# The Role of Pleiotropy in the Evolutionary Maintenance of Positive Niche Construction

# Rebecca H. Chisholm,<sup>1,\*</sup> Brian D. Connelly,<sup>2</sup> Benjamin Kerr,<sup>2</sup> and Mark M. Tanaka<sup>1,†</sup>

1. School of Biotechnology and Biomolecular Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia; and Evolution and Ecology Research Centre, University of New South Wales, Sydney, New South Wales 2052, Australia; 2. Department of Biology and BEACON Center for the Study of Evolution in Action, University of Washington, Seattle, Washington 98195

Submitted September 6, 2017; Accepted January 25, 2018; Electronically published April 25, 2018 Online enhancements: appendix, Matlab code.

ABSTRACT: Organisms often modify their environments to their advantage through a process of niche construction. Environments that are improved through positive niche construction can be viewed as a public good. If free riders appear that do not contribute to the shared resource and therefore do not incur any associated costs, the constructed niche may become degraded, resulting in a tragedy of the commons and the extinction of niche constructors. Niche construction can persist if free riders are excluded, for example, if niche constructors monopolize the resource they produce to a sufficient degree. We suggest, however, that the problem of free riders remains because it is possible that nonniche constructors with an enhanced ability to access the resource appear and invade a population of constructors. Using mathematical models we show that positive niche construction can be maintained if it is inextricably linked to a mechanism that makes free riding costly, such as a trait that confers a benefit to only niche constructors. We discuss this finding in terms of genetic interactions and illustrate the principle with a two-locus model. We conclude that positive niche construction can both evolve and be maintained when it has other beneficial effects via pleiotropy. This situation may apply generally to the evolutionary maintenance of cooperation.

*Keywords:* niche construction, tragedy of the commons, public goods, pleiotropy, epistasis, cooperation.

#### Introduction

Organisms alter their environments in ways that can impact natural selection (Laland et al. 1996, 1999; Lewontin 1982, 1983, 2000; Odling-Smee et al. 2003). A canonical example is earthworms that change the structure and chemistry of the soil they live in, which enables them to retain aquatic characteristics in a seemingly nonaquatic environment (Hayes 1983). Another example is burrowing mammals whose complex burrowing systems modulate their fertility and mortality rates (Hansell 1984). In both of these examples, the modification of the environment—or niche construction—is beneficial to the organism so that, in addition to an evolutionary process of adapting to an environment, the environment is brought closer to the organism. This positive form of niche construction can evolve under a range of conditions, including in the absence of external natural selection (Odling-Smee et al. 2003), and may lead to unexpected ecological and evolutionary outcomes, such as the fixation of otherwise deleterious alleles (Laland et al. 1996).

When it is costly for organisms to improve their environment by, for instance, contributing to a shared resource, niche-constructing organisms are vulnerable to free riders who do not pay the cost of improving the environment but still draw benefits from the modified niche. In competition with niche-constructing organisms, free riders will rise in abundance (unless there is a mechanism for reducing the cost; see Kümmerli and Brown 2010). The shared resource then shrinks, precipitating the tragedy of the commons (Hardin 1968), whereby the resource becomes exhausted and the altruistic niche constructors become extinct. This raises an evolutionary problem of how positive niche construction can emerge and be maintained if it is constantly challenged by free riders or cheaters who take advantage of the constructive work of others without incurring any fitness penalty.

An analogous problem arises in economic sciences when determining how public goods can be maintained in the face of free riders (Dionisio and Gordo 2006). Economists have identified excludability as a general principle that can allow common goods to persist (Mankiw 2012). If free riders can be excluded from exploiting the shared resource, then the tragedy of the commons can be overcome. In the context of niche construction, if constructors and their offspring can monopolize the constructed niche to a sufficient extent, then niche construction can evolve (Krakauer et al. 2009). Monop-

<sup>\*</sup> Present address: PRISM, Centre for Epidemiology and Biostatistics, Melbourne School of Population and Global Health, University of Melbourne, Parkville 3010, Australia.

<sup>&</sup>lt;sup>†</sup> Corresponding author; email: m.tanaka@unsw.edu.au.

**ORCIDs:** Chisholm, http://dx.doi.org/0000-0002-7830-793X; Connelly, http://dx.doi.org/0000-0002-9948-0379.

Am. Nat. 2018. Vol. 192, pp. 000–000. © 2018 by The University of Chicago. 0003-0147/2018/19201-57937\$15.00. All rights reserved. DOI: 10.1086/697471

oly is an example of excludability in that niche constructors exclude current and future free riders by creating privileged access to the niche for themselves and their descendants. For instance, a spider's web is clearly monopolized by constructors and their offspring in the case of social spiders. Strong spatial structure (or degree of segregation of phenotypes) has also been shown to favor cooperation or positive niche construction (Werfel and Bar-Yam 2004; Silver and Di Paolo 2006; Rendell et al. 2011) and allow a population to avert the tragedy of the commons (Kerr et al. 2006; Eshelman et al. 2010; Bachmann et al. 2013). Similarly, under kin selection, transgenerational inheritance favors offspring and other relatives of niche constructors and thereby creates a degree of monopoly over the constructed niche, preventing the tragedy of the commons (Lehmann 2007; Van Dyken et al. 2011; Van Dyken and Wade 2012). A further possibility is the punishment of free riders (or enforcement of contribution to the common good), which can stabilize public goods when it is optional to participate in maintaining them (Hauert et al. 2007). Again, this is an example of excludability in that a cost is imposed on free riders when they try to access the public goods. Another setting where free riders may undermine common goods is in mutualistic interactions between species (Bronstein 2001).

Positive niche construction is thus supported by mechanisms for excluding free riders. In cases where organisms produce a resource that can easily be accessed by other individuals, exclusion of free riders may be difficult to achieve. For example, if a resource (such as the iron-scavenging siderophore molecules secreted by Pseudomonas aeruginosa) diffuses in the environment, privileged access to that resource is eroded (Griffin et al. 2004; Kümmerli et al. 2009). Similarly, quorum sensing may be vulnerable to cheaters, although empirical evidence suggests that kin selection may prevent cheaters (Van Dyken and Wade 2012). Even if producers enjoy most of the benefit of a resource they produce as it diffuses away, they may face competition with free riders that specialize in finding high-density areas of the resource. If free riders evolve from within niche-constructing lineages, they are less constrained by spatial structure or, like their ancestors, they may possess the ability to exclude other individuals. Even in the case where a strong monopoly is apparent, a nonconstructing stronger monopolizer could chase away or kill the constructor, as has been observed in orbweaving spiders, where mature males occasionally take over webs previously occupied by immature male conspecifics (Eberhard et al. 1978). Similarly, nonconstructors might appear that can manipulate constructors into unknowingly providing the benefits of the niche to free riders. An example of this is intraspecific nest parasitism, which has been recorded in many bird species (Yom-Tov 2001). Free riders may not only exclude niche constructors but also overcome attempts by others to exclude them. Therefore, exclusion can be only a partial explanation for the persistence of positive niche construction and requires another component to deal with the possibility of non-niche-constructing niche parasites.

