispersal, sociability, network.

Introduction

A major aspect of global environmental change involves the invasion of nonnative species throughout most of the world (Vitousek et al. 1997). In particular, invasive species sometimes explode to extraordinarily high densities and wreak havoc on natural and human-influenced communities (Pimentel et al. 2005). An oft-cited "tens rule" notes, however, that of the many plant species that reach a new area, only 10% become established, and of those, only 10% become invasive (Williamson and Fitter 1996). While introduced vertebrates seem to generally exhibit higher in-

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vasion success than plants (Jeschke and Strayer 2005), variability in outcome is still the rule. A major challenge for preventing or managing invasions is thus to explain the highly variable nature of this ecologically and economically costly, epidemic-like phenomenon.

One major approach has been to identify species traits associated with invasive species (Lodge 1993; Kolar and Lodge 2001; Rehage and Sih 2004; Rehage et al. 2004; Moyle and Marchetti 2006; Sih et al. 2010; van Kleunen et al. 2010). Often the species traits that correlate with invasion success are those that promote success at many stages of the invasion process (dispersal, establishment, growth to high density, and high impact on an invaded community; Moyle and Marchetti 2006). This species-trait-based approach has had only limited success in predicting invasion success (Moyle and Marchetti 2006), in part perhaps because it can be incompatible with the existence of ecological trade-offs. In essence, different traits often appear necessary for success in different stages of the invasion process. A monomorphic population may be limited in its ability to perform well across the range of stages in the invasion process. For example, a tendency to disperse readily, which helps populations to spread through an environment quickly, might be incompatible with building up the initial densities required to overcome poor population growth at low density (the Allee effect), and traits that allow a species to do well at low densities might be incompatible with traits that allow that species to do well and have high impacts at high densities.

The notion that different traits are favored at low versus high densities has a long history in ecology associated with r and K life histories. Species with r-type life-history traits (e.g., rapid growth, early reproduction at small size, high reproductive effort, short life span, high dispersal tendencies) are thought to be good colonists that do well at low density, whereas species with K-type life histories (the opposite traits) are considered to be poor colonists who do better than r-type species at high density (Stearns 1976). Thus, if a species is made up entirely of either r-type or

K-type individuals, it should do well at either low or high density, but not both.

A new twist on the above idea has emerged from the recent interest in animal personalities (also known as behavioral syndromes). Behavioral syndromes, which have been seen in many species across a broad range of taxa (Dall et al. 2004; Sih et al. 2004; Reale et al. 2007) involve consistent individual differences in a variety of behaviors both within and across contexts, as well as correlations between behaviors (Sih et al. 2004). Individuals have different behavioral types (BTs) within the syndrome. For example, recent work reveals within-species variation in an aggression-boldness syndrome, where some individuals are more aggressive and/or bold than others across multiple contexts (Johnson and Sih 2007). Many studies have shown that behavioral types often show a relatively large genetic component, with heritability values on par with those from human personality studies (reviewed in van Oers et al. 2005).

As is the case with many life-history related traits, BTs can have striking effects on individual fitness (Dingemanse et al. 2004; Dingemanse and Reale 2005; Reale et al. 2007; Smith and Blumstein 2008) and are likely adaptive (Dall et al. 2004; Wolf et al. 2007; Duckworth 2008), with fitness effects of BTs dependent on physical, ecological, and social contexts. For example, aggression in brown trout is selected for in habitats with low physical complexity, where it is easy to defend territories, but selected against in physically complex environments (Hojesjo et al. 2004). Importantly for the invasion context, BT has recently been shown to be associated with dispersal (Fraser et al. 2001; Dingemanse et al. 2003; Clobert et al. 2009; Cote et al. 2010a, 2010b, 2010c).

The key aspect of BT that we emphasize is individual variation within species in sociability, a BT that affects density-dependent performance (Cote et al. 2008) and dispersal (Cote and Clobert 2007; Jokela et al. 2008). In common lizards, asocial individuals have increased fitness at low density, while social individuals, who actively seek out conspecifics, have increased fitness at high densities (Cote et al. 2008). This social BT by density performance interaction translates into differences in dispersal; asocial individuals disperse more at high densities, while social individuals disperse more at low densities (Cote and Clobert 2007). Dispersal decisions may generally depend on the interaction between an individual's BT and local conditions. If BT and context interact to affect an individual's expected fitness within a patch, we would expect individuals to disperse at higher rates from patches in which their BT is at a disadvantage and to stay in patches where their BT is favored. That is, dispersal may be inversely related to expected fitness gains within a patch and thus may be

an adaptive mechanism allowing BTs to display matching habitat choice (Edelaar et al. 2008).

Within-species variation in BTs and BT-dependent dispersal and performance can have important effects on invasion dynamics. Field observations of the range expansion of western bluebirds show that aggressive individuals lead the range expansion, displacing an interspecific competitor, only to be replaced themselves by less aggressive conspecifics (Duckworth 2008). In effect, the coupling of BT and dispersal led to specialization in the range expansion process. We hypothesize that local succession of life histories—and thus BTs—should be commonly observed in the spread of invasive species, deriving from this process of social or ecological context specialization. In particular, we are interested in how within-species variation in sociability, which can affect both density-dependent performance and dispersal tendencies (Cote and Clobert 2007; Cote et al. 2008, 2010c), might influence the dynamics of invasions. We imagine a BT-related life-history trade-off in which asocial individuals perform better at low densities, specialize on empty patches, and can quickly establish new patches, while social individuals perform poorly at low densities but have higher *K*. These social individuals specialize on established patches, allowing local growth to high densities. In this case, the social composition of a species may affect the invasiveness of a species. Although we develop a detailed, specific model based on individual variation in sociability, the basic logic also applies to life-history variation or variation in any other traits that exhibit a trade-off involving density-dependent performance and dispersal.

To model effects of BTs on invasions, we use a spatially explicit simulation model involving a network of patches, where the topology of the network is likely to alter the speed of spread. In network theory, small-world networks, in which most connections are local but some span longer distances, increase the speed and likelihood of the spread of agents (Watts and Strogatz 1998; Newman and Watts 1999; Kuperman and Abramson 2001). In most species, dispersal distance is limited; however, invasive species often are spread via human networks (Mack et al. 2000; Suarez et al. 2001; Floerl and Inglis 2005; Muirhead and MacIsaac 2005), which have more widely dispersed connections (Guimera et al. 2005; Colizza et al. 2006). A simple network with only short-distance connections is a ring network. Adding longer-distance connections and varying the topology of patch networks from ring to random networks can be thought of as an increase in the influence of human transportation networks on the dispersal of a species.

We examine how the population's BT composition (all social individuals, all asocial individuals, or a mix of the two) influences its rate of spread and its invader impact.

To better understand mechanisms underlying the invasion dynamics, we focus on a representative empty patch and consider how the mix of BTs affects patterns of immigration into the patch, establishment, population growth, and subsequent dispersal to new patches. We then examine how the effect of BT composition on invasion dynamics depends on (1) the dispersal environment (network connections and mortality during dispersal), (2) factors influencing dispersal rates (steepness of the effect of density and local fitness and dispersal), and (3) the magnitude of difference between asocial and social BTs in density-dependent fitness and dispersal.

Model

Within-Patch Dynamics

We consider a situation in which a species is introduced into an initially empty series of patches. We assume that the species is composed of two distinct types of individuals that differ in their fitness and dispersal responses to density (Cote et al. 2008). We will define asocial individuals as those with relatively high fitness at low densities, including a relatively small Allee effect, and social individuals as those with higher fitness at high local densities that are outperformed by asocial individuals at low densities (fig. 1*A*). We assume that the populations exhibit logistic growth with an Allee effect (Lewis and Kareiva 1993), where the equation representing the population dynamics of a single type within a single patch is

$$N_{i,j,t+1} = N'_{i,j,t} + r_i N'_{i,j,t}\left(1 - \frac{\sum_i N'_{i,j,t}}{K_i}\right)\left(\frac{\sum_i N'_{i,j,t}}{T_i} - 1\right). \quad (1)$$

