



The evolution of cooperation by the Hankshaw effect

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The evolution of cooperation—costly behavior that benefits others—faces one clear obstacle. Namely, cooperators are always at a competitive disadvantage relative to defectors, individuals that reap the benefits, but evade the cost of cooperation. One solution to this problem involves genetic hitchhiking, where the allele encoding cooperation becomes linked to a beneficial mutation, allowing cooperation to rise in abundance. Here, we explore hitchhiking in the context of adaptation to a stressful environment by cooperators and defectors with spatially limited dispersal. Under such conditions, clustered cooperators reach higher local densities, thereby experiencing more mutational opportunities than defectors. Thus, the allele encoding cooperation has a greater probability of hitchhiking with alleles conferring stress adaptation. We label this probabilistic enhancement the “Hankshaw effect” after the character Sissy Hankshaw, whose anomalously large thumbs made her a singularly effective hitchhiker. Using an agent-based model, we reveal a broad set of conditions that allow the evolution of cooperation through this effect. Additionally, we show that spite, a costly behavior that harms others, can evolve by the Hankshaw effect. While in an unchanging environment these costly social behaviors have transient success, in a dynamic environment, cooperation and spite can persist indefinitely.

KEY WORDS: Adaptation, hitchhiking, mutations, models/simulations, population structure, social evolution.

Natural selection is predicted to eliminate deleterious alleles. However, a disadvantageous allele can actually increase in frequency if it is physically linked to a beneficial allele (Hartfield and Otto 2011). Such *genetic hitchhiking* is often viewed as a passive process—the deleterious allele becomes associated with a positively selected allele purely by chance. In some cases, however, the hitchhiking allele can play an active role by increasing its probability of catching a ride. For instance, an allele that increases the genomic mutation rate may lift its chances of hitchhiking by raising the incidence of beneficial mutations, despite the deleterious mutations that it also generates (de Visser 2002). If a property of an allele increases its likelihood of hitchhiking, we term this phenomenon the “Hankshaw effect,” after the character Sissy Hankshaw from Tom Robbins’ novel *Even Cowgirls Get the Blues*. Hankshaw was born with oversized thumbs and uses this attribute to become a prolific hitchhiker. For Hankshaw, a

trait that was initially an impairment becomes her salvation on the open road. In the same way, the cost of a deleterious allele can be offset if the allele improves its own chances of hitchhiking. Here, we explore how the Hankshaw effect can promote the evolution of one costly trait that has received a great deal of attention: cooperation.

We define *cooperation* as costly behavior that improves the fitness of others. For instance, the production of costly secreted enzymes by microbes can liberate critical resources or detoxify harmful substances present in the environment. In these instances, such exoenzymes constitute public goods (Greig and Travisano 2004; Dugatkin et al. 2005; Sandoz et al. 2007; West et al. 2007a). It is the cost of cooperative behavior that makes its evolution so problematic. Specifically, a population of cooperators is susceptible to invasion by *defectors*—individuals that forego the costs of cooperation but still receive its benefits (Hardin 1968; Velicer et al. 2000; Strassmann et al. 2000; Rainey and Rainey 2003; Travisano and Velicer 2004). One recently proposed solution to

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this subversion problem involves genetic hitchhiking (Morgan et al. 2012; Quigley et al. 2012; Waite and Shou 2012; Asfahl et al. 2015). In these studies, bacteria or yeast that produce public goods (cooperators) compete against nonproducers (defectors) in a novel environment. If a beneficial mutation happens to arise first in the cooperative strain, and if the selective advantage of this mutation outweighs the cost of cooperation, then this adapted cooperator can displace defectors through genetic hitchhiking. These previous studies have focused on this hitchhiking process in well-mixed populations of cooperators and defectors. Under such conditions, cooperators do not have a greater chance of acquiring a beneficial mutation.