In this study, we develop mathematical models to examine conditions under which positive niche construction can be maintained. We consider a mechanism of exclusion that is an alternative to monopoly and spatial effects, namely, that niche constructors are (or become) better adapted to the resource than free riders. For instance, constructors may be better or more efficient at utilizing the resource. However, here too the mechanism for exclusion (resource adaptation) can become separated from niche construction, leading to the tragedy of the commons. How then can niche construction become evolutionarily stable? We show that niche construction can emerge and persist when there is either an inextricable link between niche construction and a benefit that is unavailable to nonconstructors or else a similarly inseparable link between free riding and an additional cost that is not paid by constructors. We conclude that pleiotropic effects are possible mechanisms for the long-term maintenance of genes underlying costly positive niche construction.

#### Models

First, we present a phenotypic model of niche-constructing organisms that simultaneously captures the ecological dynamics of the population and the transformation of the niche. Second, we infer the evolutionary dynamics of the system from the conditions that support the invasion of rare mutants into the population once the niche construction trait is fixed and the niche has reached a steady state. Third, we consider a possible genetic mechanism that could maintain niche construction over evolutionary time using a two-locus population-genetics model. Matlab code used to generate all figures is included in the supplementary material (available online).

#### Phenotypic Model of Niche-Constructing Organisms

Consider an asexual population consisting of *T* types (or strains) with  $n_i$  individuals in type *i*, where i = 1, ..., T. The total population size is  $N = \sum_i n_i$ . Each type is associated with a niche-constructing effect  $\phi_i$ , which affects one aspect of the environment. We call this aspect of the environment the resource or constructed niche and track it through the variable *E*. The quantities *N*, *E*, and  $\phi_i$  are all nonnegative. Organisms compete with each other and consume the resource at a rate of  $\gamma$  per capita per unit resource. The environment is restored at rate  $\rho$  and decays at rate  $\delta$  per unit resource. The population increases according to a logistic growth model (with maximum growth rate *r* and carrying capacity *K*) in the absence of niche construction ( $\phi_i = 0$ ) and in the absence of the resource (*E* = 0), and

the niche-constructing activity comes with a fitness cost  $c\phi_i$ , where  $c \ge 0$ . A summary of the parameters and variables used throughout this study is provided in table 1.

The system evolves according to

$$\frac{dn_i}{dt} = \left[ r \left( 1 - \frac{N}{K} \right) + f_i(E) - c\phi_i \right] n_i, i = 1, ..., T,$$

$$\frac{dE}{dt} = N(\overline{\phi} - \gamma E) + \rho - \delta E,$$
(1)

where *t* is time (which we consider here to be continuous rather than discrete),  $\overline{\phi} = \sum_i \phi_i n_i / N$  is the average nicheconstructing effect of the population, and  $f_i(E)$  is a function of the environmental resource describing how *E* contributes to the growth rate of strain *i*. Throughout, we consider only positive niche construction so that  $f_i(E) \ge 0$ . Similar models have been considered by Odling-Smee et al. (2003) and Krakauer et al. (2009).

Krakauer et al. (2009) showed that niche constructors can outcompete nonconstructors by monopolizing the constructed niche to a sufficient degree. In terms of the model here,  $f_i(E)$  can be set to a function of this degree of monopoly to demonstrate that principle. For example, consider the case where organisms do not degrade the niche so that  $\gamma = 0$ . If an individual has a probability m of monopolizing its own niche and a probability 1 - m of exploiting another's niche, then monopoly can be represented by setting

$$f_i(E) = g\left[m\left(\frac{E_i}{n_i}\right) + (1-m)\left(\frac{E}{N}\right)\right]$$

where g > 0 is the efficiency of resource extraction,  $E_i/n_i$  is the per individual amount of monopolized niche available to type *i* individuals, E/N is the per individual amount of available nonmonopolizable niche,  $E = \sum_i E_i$  is the total amount of resource, and

$$\frac{dE_i}{dt} = \phi_i n_i + \frac{\rho}{T} - \delta E_i.$$

Here, however, we consider an alternative mechanism. Namely, organisms can evolve to be better adapted to the resource than others (without necessarily physically excluding other types). If  $a_i$  measures how well type i is adapted to the resource, we set

$$f_i(E) = a_i E$$

to be the contribution of the resource to the growth rate.

If all types are equally adapted to the resource so that  $a_i = a$  for all *i*, only the type with the lowest contribution to niche construction (the lowest  $\phi_i$ ) can survive, while all other strains are outcompeted (for the derivation of this result, see "Analysis of the Phenotypic Model" in the appendix, available online). In the extreme case, the free-rider strain with  $\phi_i = 0$  ultimately wins. This model setting therefore represents a tragedy of the commons: the environment (including the potential new niche) is undermined by free riders, but since they incur no cost, they dominate the population. Can positive niche construction evolve if organisms vary in their degree of adaptation to the resource?

Table 1: Parameter and variable definitions for models of niche construction

Parameter	Definition	
n <sub>i</sub>	Number of type <i>i</i> organisms	
Ε	Amount of resource	
t	Time	
Т	Total number of organism types	
Ν	Total organism population size	
$\phi_i$	Per capita rate of niche construction for type <i>i</i> organisms	
$a_i$	Degree of resource adaptation for type <i>i</i> organisms	
ρ	Background rate of resource generation	
δ	Background rate of resource degradation	
γ	Per capita rate of resource degradation due to organisms	
K	Carrying capacity of population in the absence of niche construction and the resource	
С	Fitness cost to construct $\phi_i$ units of the niche for type <i>i</i> organisms	
r	Maximum reproduction rate	
α	Growth benefit due to the pleiotropic effect of the niche construction allele $A^+$ on a second trait in the model with pleiotropy	
β	Growth benefit conferred by the $B^+$ allele in the model with pleiotropy	
3	Growth benefit due to synergistic epistasis between the A and B loci in the model with pleiotropy	

## **Population Dynamics**

We approach this question analytically through the twostrain case. If we consider only the population dynamics, then the system advances toward an equilibrium where either (1) strain 1 survives and strain 2 becomes extinct so that the final population size is  $\hat{n}_1 = (K/r)(r - c\phi_1 + a_1\hat{E})$  and the final total amount of resource satisfies  $\hat{E} > 0$ ; (2) strain 2 survives and strain 1 becomes extinct so that the final population size is  $\hat{n}_2 = (K/r)(r - c\phi_2 + a_2\hat{E})$  and the final total amount of resource satisfies  $\hat{E} > 0$ ; (3) both strains coexist so that the equilibrium population size is  $\hat{N} = K\{1 - c(\phi_1 a_2 - \phi_2 a_1)/[r(a_2 - a_1)]\}$  and the total amount of resource is  $\hat{E} = c(\phi_1 - \phi_2)/(a_1 - a_2)$ ; or (4) full extinction occurs (which is stable when  $r + a_i\rho/\delta - c\phi_i < 0$  for i = 1, 2).