In this equation, $N_{i,j,t}$ and $N'_{i,j,t}$ are the population sizes of type i in patch j at time t before and after dispersal (the prime denotes population size after dispersal in time t). Thus, summing over types, i, gives us the total number of individuals in patch j at time t, and further summing over patches, j, gives us the total number of individuals in the entire network at time t. The parameters r_i, K_i, and T_i determine the strength of the density-dependent fitness trade-off between the types. K_i is the carrying capacity of type i when alone in a patch, while T_i is the Allee threshold density of type i, below which population growth is negative. The parameter r_i affects both the strength of the Allee effect for type i (i.e., the negative per capita population growth at $N \approx 0$) and the type's maximum per capita population growth. The maximum per capita population growth for each type is $\Delta N_{j,i}/N_{j,i} = [(K_i - T_i)^2/4K_iT_i]r_i$ and occurs at $N_{j,t} = (K_i + T_i)/2$. Although the types differ in r, K, and T, individuals are taken as equivalent when calculating local density. This assumption is likely to be violated in certain situations and could change the dynamics
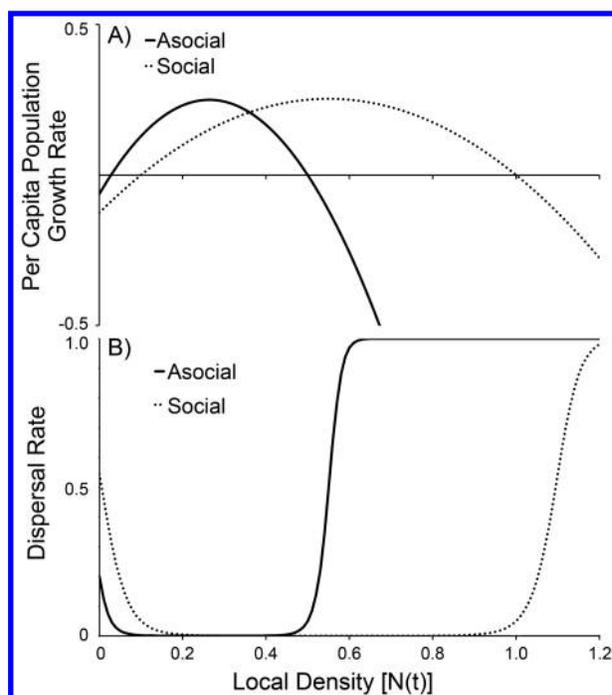

Figure 1: Population growth (*A*) and dispersal rates (*B*) for each type of individual as a function of the local patch density. Within each patch, populations experience logistic growth with an Allee effect. Negative growth due to the Allee effect is stronger and occurs over a wider range of densities in social compared with asocial individuals. However, social individuals have a higher carrying capacity. Dispersal rate is negatively related to fitness, with little dispersal occurring at densities that lead to population growth and maximal dispersal for each type occurring above the type's carrying capacity. Parameters: $r_a = 0.05$, $r_s = 0.125$, $K_a = 0.5$, $K_s = 1$, $T_a = 0.025$, $T_s = 0.1$, $\alpha = 25$, $D(K) = 0.05$.

of the model (e.g., when individuals nonrandomly distribute themselves within a patch depending on their type, asocials may stick to themselves and thereby hinder the local growth of socials); however, we leave further detailed analyses of these issues for future investigation.

To analyze effects of variation in BT on ecological dynamics in the absence of evolutionary dynamics, we make the simplifying assumption that BTs reproduce asexually. Data from many sexual systems show that BT is moderately heritable (van Oers et al. 2005). Future work examining the evolution of dispersal strategies will relax the assumption of asexual reproduction to examine effects of variation in heritability on evolutionary dynamics.

For all model analyses, we scale local density to the social carrying capacity ($K_s = 1$) and assume that socials can grow to higher local densities ($K_s > K_a$) but have a wider ($T_s > T_a$) and stronger ($r_s > r_a$) Allee effect. Finally, we assume that each type has an equal maximum per capita

growth rate, $(\Delta N_\mathrm{s}/N_\mathrm{s})^* = (\Delta N_\mathrm{a}/N_\mathrm{a})^*$, though these maxima obviously occur at different densities.

Dispersal

In addition to the local dynamics, individuals exhibit fitness-dependent dispersal, which manifests as density-dependent dispersal. Individuals disperse at higher rates as their expected fitness (we use per capita population growth rate as a proxy) decreases. Taking fitness to be $W_i(N) = \Delta N_i/N_i = r_i[1 - (N/K_i)][(N/T_i) - 1]$, we set dispersal probability, $D_i(N)$, to be

$$D_i(N) = \frac{1}{1 + e^{aW_i(N) + \ln\{[1-D(K)]/[D(K)]\}}}. \quad (2)$$

Thus, individuals disperse at a rate that depends on their expected local fitness, given the local density before dispersal. This dispersal equation, adapted from Kun and Scheuring (2006), allows for a wide variety of fitness-dependent dispersal responses. Parameter α determines how strongly dispersal rate depends on fitness, with $\alpha = 0$ corresponding to density-independent dispersal and higher values of α leading to sharper rises in dispersal rate with increasing local densities. $D(K)$ is the dispersal rate if $aW_i(N) = 0$, which occurs when α is 0 (fitness/density-independent dispersal) or when local density is equal to either the carrying capacity ($N = K_i$) or the Allee threshold ($N = T_i$) for a given type. Figure 1*B* shows each type's dispersal rate for a single set of parameter values.

Individuals that leave a patch survive the dispersal process with a probability of survival equal to S and are distributed evenly among the patches connected to their starting patch. While individuals express habitat preferences by exhibiting higher dispersal rates from low suitability patches, we assume that they cannot evaluate the density—and thus the suitability—of a new patch until after they colonize. This assumption is clearly violated in many systems, but evaluating the effects of habitat choice is beyond the scope of this article. Patches can differ in degree (number of patches connected to the focal patch), where better-connected patches tend to receive more migrants but send fewer emigrants to each neighboring patch. If $A_{j,k}$ is an indicator matrix of connections, with element (j, k) taking the value of 1 if there is a connection between patches j and k and a value of 0 otherwise, and $\mathrm{Degree}(k)$ is the total number of connections between patch k and all other patches, then the equation describing how the population changes in each patch as a result of emigration and immigration is

$$N'_{i,j,t} =$$
$$N_{i,j,t} - D_i(N_{j,t})N_{i,j,t} + \sum_k \frac{A_{j,k}}{\mathrm{Degree}(k)} D_i(N_{k,t})N_{i,k,t}S. \quad (3)$$

Substituting equation (3) into equation (1) completes the cycle of dispersal and local population growth. Thus, in each time step, dispersal depends on total density in a patch, and populations exhibit within-patch growth (birth to death), depending on density after dispersal.

Demographic Trade-Offs

The effects of BTs and the mix of BTs on invasion dynamics should depend on how different the BTs are with regard to their density-dependent fitness response. We examined this issue by comparing the spread of the three BT compositions (all social individuals, all asocial ones, or a mix of the two) over a range of demographic trade-off strengths that governed the magnitude of the difference between the two BTs in their density-dependent fitnesses. This trade-off was parameterized by fixing the parameters r_a, r_s, K_s, and T_s and varying K_a and T_a proportionally in order to keep an equal maximum per capita growth rate, $(\Delta N_\mathrm{s}/N_\mathrm{s})^* = (\Delta N_\mathrm{a}/N_\mathrm{a})^*$. If the asocial type was substantially more fit than the social type at low densities (i.e., if the asocial type had a much smaller value of T, indicating a much weaker Allee effect), then for the two BTs to have the same maximum per capita growth rate, the asocial type must also be substantially less fit than the social type at high densities (i.e., the asocial type must have a much lower value of K). We ran 10 simulations for each value of K_a ($0.125 \leq K_\mathrm{a} \leq 1$; intervals of 0.025), varying T_a accordingly.

Invasion dynamics should also depend on the shape of the fitness-dependent (thus density-dependent) dispersal curves and how different these are for the two BTs. Imagine two types of dispersal curves, one in which dispersal is independent of fitness and one in which dispersal probability is inversely related to fitness. If dispersal is fitness dependent (α is high), individuals stay in the patch during the period of fastest population growth and disperse in high numbers when densities increase, possibly allowing for faster spread than independent dispersal.

We examined the effect of fitness-dependent dispersal on spread by varying the dispersal parameters, α and $D(K)$. We evaluated the relative speed of spread for asocial and mixed-type invasions by comparing spread speed of each type for 20 realizations of the simulation at each set of parameter values α ($\alpha = 0, 5, \ldots, 50$) and $D(K)$ ($D(K) = 0.01, 0.05, \ldots, 0.41$).

Network Structure

Guided by the analogy between the spread of invasive species and the spread of other agents (e.g., information or disease), we varied the structure of connections among patches to discover conditions when an epidemic-like invasion might occur (Watts and Strogatz 1998; Kuperman and Abramson 2001). Network structures in which most links are local but some proportion p (the rewiring probability is the proportion of nonlocal links in the network) of the links spans random patches in the network have been shown to increase the likelihood, speed, and synchrony of epidemic spread (Watts and Strogatz 1998; Kuperman and Abramson 2001). We contrast spread through a range of network structures to find the effects network structure and the interaction between BT composition and network structure have on the speed of invasion spread.