However, there are circumstances where cooperators can increase their chances of adaptation. Specifically, if the population is spatially structured (in which limited dispersal leads to clustering of like types) the benefits of cooperation will be disproportionately experienced by cooperators, and cooperator-rich regions will reach higher densities. Consequently, cooperative lineages expanding within a structured population will experience more reproduction than defector lineages. A greater number of reproductive events translates to more opportunities for a beneficial mutation. Because cooperators can adapt more rapidly, they are able to competitively displace defectors when the two types meet. That is, cooperator alleles hitchhike with the beneficial mutations that are more likely to occur in their presence. In structured populations, such evolution of cooperation by the Hankshaw effect can occur if there is potential for evolutionary improvement.

There is ample opportunity for adaptation under stressful environmental conditions, as organisms experiencing such conditions are, by definition, maladapted to their environment. Evolution under harsh conditions can involve selection for mutations that allow organisms to better tolerate the stress (Lytle 2001; Bell and Collins 2008). Stressful conditions can also thin and fragment a population (Pickett and White 1985), which can lead to clustering of like-types if dispersal and migration are spatially restricted. This combination of adaptive opportunity and positive assortment sets the stage for the Hankshaw effect. Here, we build a simulation model to explore the evolution of cooperation in stressful environments.

Methods

In our agent-based model, evolution occurs in a population consisting of subpopulations connected by limited migration (i.e., a metapopulation). There are two types of individuals within these subpopulations: cooperators and defectors. Cooperation is costly, but increases the productivity of the subpopulation. The onset of stressful conditions thins the population at the beginning of the simulation, and then surviving lineages can acquire fitness-enhancing mutations to adapt to the stress.

Table 1. Parameters and baseline values.

Symbol	Parameter description	Value
c	Cost of cooperation	0.1
L	Number of adaptive loci	8
δ	Fitness effect of a beneficial allele per adaptive locus	0.3
z	Baseline fitness	1
N^2	Number of subpopulations	625
T	Number of simulation cycles	2000
S_{\min}	Minimum subpopulation size	800
S_{\max}	Maximum subpopulation size	2000
μ_c	Probability of mutation at the cooperation locus	10^{-5}
μ_a	Probability of mutation at adaptive loci	10^{-5}
m	Probability of migration	0.05
σ_d	Probability of surviving dilution	0.1
σ_t	Probability of surviving stress-induced thinning	10^{-4}
p_0	Initial cooperator proportion	0.5
E or ϵ	Average interval between environmental change events*	∞

*The parameter E refers to the interval between new stressful environmental conditions under runs when this interval is fixed. The parameter ϵ refers to the average interval between new stressful environmental conditions under runs when this interval is a random variable (picked from an exponential distribution with mean ϵ).

INDIVIDUAL GENOTYPE AND FITNESS

The genotype of each individual is a binary string. The value (allele) at the first locus, designated locus zero, determines whether the individual is a cooperator (allele 1) or a defector (allele 0). We refer to this first locus as the “cooperation locus.” Cooperation is costly, reducing individual fitness by c (model parameters and their values are listed in Table 1). Alleles at the next L positions (loci 1 through L) determine the individual’s level of adaptation to the stressful environment. We refer to these loci as “adaptive loci.” A mutation from 0 to 1 at an adaptive locus will improve individual fitness by δ regardless of the allelic states of other loci (i.e., there is no epistasis). Thus, if the allelic state of locus i is denoted a_i (with $a_i \in \{0, 1\}$), then the fitness of an individual is

$$W = z - a_0c + \sum_{i=1}^L a_i \delta, \quad (1)$$

where z is a baseline fitness (i.e., the fitness of an individual with zeros at every locus). If there are no adaptive loci ($L = 0$), then the fitnesses of a cooperator and a defector are $z - c$ and z , respectively.

POPULATION STRUCTURE AND THE BASIC SIMULATION CYCLE

Simulations track a single population with N^2 patches arranged as an $N \times N$ bounded lattice. Each patch can potentially hold a subpopulation. Simulations are run for T cycles, and all subpopulations cycle synchronously. Each cycle consists of population growth, mutation, migration, and dilution.