The steady-state resource level of an unoccupied niche is  $\rho/\delta$  in the model. A colonized niche, on the other hand, that is inhabited by a single niche-constructing strain with final population size  $\hat{n}_i$  has a steady-state resource level of  $\hat{E}_i = (\rho + \phi_i \hat{n}_i)/(\delta + \gamma \hat{n}_i)$ , where the subscript *i* indicates the sole present strain. When  $\gamma > 0$ , this is an improvement on the unoccupied niche at equilibrium if

$$\frac{\phi_i}{\gamma} > \frac{\rho}{\delta},$$

while the niche is always improved if  $\gamma = 0$ . This overall positive effect on the niche attributable to the organisms also translates into an increased final size of the population since  $\hat{n}_i$  increases linearly with  $\hat{E}_i$ . The full expressions for  $\hat{n}_1$ ,  $\hat{n}_2$ ,  $\hat{E}_1$ , and  $\hat{E}_2$  in terms of the model parameters, along with the stability conditions for the special case  $\gamma = 0$  are provided in "Analysis of the Phenotypic Model."

#### **Evolutionary** Dynamics

To understand the evolutionary dynamics of this system, we ask when a rare mutant  $(n_2)$  can invade a strain  $(n_1)$  that is fixed and the environmental resource is at equilibrium so that  $E(0) = \hat{E}_1$ ,  $n_1(0) = \hat{n}_1$ , and  $n_2(0) \ll \hat{n}_1$ . The initial per capita growth rate of the rare mutant is approximately

$$r\left(1-\frac{\hat{n}_1}{K}\right)+a_2\hat{E}_1-c\phi_2=c\phi_1-a_1\hat{E}_1+a_2\hat{E}_1-c\phi_2,$$

which is positive when

$$\hat{E}_1(a_2 - a_1) > c(\phi_2 - \phi_1).$$
(2)

Hence, mutants with a greater ability to construct the niche invade when the benefits of niche construction outweigh the associated costs. From the invasion criterion, it follows that a strain with the highest level of resource adaptation and lowest level of construction would be evolutionarily stable to invasion by all mutants differing in these traits. Thus, if free riders can arise from lineages that are highly adapted to using the resource (so that  $a_2 = a_1$ ), the tragedy of the commons applies (this point is addressed further below).

We illustrate this result in figure 1A and 1B, which shows the outputs of several realizations of an invasion process whereby rare mutants with phenotype  $(a_2, \phi_2)$  successively appear and attempt to invade a single-strain population with phenotype  $(a_1, \phi_1)$ . During each simulation of the process, at each time step a rare mutant appears that, compared with the wild-type strain, differs incrementally in both its ability to construct the niche and its degree of resource adaptation so that  $a_2 = a_1 + \Delta a$  and  $\phi_2 = \phi_1 + \Delta \phi$ . We do not impose any constraints on the direction of phenotypic change of the mutants ( $\Delta a$ ,  $\Delta \phi$ ) so that the two traits can evolve freely. The success of the invasion is determined by numerically solving the system of equations (1) with T = 2,  $f_i(E) = a_i E$ ,  $n_1(0) =$  $\hat{n}_1, E(0) = \hat{E}_1$ , and  $n_2(0) = 1$  until equilibrium. Both the evolutionary trajectories of the successfully invading strains for each realization (fig. 1A) and the corresponding plots of the niche construction trait tracked through time (where time is measured in successful invasion events; fig. 1B) reveal that, in all realizations, the tragedy of the commons applies whereby niche construction is only transiently maintained and is eventually lost because of the appearance of free riders.

We can formally demonstrate these results by considering the population dynamics of two strains when they are (1) differing only in their ability to construct the niche  $\phi_i$ and (2) differing only in their extent of resource adaptation  $a_i$ . For the latter case, a linear stability analysis of the special case  $\gamma = 0$  reveals that the only linearly stable critical point is that where the strain with the highest level of resource adaptation  $a_i$  survives and the other becomes extinct, while for the former we see that strain competition leads to the strain with the lowest level of niche construction  $\phi_i$  driving the other to extinction (for the derivation of these results, see "Analysis of the Phenotypic Model"). Therefore, if  $a_i$  and  $\phi_i$  can evolve freely, the evolutionarily stable strategy is to have as high a value for  $a_i$  and as low a value for  $\phi_i$ as possible.

#### Overcoming the Tragedy of the Commons

Our analysis shows that the degree of adaptation to a constructed resource is a way to compensate for the cost of niche construction. Given independence between traits, this compensation itself is not enough to maintain niche construction over evolutionary time because compensation can occur without niche construction and therefore the evolutionarily stable strategy is the absence of niche construction. Here we



of the commons. Here,  $\gamma = 0$ , r = 2, c = 1,  $\beta = 1$ ,  $\delta = 1$ , K = 10. *C*, *D*. Direction of trait variation is constrained such that  $(\Delta a, \Delta \phi)$  is sampled from a bivariate normal distribution with mean vector (0, 0), variances (0.01<sup>2</sup>, 0.01<sup>2</sup>), and 0, 0.1, 0.2, 0.3, 0.4, and 0.5 correlation between  $\Delta a$  and  $\Delta \phi$ , which results in the maintenance of niche construction for high correlations. Here,  $\gamma = 0.1$ , r = 1.2, c = 0.4,  $\rho = 1$ ,  $\delta = 1.9$ , K = 10. In all cases, individual simulations are identified by line type. A, C, Evolutionary trajectory of a population starting with  $(a_1, \phi_1) = (0.2, 0.2)$  is shown. B, D, Niche construction trait as a function of the number of successful invasion attempts is shown. Successful invasions are found by numerically solving to construct the niche (with  $\phi_2 = \phi_1 + \Delta \phi$ ) and their degree of resource adaptation (with  $a_2 = a_1 + \Delta a$ ). A, B, Direction of trait variation is unconstrained, which results in the tragedy Figure 1: Single realizations of an invasion process where a stable single-strain population (with trait variables  $a_1$  and  $a_1$ ) is successively invaded by rare mutants differing in their ability the system of equations (1) with T = 2,  $f_i(E) = a_i E$ ,  $n_i(0) = \hat{n}_i$ ,  $E(0) = \hat{E}$ , and  $n_2(0) = 1$ , and simulations are stopped if the niche construction effect reaches 0.

This content downloaded from 138.251.169.163 on May 02, 2018 08:35:55 AM All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

consider another possibility for the evolution of positive niche construction.

Suppose that a trade-off exists between the two traits  $a_i$ and  $\phi_i$  such that adopting the strategy of free riding (low  $\phi_i$ ) comes at the cost of a detrimental change in the degree of resource adaptation (reduced  $a_i$ ). This models the situation, for example, where an organism that does not contribute to its environment also uses resources in a wasteful manner. Or perhaps a trade-off applies such that adopting the evolutionarily unstable strategy of niche construction (high  $\phi_i$ ) comes with the additional benefit of an increased degree of adaptation to the resource (increased  $a_i$ ). For instance, organisms that construct their niche well may also use that niche well because of physical constraints. If mutants can overcome the cost of niche construction through increased adaptation to the constructed niche, then positive evolutionary feedback could emerge, leading to a further improved environment and a better resource-adapted organism. This requirement, however, depends on a strong enough trade-off between free riding and adaptation to the resource (or a strong positive relationship between niche construction and adaptation) to prevent the appearance of mutants with a high  $a_i$  and low  $\phi_i$ . In other words, the trait space must be restricted by some mechanism to exclude the subset of potential invaders with high  $a_i$  and low  $\phi_i$ .