We contrasted invasion spread through a range of 1,000 patch networks differing in rewiring probability, p, and in the average number of connections per patch, the degree, m. Dispersal was allowed in either direction along a connection. Following convention in network theory (Watts and Strogatz 1998), we began with a ring network, with $p = 0$, and each patch was connected to the $m/2$ closest patches on each side; for all patches, degree $= m$. The ring network serves as a simple, least-connected starting point. Again, following convention in network analyses, we build more random network configurations by increasing p, the probability that any given link was rewired. When a link was rewired, one end of the link was redirected from its original end point to a random patch in the network. At small to intermediate values of p, we got what network theory refers to as a small-world network (with short paths between any two patches and many local links). At higher values, the network approached a random structure (Watts and Strogatz 1998). Before simulating spread, we examined the structure of connections to ensure that no patches were disconnected from the main network.

The effect of network structure on spread was determined by allowing each of the three mixes of types to spread on a range of networks. We ran 10 replicate simulations for each rewiring probability p ($p = 0, 0.02, \ldots, 1$; $m = 4$, $S = 0.8$), each mean degree value m ($m = 2, 4, \ldots, 20$; $p = 0.7$, $S = 0.8$), and each dispersal survival value S ($S = 0, 0.05, \ldots, 1$; $m = 2$, $p = 0.7$). The default network parameters ($m = 4$, $p = 0.7$, $S = 0.8$) correspond to a network in which each patch has relatively few connections (4), but those connections are widely spread ($p = 0.7$), and dispersers are likely to survive ($S = 0.8$).

Numerical Simulations and Evaluation of Spread

We performed all numerical simulations in Matlab R2008b by iterating equations (1)–(3) for a total of 1,000 iterations on a given network structure. To initialize the system, a small number of immigrants ($N = 0.02 \times K_s$) were added in each time step into a single colonization site (patch 1). This distribution of types in the input was all social, all asocial, or a 50/50 mix of types.

Our metric of spread speed was the rate (number of newly established patches per time step) at which patches became established during the period when proportion of patches established increased from 10% of all patches to 90%. A patch was considered established once local population density reached at least T_s. Our metric of invasion impact was the total regional population size at 50 time steps after 10% of patches had been established. Qualitative results did not depend on the metrics used (i.e., results are similar when varying population size for the establishment threshold or the number of time steps for evaluating invader impact).

Results

Comparing Spread by Three BT Compositions

Under a range of conditions, the presence of a mix of types in the system simultaneously increases both the speed of the invasion front and the number of individuals present in each patch. Figure 2 compares the invasion speed for the three behavioral distributions on a representative network. Figure 2*A* and 2*B* shows how spread proceeds for asocial and social types only, respectively. It shows that growth is initially slow when the number of patches established is small and then increases steadily before slowing when most patches are full. Notice that asocials spread more quickly than the social type but that socials grow to higher local densities. Thus, the total population size in the network is comparable for these two types over this time frame (fig. 2*C*). Figure 2*D*–2*F* represents the spread of a mixed-type invasion. Figure 2*D* shows the dynamics of the asocials in the mixed-type invasion, figure 2*E* shows only the socials, and figure 2*F* shows the combined spread of both types. Comparing figure 2*D* and 2*E*, we can see that asocials lead socials in the invasion wave, with socials replacing asocials in the interior of the network. Although the input rate of each type in the mixed invasion was only half the input rate of that type in the single-type invasions, both asocials (cf. fig. 2*A*, 2*D*) and socials (cf. fig. 2*B*, 2*E*) spread faster when in a mixed-type invasion, and the total population size in a mixed-type invasion quickly outstrips either monotype (fig. 2*C*).
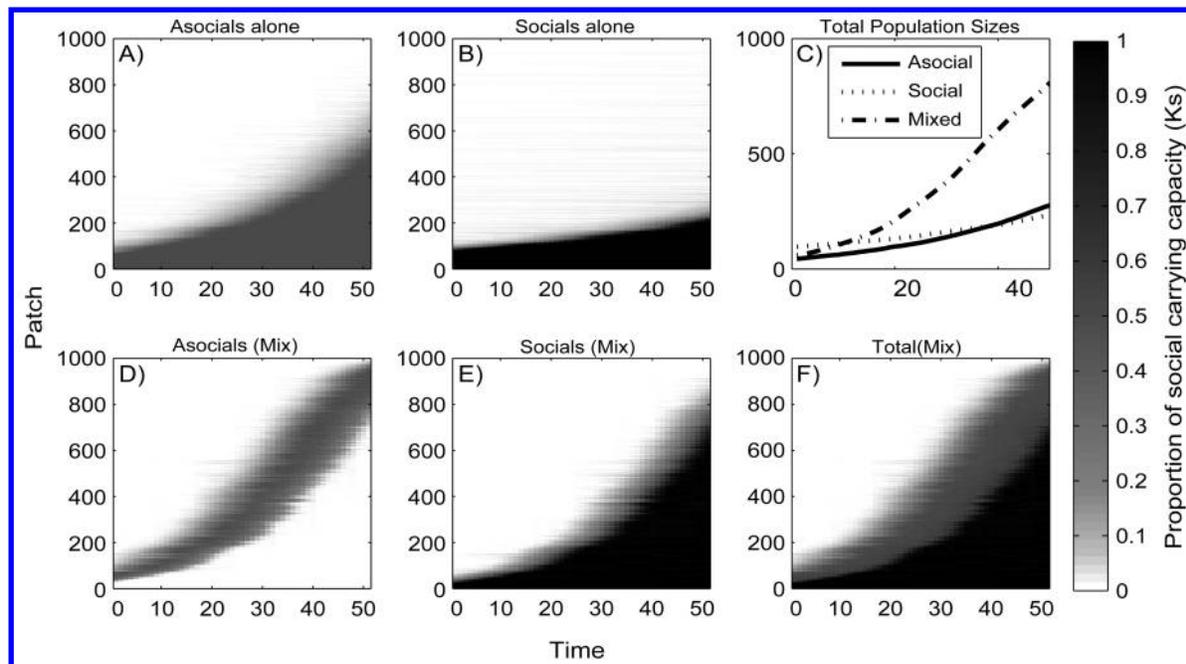
Figure 2: Invasion spread over time of three mixes of types on a representative 1,000-patch network structure. In each panel, time proceeds from left to right, while patches are arranged vertically in the order that each patch is established. *A* and *B* represent the spread of only asocials (*A*) or only socials (*B*), while *D–F* represent asocials (*D*), socials (*E*), and total individuals (*F*) in a mixed-type invasion. *C* compares the total population sizes in the three types of invasion. In all panels except *C*, the shade of gray signifies the number of individuals of the represented type in the corresponding patch at the corresponding time. The starting time ($T = 0$) for each of these panels is normalized to the time at which 10% of patches were established ($N > 0.1$ in the patch), so only the spread dynamics are compared here. Parameters: $r_a = 0.05$, $r_s = 0.125$, $K_a = 0.5$, $K_s = 1$, $T_a = 0.025$, $T_s = 0.1$, $\alpha = 25$, $D(K) = 0.05$, $S = 0.8$, $p = 0.7$.

Single-Patch Dynamics

To clarify the mechanisms leading to the increased invasion success in a mixed-type invasion seen in figure 2, we describe the typical sequence of events for each invasion type in a single patch (fig. 3). Figure 3*A*, 3*D*, and 3*G* show the patch dynamics for an asocial-type invasion. When asocials are introduced into a patch alone, they quickly establish (note the short lag, the time from first immigration—where each panel begins—to successful establishment in fig. 3*D*) as a result of their low emigration at low densities (fig. 3*G*) and relatively low Allee threshold. Once established, they begin to grow in this patch (fig. 3*D*). As their density increases, so does their propensity to leave the patch (fig. 3*D* and 3*G* illustrate how asocial emigration depends on density). As local density approaches K_a, the number of emigrants becomes sufficient to establish in connected patches and the same pattern repeats in each neighboring patch.

In contrast to asocials, when social individuals are introduced alone, they do not perform well as invaders (see fig. 2*E*). Because of the socials' stronger Allee effect, higher Allee threshold, and their concomitant tendency to dis-

perse at high rates when density is low, much larger numbers of immigrants are necessary to successfully establish in a patch. In figure 3*H*, notice that individuals begin dispersing out of the patch at low rates before the population begins to grow (fig. 3*E*). Furthermore, the population only grows once the immigration rate from neighboring patches increases to approximately double the immigration rate necessary to establish a population of asocials (cf. fig. 3*A*, 3*B*). In all, this leads to much longer within-patch lags before successful establishment (cf. fig. 3*D*, 3*E*).