SUBPOPULATION GROWTH

If p is the proportion of cooperators in a given subpopulation at the beginning of a growth cycle, then that subpopulation grows to size $S(p)$, where

$$S(p) = S_{\min} + (S_{\max} - S_{\min})p. \quad (2)$$

Therefore, a subpopulation consisting entirely of defectors ($p = 0$) reaches size S_{\min} , while a subpopulation of cooperators ($p = 1$) reaches a size of S_{\max} (with $S_{\max} \geq S_{\min}$). The function $S(p)$ gauges the benefit of cooperation, as subpopulation size increases linearly with the proportion of cooperators. During subpopulation growth, competition among genotypes occurs. Specifically, genotypes fill the $S(p)$ “slots” according to a fitness-weighted lottery (using eq. [1]), where the reproduction probability of a genotype is equal to a normalized version of its relative fitness. We are therefore modeling a form of fecundity selection in an asexually reproducing population. Such selection occurs at every occupied patch in the population.

MUTATION

For simplicity, mutation occurs after population growth. For each individual, every locus mutates independently. The cooperation locus changes allelic state with probability μ_c , while each adaptive locus changes allelic state with probability μ_a .

MIGRATION

Following mutation, individuals can migrate to new subpopulations. For each populated patch, a single neighboring destination patch is chosen. For a focal patch in the lattice, its destination patch is in its Moore neighborhood, consisting of the eight nearest patches. The population lattice has boundaries; therefore, a focal patch on the edge or corner of the lattice has fewer neighboring patches. Each individual in the focal patch migrates to the destination patch with probability m .

DILUTION

After migration, subpopulations are diluted to allow for growth in the next cycle. Each individual, regardless of its genotype, survives dilution with probability σ_d .

STRESS SURVIVAL AND ADAPTATION

Environmental stress has two effects. First, the subpopulations undergo a dramatic thinning event. For our first set of runs, this

bottleneck occurs only at the beginning of the simulation (for cases of repeated bottlenecks, see the next section). This stress-induced thinning is distinct from the mild dilution that occurs every cycle. Individuals survive the onset of the stress with probability σ_t (where $\sigma_t \ll \sigma_d$). Second, the allelic state a_i is set to 0 at each adaptive locus, as individuals are not adapted to the new stressful conditions. All simulations begin by applying these effects to full subpopulations initiated at each patch with cooperator proportion p_0 .

CHANGING ENVIRONMENTS

For some simulation runs, the population experiences a series of distinct stressful conditions. The two effects described in the previous section are applied at the onset of each new environmental condition. The intervals between consecutive stressful conditions are either fixed (E cycles) or randomly chosen from an exponential distribution (with a mean interval of ε cycles). Thus, when new stressful conditions are experienced, any fitness effects associated with adaptation to previous stress are removed.

REMOVING POPULATION STRUCTURE

Population structure can be removed by merging the entire population into a single patch, creating a well-mixed population. To control for total population size between such “unstructured” runs and the lattice runs described above, we let the size of the well-mixed population after growth be

$$S(p) = N^2 (S_{\min} + (S_{\max} - S_{\min})p). \quad (3)$$

With the exception of the migration step (which is now absent), all other steps in the simulation cycle proceed as above.

SOFTWARE ENVIRONMENT, SOURCE CODE, AND DATA ARCHIVING

Simulations used Python 2.7.10 with packages hankshaw 2.0.0, NumPy 1.10.1, and NetworkX 1.10 (Hagberg et al. 2008). Data analyses were performed with R 3.2.2 (R Core Team 2015). The simulation software, configuration files, data, and analysis scripts are available at doi: 10.6084/m9.figshare.2056563.

Results

The key aspects of the evolution of cooperation by the Hankshaw effect are: (1) stressful conditions create opportunities for adaptation, and (2) cooperators have more chances to adapt due to their relatively greater reproduction that occurs in a spatially structured population. To illustrate the importance of these components, we begin by exploring the evolution of cooperation when stress adaptation and spatial structure are either present or absent.