The invasion criterion (eq. [2]) informs us on the type of trade-off that could support the maintenance of niche construction. First, the trade-off must impinge on the direction of trait variation in the  $(a_i, \phi_i)$  trait space so that mutations are expected to result in only positively correlated changes in  $a_i$  and  $\phi_i$  so that  $(a_2 - a_1)/(\phi_2 - \phi_1) > 0$ (where the subscript 2 refers to the mutant strain and the subscript 1 to the resident strain). Second, the expected gain in the degree of resource adaptation due to an increase in the degree of niche construction must be large enough so that, on average, the invasion criterion (eq. [2]) holds true. In this case, and when the positive correlation is strong enough, then the trade-off between  $a_i$  and  $\phi_i$  is expected to prevent the invasion of free-riding mutants into a population of niche constructors.

We demonstrate this result with our stochastic evolutionary model by imposing a bias in the direction of trait variation in rare mutants. Now the change in trait values of rare mutants ( $\Delta a$ ,  $\Delta \phi$ ) are sampled from a bivariate normal distribution with a positive correlation between  $\Delta a$  and  $\Delta \phi$  and with a sufficiently large ratio  $\sigma_a/\sigma_{\phi}$  of the individual trait standard deviations (which scales the changes in trait values relative to each other) to expect that niche construction will be maintained when a strict correlation is imposed. Simulations of this constrained model (fig. 1*C*, 1*D*) reveal that niche construction can be maintained over evolutionary time if the correlation between the two traits is strong enough. However, if a reduced ratio of trait standard deviations is initially imposed, then the majority of model realizations end in the tragedy of the commons, irrespective of the correlation (see fig. 2).

When the correlation between the changes in the two traits is strong, sampling  $(\Delta a, \Delta \phi)$  from the bivariate normal distribution in the stochastic evolutionary model is comparable to constraining the resource adaptation level  $a_i$  to be an increasing linear function of niche construction ability  $\phi_i$  so that, for instance,  $a_i = a(\phi_i) = \eta \phi_i$ , where  $\eta > 0$ . When a deterministic function is used in this way to model the trade-off between  $a_i$  and  $\phi_i$ , the equilibrium level of the resource then becomes a function of  $\phi_i$ , so that  $\hat{E}_i = \hat{E}(\phi_i)$ , which allows us to further explore the conditions that support the competitive exclusion of free riders in the long run.

Suppose that  $\phi_2 > \phi_1$ . If the fitness gain due to increasing the degree of adaptation to the resource relative to the associated change in niche construction outweighs the cost of niche construction so that

$$\hat{E}(\phi_1)\left(\frac{a(\phi_2)-a(\phi_1)}{\phi_2-\phi_1}\right)>c,$$

then according to the invasion criterion (eq. [2]) the amount of niche construction will increase over evolutionary time. In the limit as  $\phi_2 - \phi_1 \rightarrow 0$ , this last condition becomes

$$\hat{E}(\phi_1)\frac{da}{d\phi_1}>c.$$

Now suppose  $\phi_2 < \phi_1$ . If the fitness loss due to decreasing the degree of adaptation to the resource relative to the associated change in niche construction is outweighed by the cost of niche construction such that

$$\hat{E}(\phi_1)\left(\frac{a(\phi_2)-a(\phi_1)}{\phi_2-\phi_1}\right) < c,$$

then niche construction will decrease over evolutionary time. In the limit as  $\phi_1 - \phi_2 \rightarrow 0$ , this last condition is equivalent to

$$\hat{E}(\phi_1)\frac{da}{d\phi_1} < c.$$

If we consider again the case where the resource adaptation level  $a_i$  is a linear function of  $\phi_i$ , so that  $a(\phi_i) = \eta \phi_i$  and  $da/d\phi_i = \eta$ , the condition for increasing levels of positive niche construction evolving becomes  $\hat{E}(\phi_i)\eta > c$ .

While the sign of  $\hat{E}(\phi_i) da/d\phi_i - c$  dictates the direction of evolutionary change, the final evolutionary outcome is



simulation are  $a_1 = 0.25$  and  $\phi_1 = 0.2$  so that the initial rate of change of  $a_i$  per unit of  $\phi_i$  required for niche construction to be maintained (as determined by the invasion criterion (eq. [2]) is approximately 0.22. When the ratio of standard deviations  $\sigma_a/\sigma_o$  is below this threshold, the tragedy of the commons is expected to occur no matter the strength of the cor-Figure 2: Frequency plots of the fraction of 40 realizations of the stochastic invasion process that end in the tragedy of the commons. Changes in the traits ( $\Delta a$ ,  $\Delta \phi$ ,) of rare mutants are selected from a bivariate normal distribution with mean (0, 0), the correlation shown along the horizontal axis of each plot with columns corresponding to the correlations  $(0.01, 0.1, 0.2, 0.3, \dots, 0.9)$ , and the variances  $(\sigma_{\alpha}^2, \sigma_{\beta}^2)$  differing between plots so that  $\sigma_a/\sigma_{\delta} = 0.1$  (A),  $\sigma_a/\sigma_{\delta} = 0.2$  (B),  $\sigma_a/\sigma_{\delta} = 0.3$  (C), and  $\sigma_a/\sigma_{\delta} = 0.6$  (D). Initial trait values of each relation between the two traits. However, when the ratio is above this threshold and the correlation is sufficiently strong, niche construction is expected to be maintained. Here,  $\sigma_a = 0.01$ ,  $\gamma = 0.1, r = 1.2, c = 0.4, \rho = 1, \delta = 1.9, \text{ and } K = 100.$ 

This content downloaded from 138.251.169.163 on May 02, 2018 08:35:55 AM All use subject to University of Chicago Press Terms and Conditions (http://www.journals.uchicago.edu/t-and-c).

further determined by the local behavior of critical points  $\phi_i = \hat{\phi}$  that satisfy

$$\left[\hat{E}(\phi_i)\frac{da}{d\phi_i}\right]_{\phi_i=\hat{\phi}} = c.$$

For instance, consider the case where  $\hat{E}(\phi_i)da/d\phi_i$  has a positive slope at the critical point  $\phi_i = \hat{\phi}$ . For values of  $\phi_i$  just above the critical point (at  $\phi_i = \hat{\phi} + \epsilon$ , where  $0 < \epsilon \ll 1$ ),  $\hat{E}(\phi_i)da/d\phi_i$  will be greater than *c* and so evolution will drive  $\phi_i$  away from the critical point toward higher values, while just below the critical point (at  $\phi_i = \hat{\phi} - \epsilon$ ),  $\hat{E}(\phi_i)da/d\phi_i < c$  and again evolution will drive  $\phi_i$  away from the critical point at  $\phi_i = \hat{\phi} - \epsilon$ ) are critical point toward lower values. Hence, a critical point at  $\phi_i = \hat{\phi}$  is locally unstable if

$$\left[\frac{d}{d\phi_i}\left(\hat{E}(\phi_i)\frac{da}{d\phi_i}\right)\right]_{\phi_i=\phi} > 0.$$
(3)

In the same way, it can be shown that if

$$\left[\frac{d}{d\phi_i}\left(\hat{E}(\phi_i)\frac{da}{d\phi_i}\right)\right]_{\phi_i=\phi} < 0, \tag{4}$$

the critical point is locally stable.