Adding social individuals to an introduction of asocials can speed the spread of an invasion (see fig. 2*C*, 2*E*). If asocial and social individuals immigrated into a patch at a moderate, constant rate, the asocials would eventually establish and begin growing in the patch (as when asocials establish alone), with socials being outperformed and emigrating out of the patch. However, in populations with a mix of BTs, immigration into an average patch is not constant and instead is pulsed (fig. 3*C*; see below for an explanation of why immigration is pulsed). A large pulsed immigration of asocials allows the population to quickly
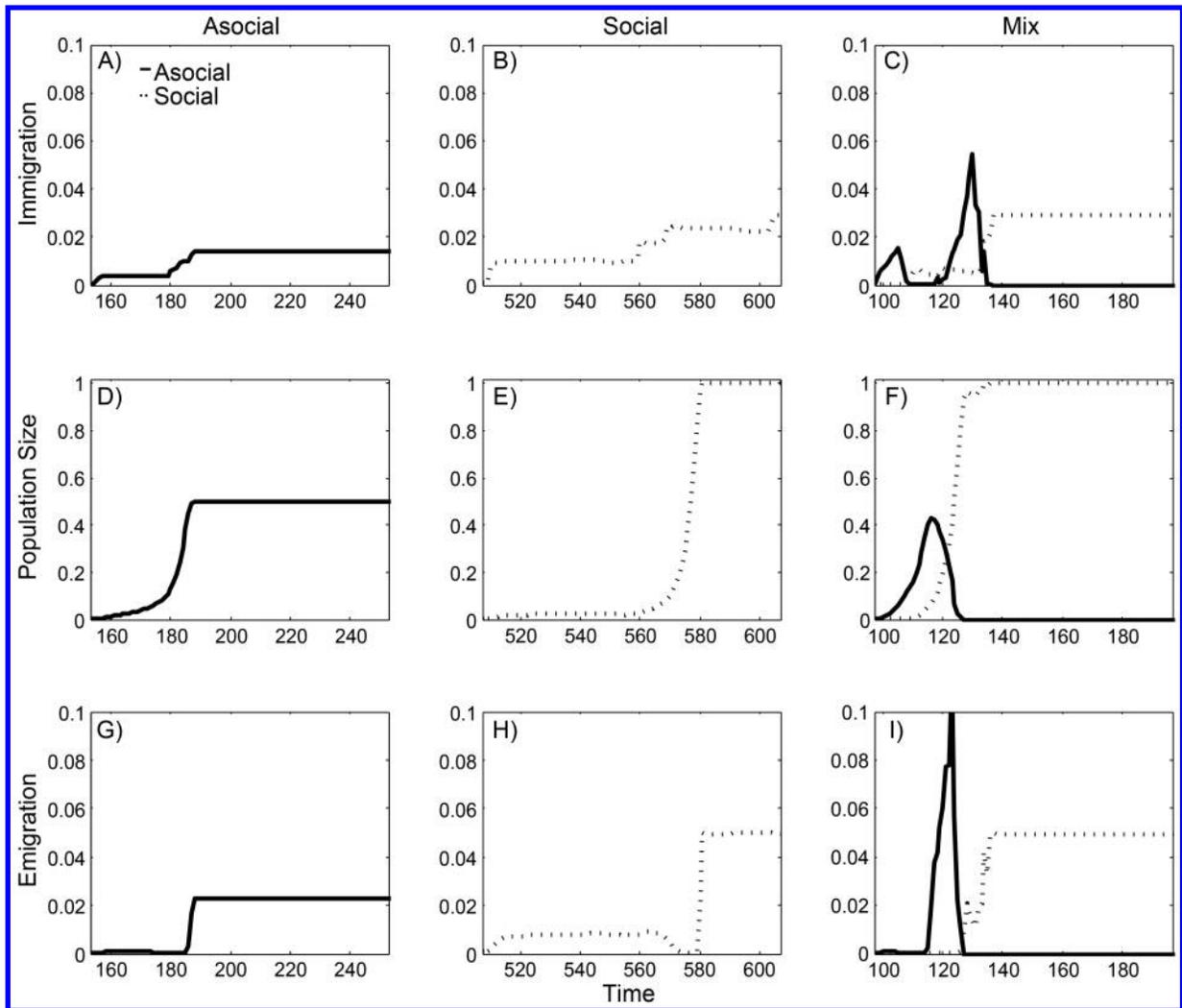
Figure 3: Comparison of immigration, population size, and emigration for three behavioral mixes at a single patch in a representative network structure. *A–C* show immigration for asocial, social, and mixed-type invasions, respectively, while *D–F* show local density and *G–I* show emigration. Immigration and emigration are the numbers entering and leaving the patch at each time rather than rates. The first time shown is the first time at which immigration was greater than 0.003, high enough to establish a patch with asocials. One hundred time steps are shown after this first immigration time. In all panels, solid lines denote asocial individuals, while dotted lines denote social individuals. Parameters: $r_a = 0.05$, $r_s = 0.125$, $K_a = 0.5$, $K_s = 1$, $T_a = 0.025$, $T_s = 0.1$, $\alpha = 25$, $D(K) = 0.05$, $S = 0.8$, $p = 0.7$.

bypass the Allee effect and establish and grow more quickly than a group of asocials with no social individuals (cf. fig. 3*E*, 3*F*). Successful establishment by asocials primes the way for socials, since local density quickly exceeds the socials' Allee threshold. Socials begin immigrating from neighboring patches (fig. 3*C*) and settling, thus quickly increasing in number (notice the lack of lag in the growth of socials in fig. 3*F* compared with fig. 3*E*). With the addition of social individuals, the local density increases beyond K_a. This increase in density beyond the maximal local density of asocials alone drastically alters the time course

of emigration. Rather than a constant emigration of asocial individuals out of the patch, there is a short pulse of emigration during which the maximum number of emigrants reaches a level approximately four times higher than with asocials alone (cf. fig. 3*I*, 3*G*). This is the source of the pulsed immigration seen in figure 3*C*.

Finally, socials disperse at the same rate they do in a social monotype (cf. fig. 3*I*, 3*H*), because the asocials are no longer present (fig. 3*F*). As seen in figure 2, these dynamics lead to differences in the spread speed of different behavioral mixes and underlie the differences in the timing

of first immigration into a representative patch in figure 3 (first immigrants arrive in the social invasion at $t \approx 155$, first immigrants in asocial invasion arrive at $t \approx 510$, and first immigrants arrive in mixed invasion at $t \approx 95$).

Demographic Trade-Off and Spread Speed

The magnitude of increase in spread speed when socials are added to asocials depends on the strength of the demographic trade-off between the two types (fig. 4). In figure 4, we vary K_a while $K_s = 1$; thus, as we move to the right, the asocial type becomes more similar to the social type. When $K_a = 1$, the types are identical. Of course, varying K_a while holding K_s constant has no effect on the demography or spread speed of a social monotype. Asocial individuals spread more rapidly as the difference between types is increased (fig. 4A), likely because as K_a is decreased, so are r_a and T_a, allowing for much better performance at low densities and quicker establishment. The impact of an asocial invasion is highest at intermediate trade-off strengths, since the maximum local density decreases as spread speed increases. Spread speed in a mix also depends on the strength of the demographic trade-off between the types (fig. 4A). When asocials and socials are either very similar or very dissimilar, there is little increase in the speed of a mixed-type invasion above the speed of asocials spreading alone. It is only when there is an intermediate similarity between types that the speed is dramatically increased. This is due to the pulsed emigration dynamics described above. When the types are very dissimilar (i.e., $K_a \approx T_s \ll K_s$), the growth rate of socials at $N = K_a$ is too low (approximately 0) to cause the rapid rise in local density above K_a that would lead to a large pulse of dispersers. Additionally, the number of asocial individuals in the patch is too low to send out large numbers of dispersers. When the types are very similar, spread becomes more similar to that of asocials alone. Indeed, when $K_a = K_s$, the types are identical. However, when similarity between types is intermediate ($K_a \approx (K_s + T_s)/2$, the density that allows for maximum growth of socials), asocials grow to intermediate densities before being pushed out in large numbers by a rapidly growing subpopulation of social individuals (fig. 3F, 3I). In general, the impact of a mixed-type invasion is enhanced by both the increased spread speed above the speed of an asocial-only invasion and the higher carrying capacity gained by including social individuals. As with spread speed, impacts are maximized when the difference between types is intermediate (fig. 4B).
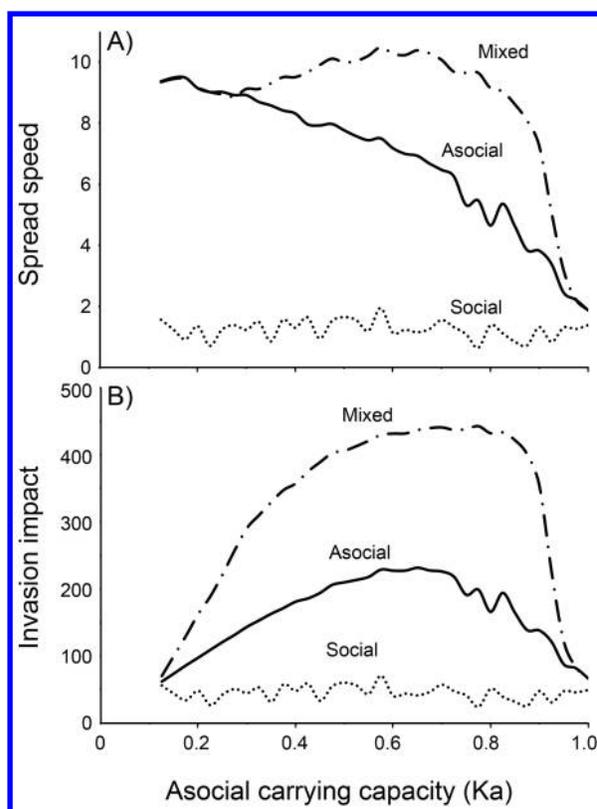