Without the opportunity for stress adaptation ($L = 0$), defectors fix rapidly (Figs. 1A and C), although structured

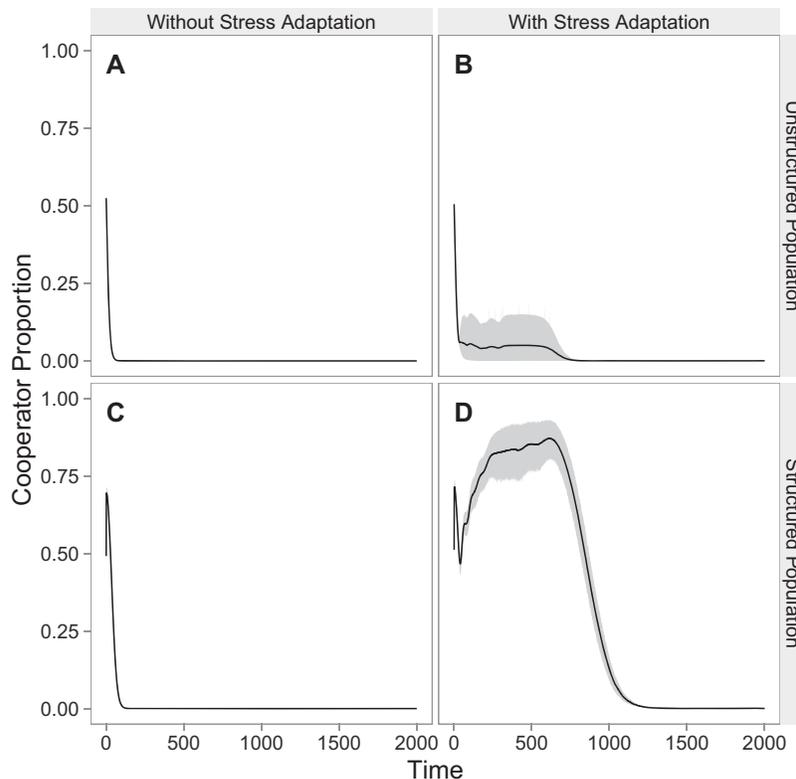


Figure 1. The evolution of cooperation by the Hankshaw effect requires population structure and adaptive opportunities. The average proportion of cooperators across 20 replicate runs is given by the black trajectory, and shaded regions indicate 95% confidence intervals. For all model parameters not specified, the baseline values listed in Table 1 were used. (A) When there is no opportunity for adaptation to the stressful conditions (i.e., L , the number of adaptive loci, is zero) and the population is well mixed, cooperators rapidly go extinct. (B) However, if adaptation to the stress can occur ($L = 8$), cooperators fare slightly better. Indeed, cooperators increase dramatically in one of the replicate runs (before eventual extinction), whereas defectors dominate quickly in the remaining set (the large variance indicates this disparity in outcomes). (C) Without stress adaptation in a structured population, cooperators crash to extinction as in part A. (D) However, if adaptation to the stress is possible ($L = 8$) in a structured population, cooperators reach high proportions. Cooperator success is ultimately transient, as defectors dominate in the long run.

populations do experience a slight initial lift in cooperator proportion (Fig. 1C). This pattern occurs because stress thins the population, leading to isolated subpopulations of either cooperators or defectors. The initial lift in cooperator proportion reflects the greater productivity of cooperator subpopulations compared to defectors. However, once migration mixes these subpopulations, cooperators are outcompeted by defectors due to the cost of cooperation. Thus, without the possibility of stress adaptation, spatial structure alone is not sufficient to maintain cooperation—cooperators experience rapid extinction in both cases.

Without spatial structure, benefits are experienced equally by both types, and the only attribute that distinguishes cooperators and defectors is the cost of cooperation. Therefore, defectors have immediate growth advantages and a greater chance of adapting (Figs. 1A and B). However, when organisms can adapt to stress ($L = 8$) in a well-mixed population, there is greater variance in outcomes (Fig. 1B). The initial variance in Figure 1B reflects the fact that in one replicate run, cooperators happen to gain the first

beneficial mutation, which allows cooperators to reach greater proportions, while in all other runs, defectors dominate after gaining the first adaptation. Cooperators in all replicate populations go extinct eventually; in the case where cooperators adapt first, the rise of de novo adapted defectors via mutation from adapted cooperators leads to cooperator extinction.