We illustrate these results in figure 3, where we show the outputs of our stochastic evolutionary model with the phenotype of organisms constrained so that their degree of adaptation to the resource  $a_i = a(\phi_i)$  is a function of their niche construction ability  $\phi_i$ . Now, the change in niche construction ability,  $\Delta \phi$ , of rare mutants compared with the wild-type strain is sampled from a normal distribution with mean 0 and standard deviation  $\sigma_{\phi}$  so that there is no underlying bias in the direction of phenotypic change. Results are shown for three different functions that model the degree of adaptation to the resource. In figure 3A-3C, the choice of *a* results in the existence of only one critical point (for the values of  $\phi_i$  considered) such that  $E(\phi_i)da/d\phi_i$  is decreasing at the critical point, as indicated by the square in figure 3A. The average level of niche construction (where the average is taken over 20 simulations of the invasion process) tracked through time (fig. 3B) converges toward the critical point from both above and below, indicating that the critical point is an evolutionarily stable strategy. In figure 3D-3F, again the choice of *a* results in the existence of only one critical point, but this time  $\tilde{E}(\phi_i) da/d\phi_i$  is increasing at the critical point, as indicated by the triangle in figure 3D. Here, the average level of niche construction tracked through time (fig. 3E) diverges away from the critical point from both above and below, indicating that the critical point is unstable. In this case, our model results in the niche construction ability of the organism evolving toward increasingly higher values if the initial resident strain's niche construction ability is high enough (so that  $\phi_1 > \hat{\phi}$ ). Otherwise, niche construction occurs only transiently and is eventually lost because of the appearance of free riders (fig. 3*E*). Finally, in figure 3*G*-3*I*, two critical points arise from the choice of *a*, the lower of which satisfies condition (4), and the other satisfies condition (3). As expected, below the higher critical point, the level of niche construction in our model converges toward the stable lower critical point, while from above the upper critical point, the niche construction ability of the organisms diverges.

# A Two-Locus Haploid Model

The analysis above shows that when a suitable trade-off exists between a niche construction trait and a trait that compensates for the cost of niche construction, the tragedy of the commons may be averted. However, a trade-off between two complex traits that affects an organism's fitness can be maintained only through evolutionary time if there is a genetic basis for that trade-off (Stearns 1977, 1989). What genetic mechanism could impose such a correlation between niche construction and this cost compensation? If there is a gene for each trait, close physical linkage may result in a transient correlation, although eventually recombination or mutation would separate the two alleles of interest. The most extreme form of a connection between two traits occurs when they are controlled by a single gene; in this case, we propose that positive niche construction can be maintained by a niche constructor allele that has pleiotropic effects on another favored trait so that if the niche construction ability is lost, so too is that other trait. Here we consider a two-locus model to explore these ideas.

Consider an isolated population of asexual haploid organisms, defined at two diallelic loci, A and B, with four possible haplotypes: (1)  $A^-B^-$ , (2)  $A^+B^-$ , (3)  $A^-B^+$ , and (4)  $A^+B^+$ . Let  $A^+$  confer the ability to niche construct, and let  $B^+$  confer compensation of the cost of niche construction so that the haplotype  $A^+B^+$  represents niche constructors compensated for the cost of constructing,  $A^+B^-$  represents noncompensated niche constructors, and free riding corresponds to the haplotypes  $A^-B^+$  and  $A^-B^-$ . The numbers of the four types of individuals with these haplotypes in the population are, respectively,  $n_1$ ,  $n_2$ ,  $n_3$ , and  $n_4$  so that the population size is  $N = \sum_i n_i$ . The dynamics are driven by competition among the four haplotypes, which can be modeled with the following ordinary differential equations:

$$\frac{dn_i}{dt} = R_i n_i, i = 1, \dots, 4, \tag{5}$$

$$\frac{dE}{dt} = (n_2 + n_4)\phi + \rho - (\delta + \gamma N)E, \qquad (6)$$

where t is time, E is the amount of resource,  $R_i$  is the growth rate of individuals with haplotype i, and all other parameters are defined as in table 1. Rather than numerically analyzing the dynamics, we will simply discuss conditions under which the niche construction allele can be maintained in a genetic system in light of the phenotypic model.

First, we show with this model how separating niche construction from cost compensation can lead to the trag-

edy of the commons. Let f(E) be the fitness advantage of using the constructed niche. To illustrate the effect of cost compensation in a two-locus system, we assume that all haplotypes have the same fitness advantage f(E) of using the niche. The growth rates of individuals with each haplotype (given in table 2) are chosen such that only niche constructors with the compensatory allele (with haplotype  $A^+B^+$ ) are able to neutralize the cost of niche construction so that  $R_1 = R_3 = R_4 > R_2$ . This leads to a neutrally unsta-



**Figure 3:** When the degree of resource adaptation *a* is a deterministic function of the niche construction ability  $\phi_i$ , the evolutionary outcome is determined by the sign of  $d/d\phi(\hat{E}_i da/d\phi_i)$  at the critical points where  $\hat{E}_i da/d\phi_i = c$ . *A*, *D*, *G*,  $\hat{E}_i da/d\phi_i - c$  is shown as a function of  $\phi$ . Here, arrows indicate the direction of evolutionary change, triangles correspond to locally unstable critical points, and squares correspond to locally stable critical points. *B*, *E*, *H*, Niche construction ability  $\phi_i$  of the organisms averaged over 20 simulations of the stochastic invasion process is shown as a function of the number of invasion attempts. *C*, *F*, *I*,  $\hat{E}_i da/d\phi_i$  averaged over 20 simulations of the stochastic invasion process is shown as a function of the number of invasion attempts. *A*–*C*, When  $a(\phi_i) = 1 - 0.3(\phi_i - 1)^2$  (for  $\phi_i < 1$ ), niche construction is maintained because at the critical point,  $d/d\phi(\hat{E}_i da/d\phi_i) < 0$ , and hence the critical point is stable. *D*–*F*, When  $a(\phi_i) = 1 + 0.3\phi_i^2$  (for  $\phi_i > 0$ ), the critical point is unstable because at the critical point,  $d/d\phi(\hat{E}_i da/d\phi_i) > 0$ . Hence, niche construction is maintained if the initial resident strain has a niche construction ability greater than that at the critical point  $\phi_i = \hat{\phi}$ , otherwise the tragedy of the commons applies. *G*–*I*, When  $a(\phi_i) = 1/2[1 + (\phi_i - 1)^3]$  (for  $\phi_i > 0$ ), two critical points exist and niche construction is maintained at a level determined by the initial value of  $\phi_i$  with respect to the lower critical point. Here, r = 1.2, K = 10, c = 0.4,  $\rho = 1$ ,  $\delta = 1.9$ ,  $\gamma = 0.1$ .