Figure 4: Spread speed (*A*) and invasion impact (*B*) during invasion for the three behavioral mixes as a function of asocial carrying capacity. When K_a is smaller, types are more dissimilar. Spread speed is measured as the rate of patch establishment after 10% of patches are established. Invasion impact is measured as the total population size in the network 50 time steps after 10% of patches are established. This measurement takes both local patch density and spread speed into account. In order to keep maximum per capita growth rates comparable between social and asocial individuals, the asocial Allee threshold varies with asocial carrying capacity ($T_a = K_a - 2^{3/2}(K_a + 2)^{1/2} + 4$). Parameters: $r_a = K_a/8$, $r_s = 0.125$, $K_s = 1$, $T_s = 0.1$, $\alpha = 25$, $D(K) = 0.05$, $S = 0.9$, $p = 0.7$.

Network Structure and Spread Speed

While behavioral heterogeneity is necessary for fast spread through a network, the structure of network connections moderates the strength of this effect. For a mix of types to increase the rate of spread, connection heterogeneity is necessary (fig. 5A). On a homogenous ring network, the speed increase is minimal. As each new patch is established, only one additional new patch becomes available for new establishment. Thus, the invasion cannot accelerate. As connection heterogeneity increases, however, newly established patches are more likely to be connected to empty patches. Spread from these areas leads to acceleration in the number of patches established over time, and the con-
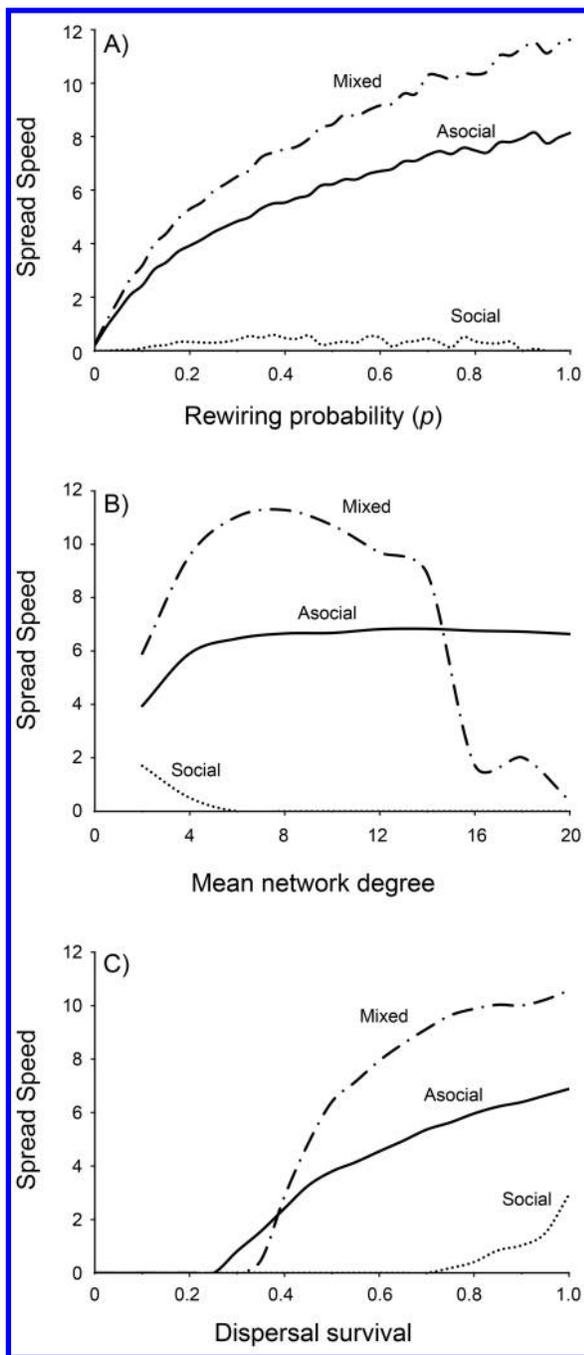
Figure 5: Spread speed during invasion for the three behavioral mixes as a function of the amount of randomness in the network's connections (p; A), the mean number of network connections (m; B), and the probability of survival during dispersal (S; C). Values presented are averages of 10 realizations of the simulation for each value of the independent variable. Simulations were run for 41 levels of p, 10 levels of network connection, and 21 levels of S. Parameters: $r_a = 0.05$, $r_s = 0.125$, $K_a = 0.5$, $K_s = 1$, $T_a = 0.025$, $T_s = 0.1$, $\alpha = 25$, $D(K) = 0.05$ (A–C); $S = 0.8$ (A, B); $p = 0.7$ (B, C); $m = 2$ (A, C).

sequence of socials pushing asocials along is faster acceleration with a mix than with asocials alone. Socials spread slowly regardless of the network structure.

As the mean degree of the network increases, the spread speed of asocials remains relatively unaffected; increasing degree means more patches are available to be established but also fewer immigrants arriving in each patch per time step, since the number of emigrants from a patch are evenly distributed among the connections of that patch. This trade-off between degree and number of immigrants arriving in empty patches has a minimal effect on asocial spread (fig. 5B), since the increased time to establish is offset by the number of patches established. Social-type spread is negatively affected by increasing degree (fig. 5B), since they need a minimum number of immigrants arriving per time step to compensate for their high dispersal rates and low fitness at low densities and successfully establish. Increasing degree decreases the number of immigrants arriving to a point where establishment becomes impossible. In mixed-type invasions, speed initially rises with network degree, since the pulses of dispersal provide enough immigrants to establish many patches quickly. As degree continues to increase, however, the speed of spread drops precipitously as the pulses of emigrants are diluted over too large a number of target patches and are no longer able to quickly establish all these patches (fig. 5B). If given enough time, the reduced number of asocial immigrants per patch would be able to successfully establish, but the transience of the emigration pulse (fig. 3I) prevents establishment in this shorter time frame. In highly connected networks, asocial populations spread most quickly as a result of their continued dispersal after establishment.

As one would predict, increasing dispersal survival enhanced spread speed for each of the behavioral distributions (fig. 5C). Socials are unable to spread unless survival is very high, while asocials can spread even with relatively poor survival during dispersal. The mixed-type invasion spreads most quickly when survival is high but does not perform as well as an asocial invasion at the lowest survival rates. The mechanism is similar to the one previously discussed for very high degree networks: low survival dilutes the pulse of asocial dispersers too much to successfully establish new patches.

Fitness-Dependent Dispersal and Spread Speed

Finally, these results depend strongly on the strength of the relationship between fitness and dispersal rate. Figure 6 shows the speed of invasion for each behavioral mix as a function of the dispersal parameters. As in all previous analyses, socials are unable to spread effectively in a monotype. However, they do best when dispersal is relatively high (~20% of the population) independently of fitness
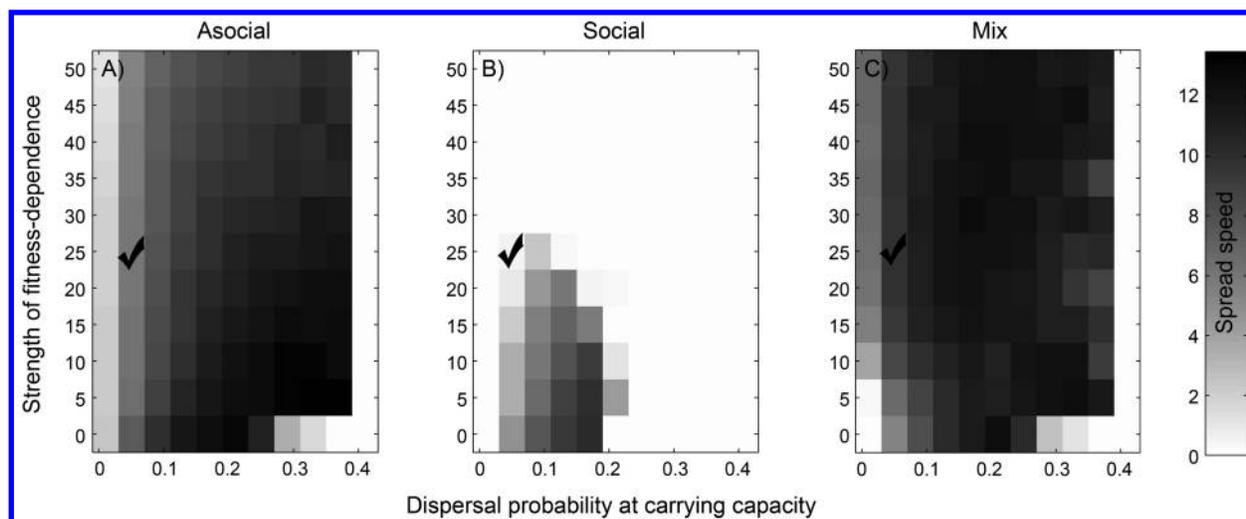
Figure 6: Spread speed of asocial (*A*), social (*B*), and mixed-type (*C*) invasions as a function of dispersal parameters (strength of density dependence = α, dispersal probability at carrying capacity = $D(K)$). Values for each set of parameters correspond to the average speeds obtained from 10 iterations of the invasion simulation. Darker shades indicate faster spread. Check marks indicate the default parameters in other simulations. Parameters: $r_a = 0.05$, $r_s = 0.125$, $K_a = 0.5$, $K_s = 1$, $T_a = 0.025$, $T_s = 0.1$, $S = 0.8$, $p = 0.7$.