When both the opportunity to adapt to stress and spatial structure are present, a dramatically different picture emerges (Fig. 1D). The greater productivity of isolated cooperator subpopulations creates more mutational opportunities, enabling a faster rate of adaptation to the stress. When cooperators and defectors meet through migration, the fitter cooperators can now competitively displace the defectors despite the cost of cooperation. More generally, cooperator subpopulations are epicenters of rapid adaptation, spreading, and displacing defector-dominated subpopulations. Not surprisingly, cooperators fare better as the number of adaptive loci increases, the benefit of cooperation increases, or the cost decreases (Fig. S1).

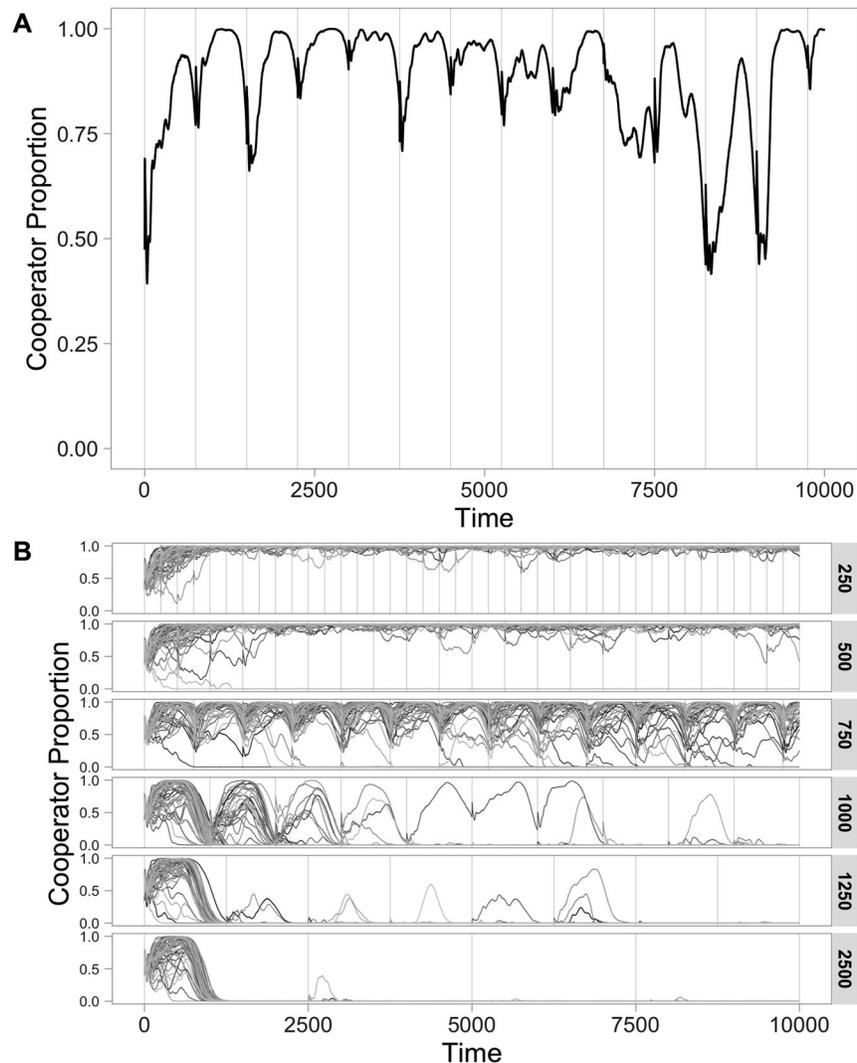


Figure 2. Evolution of cooperation in changing environments. (A) When new stressful conditions occur every 750 cycles (faint vertical lines), cooperators are able to remain at high proportion for long periods of time (baseline parameter values from Table 1 are used here, and one sample replicate is shown). (B) Each panel shows the proportion of cooperators over time in 50 replicate populations for a given interval between consecutive environmental changes (the number on the right side of each panel). This interval must be sufficiently small (less than 1250 cycles) for cooperators to have a sustained presence.

Although cooperators rise to high proportions, this increase is ultimately transient. Because the number of adaptive loci is finite, cooperators eventually discover the genotype that is most adapted to the stress. At this point, any *de novo* defectors will be equally stress-adapted but will save on the cost of cooperation, and thereafter displace cooperators. We note that if mutation at the cooperation locus does not occur ($\mu_c = 0$), cooperators reach fixation in the majority of replicates (Fig. S3).