Haplotype	Number	Growth rate
$A^{-}B^{-}$	$n_1$	$R_1 = r\left(1 - \frac{N}{K}\right) + f(E)$
$A^+B^-$	<i>n</i> <sub>2</sub>	$R_2 = r\left(1 - \frac{N}{K}\right) + f(E) - c\phi$
$A^-B^+$	<i>n</i> <sub>3</sub>	$R_3 = r\left(1 - \frac{N}{K}\right) + f(E)$
$A^+B^+$	$n_4$	$R_4 = r\left(1 - \frac{N}{K}\right) + f(E)$

 Table 2: Growth rates of haplotypes in the simple compensation model

ble system where the  $A^+B^-$  haplotype is eliminated and the  $A^+B^+$  haplotype does not remain stably fixed. Through mutation and genetic drift, the niche-constructing type  $A^+B^+$  can be replaced by nonniche constructors  $A^-B^+$  or  $A^-B^-$ . If the compensatory allele  $B^+$  already brings benefits in the absence of niche construction so that  $R_3 > R_1 = R_4 > R_2$ , then the haplotype  $A^-B^+$  will have the highest fitness ( $R_3$ ) and niche construction is outcompeted. Hence, when the niche construction trait and cost compensation trait are controlled by different loci, the tragedy of the commons applies.

## Pleiotropy Maintains Positive Niche Construction

Now let the niche construction locus *A* influence another trait pleiotropically. The second trait is also influenced by a second locus *B*. Here, allele  $A^+$  confers niche construction, the cost of niche construction, and an additional benefit  $\alpha > 0$  because of its effect on the second trait, while allele  $B^+$  confers benefit  $\beta > 0$  so that  $R_3 > R_1$  and  $R_4 > R_2$ . We also allow a synergistic interaction between loci (epistasis) to produce an additional benefit of  $\varepsilon \ge 0$  for the  $A^+B^+$  haplotype.

Under this model, positive niche construction is locked in with haplotype  $A^+B^+$  provided that  $\alpha + \varepsilon - c\phi > 0$  as seen by comparing growth rates of haplotypes, given in table 3 and illustrated in figure 4. Initial numerical exploration of an extended model suggests that these results hold when recombination can occur (for a description of this extended model and additional numerical results, see "Model Extension Incorporating Recombination"; fig. A1, available online). Therefore, positive niche construction is maintained if (1) the pleiotropic effect of the niche-constructing allele is strong enough so that  $R_2 > R_1$  and  $R_4 > R_3$  (fig. 5A-5D), (2) the synergistic epistasis is strong enough so that  $R_4 > R_3$  even though  $R_1 > R_2$  (fig. 5E), or (3) both the pleiotropic and synergistic epistasis effects are strong enough so that  $R_4 > R_3$ and  $R_2 > R_1$  (fig. 5A-5D). When neither the pleiotropic effect of the niche-constructing allele nor the synergistic epistasis effect are strong enough so that  $R_3 > R_4$  and  $R_1 > R_2$ , then the tragedy of the commons applies (fig. 5F, 5G).

In the case of the epistasis, the additional growth benefit arises from the pleiotropic contribution made by the nicheconstructing allele to the second trait. Indeed, comparing the growth rates of  $A^-B^-$  and  $A^+B^-$ , the second locus is not needed if the (additive) pleiotropic effect  $\alpha$  of locus Aby itself outweighs the cost  $c\phi$ . Therefore, pleiotropy can promote the long-term maintenance of positive niche construction.

#### Discussion

Positive niche construction is potentially fragile in that it can be eliminated when a cheater that pays zero cost appears and outcompetes the niche constructors. It is not obvious how niche construction can persist over evolutionary time when faced with such free riders. Available explanations center on niche constructors being able to compensate for the cost of their altruism by, in part, excluding free riders from the benefits of the constructed niche (Silver and Di Paolo 2006; Lehmann 2007; Krakauer et al. 2009). We offer another similar explanation here: that niche constructors are better adapted to the resource. For example, Pseudomonas aeruginosa requires specific outer membrane transporters to internalize ferric-siderophore complexes (Voulhoux et al. 2006). If siderophore producers also have a considerably higher level of expression of these membrane transporters than nonproducers, then we would ex-

 Table 3: Growth rates of haplotypes in the model with pleiotropy

Haplotype	Number	Growth rate
$A^-B^-$	$n_1$	$R_1 = r\left(1 - \frac{N}{K}\right) + f(E)$
$A^+B^-$	<i>n</i> <sub>2</sub>	$R_2 = r\left(1 - \frac{N}{K}\right) + f(E) - c\phi + \alpha$
$A - B^+$	<i>n</i> <sub>3</sub>	$R_3 = r\left(1 - \frac{N}{K}\right) + f(E) + \beta$
$A^+B^+$	$n_4$	$R_4 = r\left(1 - \frac{N}{K}\right) + f(E) - c\phi + \alpha + \beta + \varepsilon$



**Figure 4:** Genetic interactions in a model of niche construction with pleiotropy and epistasis affecting other traits. This schematic illustrates the action of genes in the two-locus model presented in table 3. Here, the niche construction allele A+ contributes to niche construction through parameter  $\phi$ , but this ability incurs cost c. The allele also pleiotropically affects another trait, conferring benefit  $\alpha$ . The other trait confers an additional benefit  $\beta$  in the presence of allele B+ at the second locus. The alleles A+ and B+ produce benefit  $\varepsilon$  together through epistatic interaction.

pect these producers to be better adapted to using the resource because of their increased uptake rate and thus be able to outcompete cheaters. However, these explanations all suffer from the problem that the niche-constructing trait can become separated from any mechanism that compensates for the cost of niche construction. In the case of adaptation to the resource, when the niche construction and adaptation traits are independent, highly adapted free riders can prevent the maintenance of positive niche construction.

Here we hypothesize that if genes influencing nicheconstructing abilities have pleiotropic effects on other traits so that free riding becomes costly, then niche construction can be maintained in the long run. For example, if a cheater mole loses its ability to dig a burrow, it is possible that the free rider is also compromised in its ability to forage efficiently for earthworms. A more concrete example is the coregulation of genes involved in siderophore synthesis and uptake through the repressor protein FUR. If mutations in such regulators compromise production, they would also compromise regulation of uptake (Visca et al. 2007). Any protein complex influencing multiple systems, including complexes of factors regulating transcription, would similarly be subject to mutations with multiple pleiotropic effects. These are examples of bow tie architectures that are widespread in nature and have been noted to promote robustness (Kitano 2004). We note that even in such cases, rare combinations of mutations could conceivably unlink positive niche construction from other traits. We nevertheless propose that pleiotropic effects associated with niche construction may constrain evolution so that free riders cannot emerge.

Pleiotropy is viewed as an impediment to adaptation because the speed of adaptation, which scales with the inverse of the degree of pleiotropy, is reduced on average by deleterious pleiotropic effects (Orr 2000; Welch et al. 2003; Otto 2004; Guillaume and Otto 2012). Thus, genomes might have evolved in a way to minimize pleiotropy or to contain pleiotropic effects within modules (Wang et al. 2010). However, pleiotropy is favored under weak functional trade-offs between traits, which may explain the general persistence of pleiotropy (Guillaume and Otto 2012). In this study, we propose that deleterious pleiotropic effects offer the benefit of preventing the invasion of free riders. Our hypothesis implies that niche construction and cost compensation persist together when they are linked through pleiotropy. It is possible that this advantage in turn contributes to the persistence of pleiotropy; models such as those of Guillaume and Otto (2012), which consider the evolution of pleiotropy through modifier loci, could be further explored to study the potential role of niche construction.