($\alpha \approx 0$). Both the asocial and mixed-type invasions can spread effectively over a much wider range of dispersal parameters, but spread speeds show a different pattern of dependence on the dispersal parameters. The asocial monotype spreads best when baseline dispersal rates are high ($0.2 < D(K) < 0.4$) and fitness dependence is low ($\alpha < 10$). In this situation, there are relatively high levels of dispersal, regardless of the local density. The mixed-type invasion, on the other hand, progresses most quickly when dispersal is strongly fitness dependent ($\alpha > 25$) and $D(K)$ is intermediate. In this situation, there is strong density dependence; when densities are favorable for a type, their dispersal rate is very low but rapidly rises as densities become unfavorable (see fig. 1). When we compare the spread of the mixed-type invasions to the spread of asocial invasions, we see that mixed invasions have a large advantage whenever density-independent dispersal is lower (lower $D(K)$) and when dispersal is more sensitive to changes in density (α). The combination of a lower $D(K)$—and thus lower dispersal when conditions are good—and strong density dependence (high α) leads to a buildup of asocials while the population is growing, followed by large pulses of dispersing asocials when socials force densities above K_a. In this region of parameter space, the spread of asocial monotypes is limited by low dispersal. Without social individuals present, densities never rise above K_a, so strong density dependence and low dispersal at carrying capacity means very little movement by asocials. As fitness dependence is reduced and $D(K)$ is increased, dispersal becomes less dependent on large pulses

of asocials to quickly establish neighboring patches and more reliant on the consistently high dispersal rate of any asocials present. Thus, the dynamics of spread for the two behavioral mixes are similar but skewed slightly toward faster spread by asocials (since dispersing socials do not provide additional help in the establishment phase).

Discussion

Invasive species that attain pest status often spread across a landscape at surprisingly rapid speeds and subsequently grow quickly to problem densities in all suitable habitats (Mack et al. 2000; Kolar and Lodge 2001; Sakai et al. 2001). Analyses of invasions emphasize that it is a multistage process (Kolar and Lodge 2001; Colautti and MacIsaac 2004); successful invasion requires a species to get to a new area, establish, grow locally, spread, and grow regionally. Ecological theory and empirical research suggest that different traits are favored in different stages of this process (Kolar and Lodge 2001; Sakai et al. 2001). Traits that enhance success in empty patches (e.g., tendency to stay in empty patches, aggressiveness, *r*-type life history) may be incompatible with traits allowing spread (high dispersal rate) or growth to high densities (tolerance of high densities, *K*-type life history). Thus, in theory, species with traits that do well in one stage of an invasion should not do well in other stages. In this article, we suggest a mechanism that can offset trade-offs inherent in the invasion process. Below, we (1) summarize the basic idea of our model and its key results, (2) note that the basic mech-

anism in our model is very general, (3) discuss more specific assumptions and results in more detail, and (4) outline some future directions of study.

The key general insight from our model is that the inherent problem of trade-offs in invasions can be solved by the existence of within-species variation in traits. In particular, we model the situation where life-history-related BT variation (where different BTs specialize on different densities and disperse accordingly) increases the speed of invasions above a monotype of either social or asocial BTs alone and also allows for high densities in each patch. Social types that do poorly at low density spread slowly because they grow slowly within each new patch they encounter, leading to long time lags between establishment of each successive patch. This type does, however, eventually grow to high densities within each patch. In contrast, asocials spread more quickly than socials as a result of their higher growth rate at low densities, allowing for quick establishment and shorter lags between establishment of new patches. However, this type is unable to grow to high densities in each patch. A mix of types allows for both faster spread than asocials alone and for socials to grow to high local densities more quickly than they do alone.

While our model is based on variation in sociability, the logic should generally apply to any traits that exhibit a density-dependent performance trade-off with associated density-dependent dispersal. For example, parallel dynamics have also been suggested for another BT axis: aggressiveness, where dispersers are more aggressive than residents (Duckworth and Badyaev 2007). In an ongoing range expansion, western bluebirds have been able to displace an interspecific competitor, the mountain bluebird, since aggressive individuals of the former species are able to competitively exclude individuals of the latter species. These aggressive individuals are also more highly dispersive (Duckworth and Badyaev 2007; Duckworth 2008; Duckworth and Kruuk 2009); this coupling of dispersal and aggression has led to a wave of range expansion, with highly aggressive types dispersing to the front of range expansion and displacing the competitor species. In established patches, however, aggression is selected against. As a result, populations in the interior of the range expansion are less aggressive than those at the edge of range expansion. These results are similar to our basic results: individual differences in context-dependent performance, correlated to differences in dispersal, lead to a spatial pattern of spread in which one type leads and the other type follows, slowly replacing the former type as it spreads. Our results add the important insight that under a broad range of conditions, behavioral heterogeneity (variation among individuals in BT) can actually speed the spread of an invasion.

The basic logic in our model can also apply to non-behavioral phenotypic traits. For example, individuals in many species vary in defensive morphology (e.g., Tollrian and Harvell 1998; DeWitt et al. 1999). Individuals that are well defended can cope better with predators but typically have lower feeding, growth, or reproductive rates when predation risk is low. Invasive species sometimes enjoy a reduction in predation pressure when they first colonize a new site, either because predators do not recognize the invader as prey or as a result of density-dependent targeting effects (e.g., Ioannou et al. 2009). At low density, selection would favor individuals that do not build an antipredator morphology and that tend to have a higher potential r, which should help make them good colonists. However, if predation pressure increases with increasing prey density, individuals who have invested in antipredator defense will now be favored. With high predation risk at high densities, poorly defended individuals should disperse readily (and potentially colonize new habitats) and be replaced by better-defended ones. As a result, with a mix of the defensive phenotypes, the species should spread faster than it would with only a single type.

Furthermore, the basic dynamics we describe also generalize beyond variation in traits within a single species to also apply to how variation between species can affect community dynamics. The scenario where one type does well in empty patches in an early stage of colonization before being joined and replaced by a type that cannot colonize alone is a familiar pattern in ecological succession where the two species might vary, for example, in life history, with one r-selected type and one K-selected type (Connell and Slatyer 1977; Sousa 1979; Turner et al. 1998). The parallels between the successional process and the invasion dynamics we present are striking. The r-type species (asocials, who perform better at low densities and generally disperse more) colonizes empty areas before being joined and eventually replaced by the K-type species (socials, who have higher K in our situation). Moreover, as is often the case in succession, we see facilitation effects of colonizer-type individuals on the later establishment of successional species that cannot quickly establish on their own.

Broadly speaking, our results add to the growing literature indicating that acknowledging variation changes how we view ecological and evolutionary processes. For example, in fish shoals, groups with both bold and shy individuals forage more efficiently than groups with only one type (Dyer et al. 2009). Likewise, within-group social variation in social spider webs enhances fitness for all; asocial individuals capture food effectively but fight when encountering other asocials (Pruitt and Reichert 2010). In water striders, the mix of types can determine the strength and direction of sexual selection acting on males, since

certain hyperaggressive males can disrupt the entirety of the mating system (Sih and Watters 2005). At a broader scale, consistent individual differences may favor the evolution of cooperation (McNamara et al. 2004; Bergmüller et al. 2010), mediated by the evolution of social awareness (McNamara et al. 2009). In general, incorporating knowledge about individual variation can lead to a richer understanding of ecological and evolutionary processes (Bolnick et al. 2003; Sih et al. 2004).