For all of the results above, populations adapt in response to a single stressful environment. If populations instead face a series of stressful environments, we see that cooperator proportion can be maintained at high values (Fig. 2A). Here, cooperators are able to continue to gain adaptations, which is made possible by en-

vironmental changes. However, the length of the period between consecutive environmental changes is crucial. This interval must be lower than a critical value in order for cooperators to avoid extinction (Fig. 2B). When environments change too slowly, populations become fully adapted, and defectors dominate as we saw in Figure 1D. If the period is sufficiently low, however, a fresh round of adaptation salvages an otherwise doomed cooperator lineage. When the environment changes extremely rapidly, there is not sufficient time for adaptation to any new stress (given the barrage of changing harsh conditions, see Fig. S4). Cooperators fare well in these quickly changing environments solely due to the continual thinning effect associated with stress and the ensuing positive assortment.

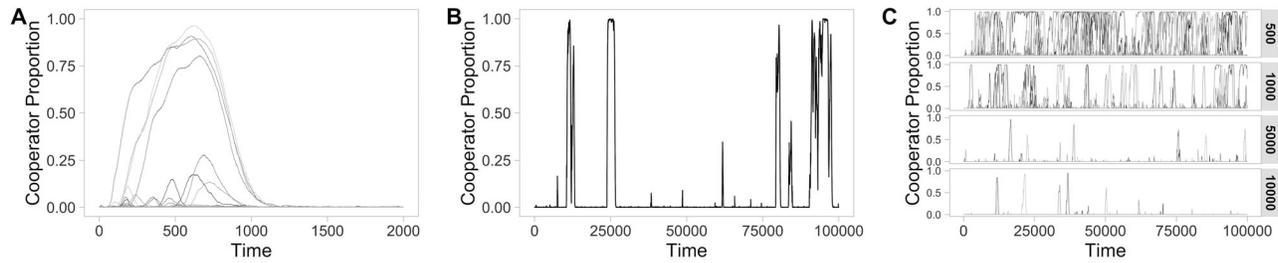


Figure 3. Cooperator invasion in changing environments. When initially absent ($p_0 = 0$), cooperator invasion occurs with some probability by the Hanksaw effect. (A) Without periodic environmental change, cooperators are able to invade from rare and reach high proportions in a small minority of replicate simulations (4 out of 500). Here, we use our baseline parameter values, except the initial cooperator proportion, p_0 , is zero. (B) The interval between environmental changes is a random exponentially distributed variable. On average, environmental changes occur every 500 cycles ($\varepsilon = 500$). De novo cooperators arise via mutation and reach high proportions several times, as shown in this representative replicate. (C) Cooperator success depends on the length of the period between environmental changes. Each panel shows the proportion of cooperators over time in 50 replicate populations for a given expected interval between environmental change events.

Up until this point, we have been exploring situations in which cooperators and defectors start at equal proportions. Therefore, our results thus far address the *maintenance* of cooperation as opposed to its *emergence*. Interestingly, under our baseline parameter values (Table 1), cooperators are able to increase to high levels from extreme rarity in a small fraction of the runs (Fig. 3A). This phenomenon has important implications for the evolution of cooperation under more realistic environmental change scenarios. For instance, the intervals between environmental change events may vary over time. As described above, when the period becomes too large, cooperators crash (Fig. 2B). However, even after such a crash, cooperators can reemerge through mutation and rise in abundance via the Hanksaw effect in recently thinned environments. Therefore, with enough change events, cooperators can recover from rarity with reasonable likelihood. Further, this pattern can happen repeatedly (Fig. 3B). The possibility of cooperator invasion expands the set of environmental change regimes that allow sustained persistence of cooperation (Fig. 3C and Fig. S5).