In many cases, it is unrealistic to expect a single gene to control multiple sophisticated functions: many genes are likely to contribute to the ability to build nests or dams. Thus, many instances of niche construction may be underpinned by complex interactions between genes and traits, a relatively simple example of which is shown in figure 4. A corollary of our hypothesis is that simpler instances of niche construction tend to be fragile. That is, if a single gene and trait are responsible for a niche construction trait, it is easier for zero-cost paying mutants to appear and invade. One would also expect that the kinds of niche construction found in nature would tend to be the ones that are robust and underpinned by complex interactions between genes and traits, since fragile cases with simpler genetic interactions tend to be destroyed through evolutionary time, leaving behind only robust examples. An empirical test of our



**Figure 5**: Single realizations of an invasion process where a single-haplotype population (with initial haplotype  $A^{-}B^{-}$ ) is invaded by rare mutants at a rate  $\mu N$ , where  $\mu$  is the mutation  $A^+B^-$  or  $A^-B^+$  (with equal probability  $n_4/(2N)$ ). Both N and  $n_i$  are calculated at the time of invasion. In all panels, the sizes of the haplotype populations  $n_i$  are shown as a function of time ergistic epistasis is strong enough (E), or both the pleiotropic effect of the niche-constructing allele and synergistic epistasis is strong (A-D). F-G. Free-rider strains invade because neither rate of the population set here to be  $10^{-6}$  mutations per gene per unit time. Mutations occur at exponentially distributed time intervals (with rate parameter  $\mu N$ ) and result in either  $A^{-}B^{-} \rightarrow A^{+}B^{-}$  or  $A^{-}B^{+}$  (with equal probability  $n_{1}/(2N)$ ),  $A^{+}B^{-} \rightarrow A^{-}B^{-}$  or  $A^{+}B^{+}$  (with equal probability  $n_{2}/(2N)$ ),  $A^{-}B^{+} \rightarrow A^{-}B^{-}$  or  $A^{+}B^{+}$  (with equal probability  $n_{3}/(2N)$ ), or  $A^{+}B^{+} \rightarrow A^{-}B^{-}$  or  $A^{+}B^{+}$  (with equal probability  $n_{3}/(2N)$ ), or  $A^{+}B^{+} \rightarrow A^{-}B^{-}$  or  $A^{+}B^{+}$  (with equal probability  $n_{3}/(2N)$ ), or  $A^{+}B^{+} \rightarrow A^{-}B^{-}$  or  $A^{+}B^{+}$  (with equal probability  $n_{3}/(2N)$ ), or  $A^{+}B^{+} \rightarrow A^{-}B^{-}$  or  $A^{+}B^{+}$  (with equal probability  $n_{3}/(2N)$ ). since the beginning of the invasion process t. A–E. Niche construction strains invade because either the pleiotropic effect of the niche-constructing allele is strong enough (A–D), the syn- $= 100, r = 1.5, c = 2, \rho = 1, \delta = 1.9, \gamma = 0.1, a = 2, \alpha = 1; \phi = 1, \sigma = 1, \sigma$  $0.25, \beta = 0.6, \varepsilon = 0.2, (A, B); \phi = 0.25, \beta = 0.4, \varepsilon = 0.2, (C, D); \phi = 0.55, \beta = 0.4, \varepsilon = 0.2, (B; \phi = 0.55, \beta = 0.4, \varepsilon = 0.05, (B; \phi = 0.55, \beta = 0.02, \varepsilon = 0.05, (G).$ he pleiotropic effect of the niche-constructing allele nor the synergistic epistasis is strong enough. Parameter set: K

The problems we have highlighted with positive niche construction generally apply to the evolutionary maintenance of cooperation and mutualism. Cooperation is expected to be lost eventually, unless there is a mechanism to bind cooperation to the ability to outcompete defectors (or cheaters). Hammarlund et al. (2016) have suggested such a mechanism: if cooperator alleles create conditions by which they improve the chances of producing adaptive genetic changes elsewhere in the genome, they can hitchhike to fixation with those adaptive changes. This has been termed the Hankshaw effect. Connelly et al. (2016) have further suggested that the opportunities for adaptation and hitchhiking are continually renewed if organisms alter the environment through negative niche construction (Laland et al. 1999). Cooperators thus beat defectors by generating beneficial mutations faster to stay ahead on an evolutionary treadmill. The analogous problem of cheaters also appears in mutualistic interactions where cooperation occurs between species (Bronstein 2001). A mutualist constructs its niche by benefiting another species, which in turn benefits the first species, and here again this interaction is vulnerable to cheaters that gain benefits without contributing to the symbiosis. As a solution to this problem, Ferriere et al. (2002) proposed that an asymmetry in competition prevents the invasion of cheaters. Here, we have explored an alternative mechanism in the context of positive niche construction, namely, that cooperators are bound to the ability to exclude defectors through pleiotropic effects in underlying genes or control sequences. In cellular systems, cooperation without public goods has been found to be bolstered by pleiotropic connections between cheating and personal costs (Queller et al. 2003; Foster et al. 2004). For example, in the social amoeba Dictyostelium discoideum, the pleiotropic effects of the gene *dimA* limit cheating by ensuring cells that defect from stalk formation are competitively excluded from contributing to the next generation (Foster et al. 2004). Protection of cooperative traits through pleiotropic connections is also found in cellular systems where cooperation involves the production of public goods (Dandekar et al. 2012) and is stabilized further when the individual cost of the cooperative trait is small (Mitri and Foster 2016). Genetic interaction, therefore, may play a key role in the maintenance of altruistic traits.

# Acknowledgments

We thank Kevin Laland for discussions and encouragement, Mike Kasumovic for discussions about spider behavior, and Jai Tree for discussions about bacterial gene regulation. We gratefully acknowledge support from the Australian Research Council (grant FT140100398 to M.M.T.) and the University of New South Wales.