A key assumption in our model is that sociability affects fitness in a density-dependent manner. Several common mechanisms support this assumption. For example, predators are generally more likely to recognize and attack larger groups (presumably composed of higher-sociability individuals; Krause and Ruxton 2002; Ioannou and Krause 2008; Ioannou et al. 2009), but as groups become very large, the predator's targeting of individuals degrades (Ioannou et al. 2009). As a result, social individuals may be protected only in very large groups and, thus, in areas where densities are very high. Similarly, the density-dependent link between social tendency and fitness might be explained by differences in foraging strategies, with asocial individuals representing producers seeking to avoid scroungers while scroungers need others to acquire social information and thus are more social (Barnard and Sibly 1981; Kurvers et al. 2009). At low density, asocial, solitary foragers will likely find dispersed food items, while social scroungers will likely have trouble finding and following asocial producers. In contrast, at high density, social scroungers will readily locate and scrounge from producers.

Beyond the key prediction that under a broad range of conditions, having a mix of BTs (or, more broadly, a mix of phenotypes) facilitates ecological invasions, we further show that the relationship between expected fitness and dispersal can have a strong impact on the relative speed of invasion. When individuals display fitness-independent dispersal (and thus density-independent dispersal), asocial individuals spread most rapidly. Conversely, when potential dispersers are more sensitive to the fitness consequences of remaining in their current patch (and thus patch density), mixed-type invasions can spread more quickly. Theoretical investigations into the evolution of density-dependent dispersal (Travis et al. 1999; Kun and Scheuring 2006; Enfjäll and Leimar 2009) show that a sigmoid density-dispersal curve, where dispersal is negligible below some threshold density but accelerates above this density, is the evolutionarily stable strategy (ESS). The ESS sigmoid density-dependent dispersal curves are strikingly similar to those curves that promote the speed of invasion spread in mixed-type invasions in our analyses. Importantly, empirical studies generally confirm this functional form for dispersal, with few individuals emigrating from low-density patches and many more dispersing once density exceeds some threshold (Denno et al. 1991; Fonseca and Hart 1996; Moksnes 2004; Enfjäll and Leimar 2005; Matthysen 2005). Other empirical studies of dispersal, however, have found both positive and negative density-dependent dispersal within a species (Cote and Clobert 2007; Kim et al. 2009). If individuals in these species display matching habitat choice, then individuals that do better at low density may be more likely to leave at high density and vice versa (Edelaar et al. 2008). Further modeling is needed to examine how BTs combined with this pattern of density-dependent dispersal might influence invasion dynamics.

Our results also show that the structure of the dispersal network can have important effects on the speed of invasion spread. Work in network theory has repeatedly shown that the spread of agents on a network is quite sensitive to the pattern of connections between points on the network (Kuperman and Abramson 2001; Pastor-Satorras and Vespignani 2001; Newman 2002). Our study extends these results into an ecological context by showing that invasion spread is likely to be fastest when the proportion of nonlocal connections is high. This proportion, which describes whether dispersers are more likely to find themselves in neighboring or faraway patches, is likely to depend on several factors. First, the physical configuration of patches in the environment, including a consideration of the matrix areas and corridors between them, will strongly influence the topology of a dispersal network. For example, ring networks are more likely to approximate a less disturbed, continuous habitat, such as a series of bays along a coastline, while disturbed habitats may force more long-distance dispersal. Second, the topology of a dispersal network will depend on the dispersal biology of the species in question, taking into account the dispersal kernel of the species (more long-distance dispersal may lead to more nonlocal network links), variation in dispersal distance by BT (Fraser et al. 2001), and the spatial scale at which habitats appear continuous. To a species with planktonic larvae, a series of bays may not approximate a ring network for dispersal. Finally, we must take into account the pattern of connections provided by human-aided transport vectors, since many invasive species are human dispersed (Lodge 1993; Mack et al. 2000; Sakai et al. 2001; Suarez et al. 2001; Floerl and Inglis 2005; Muirhead and MacIsaac 2005), and human transportation networks are designed to efficiently spread over wide areas, with few stops (Newman 2002; Guimera et al. 2005; Colizza et al. 2006). In order to predict invasion spread, we would need to know the propensity of the species or BTs in particular to be transported via human transportation networks (e.g., bolder individuals may be more likely to venture into human-dominated areas and into ships or airplanes).

Our model involves asocials spreading into empty patches, being followed later by socials that quickly increase density, leading to enhanced asocial dispersal. When taken to the logical conclusion, we are left with only social individuals. Our model presents no mechanism for long-term coexistence of BTs. Analogous work, however, both theoretical and empirical, has been done on the coexistence of life-history types in successional systems (McPeek and Holt 1992; Nee and May 1992; Tilman 1994). The existence of a competition-colonization trade-off in succession generally necessitates either ongoing disturbance to continually create new patches for recolonization by the dispersive type—here asocials (Hastings 1980; Sousa 1984; Nee and May 1992)—or spatial variation, which may offer asocials refuge from competitive exclusion. In an invasion context, the successional dynamics could lead to consistently biased misidentification of the traits shared by successful invasive species. If surveys of traits within populations of invasive species are not performed until the species has become successfully established as an invasive, then it is likely that the traits that actually facilitate spread would be missed. The classification of invasive species based on outcomes rather than process could lead to under- or overestimates of the invasiveness of potentially invasive species, depending on whether leading or following traits are more prevalent in a population. By correctly classifying species phenotypes as leading and following phenotypes, we may be able to better predict when a population is likely to quickly grow within a patch and which patches may be more vulnerable to control measures targeting certain behavioral phenotypes. Furthermore, by controlling which BTs are introduced into a population, we may be able to limit the likelihood of invasive spread.

Finally, we focused our attention on a dichotomous mix of a single behavioral axis in a landscape of identical patches connected in a variety of ways, but nature is much more complex. First, BTs are usually continuous, not categorical. With respect to our current model, populations with continuous behavioral variation are likely to spread even more quickly than dichotomous BTs, since we should expect to see a range of individuals that are well adapted to each density, with more limited distributions of types locally leading to faster growth in each patch. If each individual has some threshold dispersal density, then as local density increases, so should the social tendencies of dispersers. Thus, the pool of dispersers should be well equipped both to establish new populations and to reinforce growing nearby populations. In addition, animals vary not only in sociability but also in traits such as boldness, aggressiveness, and exploratory tendencies (Reale et al. 2007). Furthermore, habitats vary not only in population density but also along many ecological axes, including predation, competition, and resource availability.

Each combination of BT and ecological challenge is likely to produce a different pattern for how BT and ecological context interact to govern fitness and dispersal. If there are correlations between BT axes and if the distribution of ecological conditions in a patchy landscape is idiosyncratic, general patterns for the spread of invasions may be difficult to predict. If, however, consistent relationships exist between different behavioral axes, and if there are spatial autocorrelations between parameters in connected patches in a landscape, we anticipate that general, intuitively understandable predictions should emerge. A better understanding of how mixes of BTs interact with ecological conditions to influence the susceptibility of different environments to costly invasions is an important issue for further theoretical and empirical study.

Acknowledgments

Literature Cited

Barnard, C. J., and R. M. Sibly. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour 29:543–550.

Bergmüller, R., R. Schürch, and I. M. Hamilton. 2010. Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2751–2764.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161:1–28.

Clobert, J., J. F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Colautti, R. I., and H. J. MacIsaac. 2004. A neutral terminology to define "invasive" species. Diversity and Distributions 10:135–141.

Colizza, V., A. Barrat, M. Barthélemy, and A. Vespignani. 2006. The role of the airline transportation network in the prediction and predictability of global epidemics. Proceedings of the National Academy of Sciences of the USA 103:2015–2020.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119–1144.

Cote, J., and J. Clobert. 2007. Social personalities influence natal dispersal in a lizard. Proceedings of the Royal Society B: Biological Sciences 274:383–390.

Cote, J., A. Dreiss, and J. Clobert. 2008. Social personality trait and fitness. Proceedings of the Royal Society B: Biological Sciences 275: 2851–2858.

Cote, J., J. Clobert, T. Brodin, S. Fogarty, and A. Sih. 2010a. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philosophical Transactions of the Royal Society B: Biological Sciences 365:4065–4076.

Cote, J., S. Fogarty, T. Brodin, K. Weinersmith, and A. Sih. 2010b. Personality-dependent dispersal in the invasive mosquitofish: group composition matters. Proceedings of the Royal Society B: Biological Sciences, doi:10.1098/rspb.2010.1892.

Cote, J., S. Fogarty, K. Weinersmith, T. Brodin, and A. Sih. 2010c. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). Proceedings of the Royal Society B: Biological Sciences 277:1571–1579.

Dall, S. R. X., A. I. Houston, and J. M. McNamara. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters 7:734–739.

Denno, R. F., G. K. Roderick, K. L. Olmstead, and H. G. Dobel. 1991. Density-related migration in planthoppers (Homoptera: Delphacidae): the role of habitat persistence. American Naturalist 138:1513–1541.