Discussion

Although the first models that explored hitchhiking focused on neutral alleles (Maynard Smith and Haigh 1974), this process can also explain the spread of deleterious alleles (Hartfield and Otto 2011). In our model, costly cooperation evolves through a form of hitchhiking. In order for cooperation to hitchhike, “rides” must be available; that is, there must be opportunities to gain beneficial mutations. In our simulated scenario, a stressful environment provides such opportunities for adaptation. However, evolution by the Hanksaw effect involves more than simple hitchhiking; rather, it requires that cooperators have a greater chance of catching a ride than defectors, which can occur if cooperators have

more reproductive opportunities (Fig. S1C). In our simulation, the combination of stress-induced population thinning and spatially limited dispersal produces positive assortment, and higher cooperator productivity follows. With both adaptive opportunities and limited dispersal, cooperators can experience sustained increases in frequency (Fig. 1), and can even invade populations of defectors (Fig. 3).

In the process we have outlined, the cooperation allele is a hitchhiking passenger with a “driving” allele that confers stress adaptation. While the pace of stress adaptation depends on social traits, the stress adaptation itself is inherently non-social. The idea that adaptation to non-social aspects of the environment can affect social evolution has been explored both empirically (Morgan et al. 2012; Waite and Shou 2012; Asfahl et al. 2015) and theoretically (Morgan et al. 2012; Quigley et al. 2012). These previous studies focus on well-mixed populations of cooperators and defectors, where a beneficial mutation can arise in either background with equal probability. If this mutation occurs in the cooperator background, and if the benefit of this mutation outweighs the cost of cooperation, then cooperators may displace defectors. This process has been termed an “adaptive race” (Waite and Shou 2012) in the sense that the cooperator and defector are in a race to gain the first adaptive mutation. This may be a race to obtain the first mutation to an abiotic stress (Morgan et al. 2012; Waite and Shou 2012), or a biotic stress (Morgan et al. 2012; Quigley et al. 2012). In an adaptive race, the cooperation allele does not have a greater chance of hitchhiking than the defection allele. In the experiments of Morgan et al. (2012), defector frequency must be relatively low in order for cooperators to purge defectors (see their Fig. 3). Consequently, the average proportion of cooperators (e.g., across many replicate populations) is not expected to increase (Fig. 1B). In contrast, in a spatially structured population, the cooperation allele directly increases its probability of catching a lift,

leading to an actual increase in the average cooperator proportion (Fig. 1D). Indeed, as we see in Figure 3, the Hankshaw effect even allows cooperators to invade from rarity; such invasion would be exceedingly unlikely under the adaptive race.

As Hamilton's pioneering work demonstrated (Hamilton 1963, 1964), any mechanism that enables cooperators to cluster together facilitates the evolution of cooperation (Hamilton 1975; Wilson 1975; Pepper and Smuts 2002; Nowak 2006; West et al. 2007b; Fletcher and Doebeli 2009; Nadell et al. 2010). In our model, there are two features that lead to spatial clustering. First, at the beginning of each simulation, only a few individuals survive the onset of the stressful conditions; thus the majority of subpopulations are founded by single individuals. Reproduction within these subpopulations will create immediate positive assortment of types. Second, spatially restricted dispersal within the population maintains this clustering. Interestingly, cooperators can still fare well if these features of spatial clustering are removed or diminished. Even in the absence of the initial stress-induced thinning, cooperators can beat defectors in an adaptive race, thereby jump-starting their success by the Hankshaw effect (Fig. S6). Additionally, as more subpopulations become connected through migration, thus increasing dispersal, cooperators continue to reach high proportions (Fig. S7). While some degree of population structure is required, the Hankshaw effect is robust to the exact form of this structure.

The evolution of cooperation by the Hankshaw effect is additionally robust to other changes in our model. For instance, the process still occurs when fecundity selection is replaced by viability selection (Fig. S8), when the shapes of benefit and fitness functions are altered (Fig. S9 and Fig. S10, respectively), when subpopulation sizes are varied (Fig. S11), and when the initial cooperation proportion is varied (Fig. S12). Our results suggest that cooperation can succeed under a broad set of conditions.