#### Literature Cited

- Bachmann, H., M. Fischlechner, I. Rabbers, N. Barfa, F. B. dos Santos, D. Molenaar, and B. Teusink. 2013. Availability of public goods shapes the evolution of competing metabolic strategies. Proceedings of the National Academy of Sciences of the USA 110:14302–14307.
- Bronstein, J. L. 2001. The exploitation of mutualisms. Ecology Letters 4:277–287.
- Connelly, B. D., K. J. Dickinson, S. P. Hammarlund, and B. Kerr. 2016. Negative niche construction favors the evolution of cooperation. Evolutionary Ecology 30:267–283.
- Dandekar, A. A., S. Chugani, and E. P. Greenberg. 2012. Bacterial quorum sensing and metabolic incentives to cooperate. Science 338:264– 266.
- Dionisio, F., and I. Gordo. 2006. The tragedy of the commons, the public goods dilemma, and the meaning of rivalry and excludability in evolutionary biology. Evolutionary Ecology Research 8:321–332.
- Eberhard, W. G., M. Barreto, and W. Pfizenmaier. 1978. Web robbery by mature male orb-weaving spiders. Bulletin of the British Arachnological Society 4:228–230.
- Eshelman, C. M., R. Vouk, J. L. Stewart, E. Halsne, H. A. Lindsey, S. Schneider, M. Gualu, A. M. Dean, and B. Kerr. 2010. Unrestricted migration favours virulent pathogens in experimental metapopulations: evolutionary genetics of a rapacious life history. Philosophical Transactions of the Royal Society B 365:2503–2513.
- Ferriere, R., J. L. Bronstein, S. Rinaldi, R. Law, and M. Gauduchon. 2002. Cheating and the evolutionary stability of mutualisms. Proceedings of the Royal Society B 269:773–780.
- Foster, K. R., G. Shaulsky, J. E. Strassmann, D. C. Queller, and C. R. Thompson. 2004. Pleiotropy as a mechanism to stabilize cooperation. Nature 431:693–696.
- Griffin, A. S., S. A. West, and A. Buckling. 2004. Cooperation and competition in pathogenic bacteria. Nature 430:1024–1027.
- Guillaume, F., and S. P. Otto. 2012. Gene functional trade-offs and the evolution of pleiotropy. Genetics 192:1389–1409.
- Hammarlund, S. P., B. D. Connelly, K. J. Dickinson, and B. Kerr. 2016. The evolution of cooperation by the Hankshaw effect. Evolution 70:1376–1385.
- Hansell, M. H. 1984. Animal architecture and building behaviour. Longman, New York.
- Hardin, G. 1968. The tragedy of the commons. Science 162:1243-1248.
- Hauert, C., A. Traulsen, H. Brandt, M. A. Nowak, and K. Sigmund. 2007. Via freedom to coercion: the emergence of costly punishment. Science 316:1905–1907.
- Hayes, M. H. B. 1983. Darwin's "vegetable mould" and some modern concepts of humus structure and soil aggregation. Pages 19–33 *in* J. E. Satchell, ed. Earthworm ecology: from Darwin to vermiculture. Chapman & Hall, London.
- Kerr, B., C. Neuhauser, B. J. Bohannan, and A. M. Dean. 2006. Local migration promotes competitive restraint in a host-pathogen "tragedy of the commons." Nature 442:75–78.
- Kitano, H. 2004. Biological robustness. Nature Reviews Genetics 5: 826-837.

## 000 The American Naturalist

- Krakauer, D. C., K. M. Page, and D. H. Erwin. 2009. Diversity, dilemmas, and monopolies of niche construction. American Naturalist 173:26–40.
- Kümmerli, R., and S. P. Brown. 2010. Molecular and regulatory properties of a public good shape the evolution of cooperation. Proceedings of the National Academy of Sciences of the USA 107:18921– 18926.
- Kümmerli, R., A. S. Griffin, S. A. West, A. Buckling, and F. Harrison. 2009. Viscous medium promotes cooperation in the pathogenic bacterium *Pseudomonas aeruginosa*. Proceedings of the Royal Society B 276:3531–3538.
- Laland, K. N., F. J. Odling-Smee, and M. W. Feldman. 1996. The evolutionary consequences of niche construction: a theoretical investigation using two-locus theory. Journal of Evolutionary Biology 9:293–316.
- . 1999. Evolutionary consequences of niche construction and their implications for ecology. Proceedings of the National Academy of Sciences of the USA 96:10242–10247.
- Lehmann, L. 2007. The evolution of trans-generational altruism: kin selection meets niche construction. Journal of Evolutionary Biology 20:181–189.
- Lewontin, R. C. 1982. Organism and environment. Pages 151–170 in H. C. Plotkin, ed. Learning, development, and culture. Wiley, New York.
- . 1983. Gene, organism and environment. Pages 273–285 in
   D. S. Bendall, ed. Evolution from molecules to men. Cambridge University Press, Cambridge.
- ——. 2000. The triple helix: gene, organism, and environment. Harvard University Press, Cambridge, MA.
- Mankiw, N. G. 2012. Principles of economics. 6th ed. South-Western, Mason, OH.
- Mitri, S., and K. R. Foster. 2016. Pleiotropy and the low cost of individual traits promote cooperation. Evolution 70:488-494.
- Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 2003. Niche construction: the neglected process in evolution. Monographs in Population Biology 37. Princeton University Press, Princeton, NJ.
- Orr, H. A. 2000. Adaptation and the cost of complexity. Evolution 54:13–20.
- Otto, S. P. 2004. Two steps forward, one step back: the pleiotropic effects of favoured alleles. Proceedings of the Royal Society B 271: 705–714.

- Queller, D. C., E. Ponte, S. Bozzaro, and J. E. Strassmann. 2003. Single-gene greenbeard effects in the social amoeba *Dictyostelium discoideum*. Science 299:105–106.
- Rendell, L., L. Fogarty, and K. N. Laland. 2011. Runaway cultural niche construction. Philosophical Transactions of the Royal Society B 366:823–835.
- Silver, M., and E. Di Paolo. 2006. Spatial effects favour the evolution of niche construction. Theoretical Population Biology 70:387–400.
- Stearns, S. C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. Annual Review of Ecology and Systematics 8:145–171.
- . 1989. Trade-offs in life-history evolution. Functional Ecology 3:259–268.
- Van Dyken, J. D., T. A. Linksvayer, and M. J. Wade. 2011. Kin selection–mutation balance: a model for the origin, maintenance, and consequences of social cheating. American Naturalist 177:288–300.
- Van Dyken, J. D., and M. J. Wade. 2012. Detecting the molecular signature of social conflict: theory and a test with bacterial quorum sensing genes. American Naturalist 179:436–450.
- Visca, P., F. Imperi, and I. L. Lamont. 2007. Pyoverdine siderophores: from biogenesis to biosignificance. Trends in Microbiology 15:22– 30.
- Voulhoux, R., A. Filloux, and I. J. Schalk. 2006. Pyoverdine-mediated iron uptake in *Pseudomonas aeruginosa*: the Tat system is required for PvdN but not for FpvA transport. Journal of Bacteriology 188: 3317–3323.
- Wang, Z., B.-Y. Liao, and J. Zhang. 2010. Genomic patterns of pleiotropy and the evolution of complexity. Proceedings of the National Academy of Sciences of the USA 107:18034–18039.
- Welch, J. J., D. Waxman, and D. Houle. 2003. Modularity and the cost of complexity. Evolution 57:1723–1734.
- Werfel, J., and Y. Bar-Yam. 2004. The evolution of reproductive restraint through social communication. Proceedings of the National Academy of Sciences of the USA 101:11019–11024.
- Yom-Tov, Y. 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. Ibis 143:133– 143.

Associate Editor: Scott L. Nuismer Editor: Alice A. Winn



"Palmer's variety of the Curved-billed Mocking-thrush." From "Some United States Birds, New to Science, and Other Things Ornithological" by Elliott Coues (*The American Naturalist*, 1873, 7:321–331).