DeWitt, T. J., A. Sih, and J. A. Hucko. 1999. Trait compensation and cospecialization in a freshwater snail: size, shape and antipredator behaviour. Animal Behaviour 58:397–407.

Dingemanse, N. J., and D. Reale. 2005. Natural selection and animal personality. Behaviour 142:1159–1184.

Dingemanse, N. J., C. Both, A. J. van Noordwijk, A. L. Rutten, and P. J. Drent. 2003. Natal dispersal and personalities in great tits (*Parus major*). Proceedings of the Royal Society B: Biological Sciences 270:741–747.

Dingemanse, N. J., C. Both, P. J. Drent, and J. M. Tinbergen. 2004. Fitness consequences of avian personalities in a fluctuating environment. Proceedings of the Royal Society B: Biological Sciences 271:847–852.

Duckworth, R. A. 2008. Adaptive dispersal strategies and the dynamics of range expansion. American Naturalist 172(suppl.):S4–S17.

Duckworth, R. A., and A. V. Badyaev. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proceedings of the National Academy of Sciences of the USA 104:15017–15022.

Duckworth, R. A., and L. E. B. Kruuk. 2009. Evolution of genetic integration between dispersal and colonization ability in a bird. Evolution 63:968–977.

Dyer, J. R. G., D. P. Croft, L. J. Morrell, and J. Krause. 2009. Shoal composition determines foraging success in the guppy. Behavioral Ecology 20:165–171.

Edelaar, P., A. M. Siepielski, and J. Clobert. 2008. Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. Evolution 62:2462–2472.

Enfjäll, K., and O. Leimar. 2005. Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxia*. Oikos 108:465–472.

———. 2009. The evolution of dispersal: the importance of information about population density and habitat characteristics. Oikos 118:291–299.

Floerl, O., and G. J. Inglis. 2005. Starting the invasion pathway: the interaction between source populations and human transport vectors. Biological Invasions 7:589–606.

Fonseca, D. M., and D. D. Hart. 1996. Density-dependent dispersal of black fly neonates is mediated by flow. Oikos 75:49–58.

Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. American Naturalist 158:124–135.

Guimera, R., S. Mossa, A. Turtschi, and L. A. N. Amaral. 2005. The worldwide air transportation network: anomalous centrality, community structure, and cities' global roles. Proceedings of the National Academy of Sciences of the USA 102:7794–7799.

Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology 18:363–373.

Hojesjo, J., J. Johnsson, and T. Bohlin. 2004. Habitat complexity reduces the growth of aggressive and dominant brown trout (*Salmo trutta*) relative to subordinates. Behavioral Ecology and Sociobiology 56:286–289.

Ioannou, C. C., and J. Krause. 2008. Searching for prey: the effects of group size and number. Animal Behaviour 75:1383–1388.

Ioannou, C. C., L. J. Morrell, G. D. Ruxton, and J. Krause. 2009. The effect of prey density on predators: conspicuousness and attack success are sensitive to spatial scale. American Naturalist 173:499–506.

Jeschke, J. M., and D. L. Strayer. 2005. Invasion success of vertebrates in Europe and North America. Proceedings of the National Academy of Sciences of the USA 102:7198–7202.

Johnson, J. C., and A. Sih. 2007. Fear, food, sex and parental care: a syndrome of boldness in the fishing spider (*Dolomedes triton*). Animal Behaviour 74:1131–1138.

Jokela, M., M. Elovainio, M. Kivimäki, and L. Keltikangas-Järvinen. 2008. Temperament and migration patterns in Finland. Psychological Science 19:831–837.

Kim, S. Y., R. Torres, and H. Drummond. 2009. Simultaneous positive and negative density-dependent dispersal in a colonial bird species. Ecology 90:230–239.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology & Evolution 16:199–204.

Krause, J., and G. Ruxton. 2002. Living in groups. Oxford University Press, Oxford.

Kun, A., and I. Scheuring. 2006. The evolution of density-dependent dispersal in a noisy spatial population model. Oikos 115:308–320.

Kuperman, M., and G. Abramson. 2001. Small world effect in an epidemiological model. Physical Review Letters 86:2909–2912.

Kurvers, R. H. J. M., H. H. T. Prins, S. E. van Wieren, K. van Oers, B. A. Nolet, and R. C. Ydenberg. 2009. The effect of personality on social foraging: shy barnacle geese scrounge more. Proceedings of the Royal Society B: Biological Sciences 277:601–608.

Lewis, M. A., and P. Kareiva. 1993. Allee dynamics and the spread of invading organisms. Theoretical Population Biology 43:141–158.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology & Evolution 8:133–137.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403–416.

McNamara, J. M., Z. Barta, and A. I. Houston. 2004. Variation in behaviour promotes cooperation in the prisoner's dilemma game. Nature 428:745–748.

McNamara, J. M., P. A. Stephens, S. R. X. Dall, and A. I. Houston. 2009. Evolution of trust and trustworthiness: social awareness favours personality differences. Proceedings of the Royal Society B: Biological Sciences 276:605–613.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140:1010–1027.

Moksnes, P. O. 2004. Interference competition for space in nursery habitats: density-dependent effects on growth and dispersal in juvenile shore crabs *Carcinus maenas*. Marine Ecology Progress Series 281:181–191.

Moyle, P. B., and M. P. Marchetti. 2006. Predicting invasion success: freshwater fishes in California as a model. BioScience 56:515–524.

Muirhead, J. R., and H. J. MacIsaac. 2005. Development of inland lakes as hubs in an invasion network. Journal of Applied Ecology 42:80–90.

Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. Journal of Animal Ecology 61:37–40.

Newman, M. E. J. 2002. Assortative mixing in networks. Physical Review Letters 89:208701.

Newman, M. E. J., and D. J. Watts. 1999. Scaling and percolation in the small-world network model. Physical Review E 60:7332–7342.

Pastor-Satorras, R., and A. Vespignani. 2001. Epidemic spreading in scale-free networks. Physical Review Letters 86:3200–3203.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52:273–288.

Pruitt, J. N., and S. E. Reichert. 2010. How within-group behavioural variation and task efficiency enhance fitness in a social group. Proceedings of the Royal Society B: Biological Sciences, doi: 10.1098/rspb.2010.1700.

Reale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews 82:291–318.

Rehage, J. S., and A. Sih. 2004. Dispersal characteristics and boldness: a comparison of *Gambusia* species of varying invasiveness. Biological Invasions 6:379–391.

Rehage, J. S., B. K. Barnett, and A. Sih. 2004. Behavioral responses to novel predation and competition in invasive mosquitofish and their non-invasive relatives (*Gambusia* sp.). Behavioral Ecology and Sociobiology 57:256–266.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, et al. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305–332.

Sih, A., and J. V. Watters. 2005. The mix matters: behavioural types and group dynamics in water striders. Behaviour 142:1417–1431.

Sih, A., A. M. Bell, J. C. Johnson, and R. E. Ziemba. 2004. Behavioral syndromes: an integrative overview. Quarterly Review of Biology 79:241–277.

Sih, A., D. I. Bolnick, B. Luttbeg, J. L. Orrock, S. D. Peacor, L. M. Pintor, E. Preisser, J. S. Rehage, and J. R. Vonesh. 2010. Predator-prey naivete, antipredator behavior, and the ecology of predator invasions. Oikos 119:610–621.

Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis. Behavioral Ecology 19:448–455.

Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs 49:227–254.

———. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353–391.

Stearns, S. C. 1976. Life-history tactics: review of ideas. Quarterly Review of Biology 51:3–47.

Suarez, A. V., D. A. Holway, and T. J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proceedings of the National Academy of Sciences of the USA 98:1095–1100.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Tollrian, R., and C. D. Harvell. 1998. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, NJ.

Travis, J. M. J., D. J. Murrell, and C. Dytham. 1999. The evolution of density-dependent dispersal. Proceedings of the Royal Society B: Biological Sciences 266:1837–1842.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511–523.

van Kleunen, M., W. Dawson, D. Schlaepfer, J. M. Jeschke, and M. Fischer. 2010. Are invaders different? a conceptual framework of comparative approaches for assessing determinants of invasiveness. Ecology Letters 13:947–958.

van Oers, K., G. de Jong, A. J. van Noordwijk, B. Kempenaers, and P. J. Drent. 2005. Contribution of genetics to the study of animal personalities: a review of case studies. Behaviour 142:1185–1206.

Vitousek, P. M., C. M. Dantonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21: 1–16.

Watts, D. J., and S. H. Strogatz. 1998. Collective dynamics of "small-world" networks. Nature 393:440–442.

Williamson, M., and A. Fitter. 1996. The varying success of invaders. Ecology 77:1661–1666.

Wolf, M., G. S. van Doorn, O. Leimar, and F. J. Weissing. 2007. Life-history trade-offs favour the evolution of animal personalities. Nature 447:581–584.