The basic assumptions of our model are fundamental features of many natural systems. For instance, cooperation in the form of public good production or competitive restraint in the use of common resources has been shown to increase population size (Kerr et al. 2006; Diggle et al. 2007; Eshelman et al. 2010; Xavier et al. 2011; Drescher et al. 2014), a critical assumption of our model. Moreover, many populations are naturally structured, from microbial biofilms to passively dispersed plants to sessile or territorial animals (Hutchings 1986; Tilman and Kareiva 1997; Nadell et al. 2009). Finally, in natural systems, harsh environmental conditions can impact the survival and reproduction of organisms (Lytle 2001). In fact, the edges of a species' range can be delimited by stressful conditions (Connell 1961; Sexton et al. 2009; Hargreaves et al. 2014). It is likely that these assumptions will be simultaneously satisfied in many natural contexts.

Cooperation is not the only kind of social trait that can evolve by the Hankshaw effect. Indeed, any social trait that leads to a

greater opportunity for adaptation could evolve through this process. For instance, it is possible that spiteful traits (i.e., phenotypes that harm others at a personal cost; Hamilton 1970; Gardner and West 2006) may also create opportunities to hitchhike within structured populations. For example, the production of toxins by bacteria (bacteriocins; Chao and Levin 1981; Kerr et al. 2002; Riley and Wertz 2002; Inglis et al. 2009) or characteristics that enhance flammability in plants (Mutch 1970; Williamson and Black 1981; Schwilk 2003) are spiteful traits that could evolve through the Hankshaw effect. Specifically, individuals with these traits create empty patches in their population at an extreme personal cost (by lysing or burning); and adaptation by relatives (clone mates or offspring) may therefore occur at a higher rate (see Schwilk and Kerr 2002 for discussion). In the Supplement, we adjust our model to explore spiteful interactions, and demonstrate that spite can also evolve by the Hankshaw effect (Fig. S13).

In our model, the success of costly social traits (cooperation or spite) is merely transient when mutants that evade the costs (i.e., defectors or nonspiteful types) can arise and stress adaptation is limited. However, these social traits can experience long-term success if the environment changes continually (Fig. 2 and Fig. S13C). Environmental change is ubiquitous in natural systems; indeed, periodic change (e.g., diurnal or seasonal cycles) is experienced by many biological populations (Fretwell 1972; McClung 2006). Ultimately, however, this places the evolving population at the mercy of the external environment.

However, new selective conditions can originate from the evolving system itself. For instance, in antagonistic coevolutionary systems, changes in one species (e.g., a parasite) may create new adaptive trajectories for an interacting species (e.g., a host), allowing for hitchhiking possibilities (Quigley et al. 2012). More generally, organisms continually alter their biotic and abiotic environments, a process termed "niche construction" (Laland et al. 1999; Odling-Smee et al. 2003). As a result, cycles of environmental change can be generated by the evolving system itself. In "relocation niche construction," organisms gain access to a new environment (e.g., by moving into it). For instance, mutations at adaptive loci could enable the invasion of a new territory, which could also serve to create population structure (this process is explored by Wilder and Stanley 2015). Alternatively, in "perturbation niche construction," organisms physically change their environment through their actions. Extending upon the model used in this paper, we have shown that when individuals alter their local environments in ways that generate new adaptive opportunities (i.e., negative perturbation niche construction), cooperation can be maintained at high proportion indefinitely through the Hankshaw effect (Connelly et al. 2015).

There are several extensions of our model that warrant future exploration. First, we have restricted our attention to a specific

form of cooperation (termed “multilevel altruism” in Kerr et al. 2004; see SI Section 14 for discussion). However, other forms of cooperation are likely to occur in natural systems (Doebeli and Hauert 2005; Powers et al. 2011). For instance, under the so-called “snowdrift game,” cooperators can increase when rare, which we may expect to jumpstart the Hawkshaw effect. Second, we have also focused on a particular kind of adaptation, involving positive selection. It would be worthwhile to extend the model to include diversifying selection. In fact, when there is selection for genetic diversity within subpopulations of a population, alleles encoding cooperation can hitchhike via linkage with rare alleles (Santos and Szathmáry 2008). Third, an important extension would involve the incorporation of recombination. While recombination can reduce the genetic load in a population (Lynch and Gabriel 1990; Hadany and Feldman 2005), it would also uncouple the cooperation allele from beneficial alleles at adaptive loci. Nonetheless, Schwilk and Kerr (2002) demonstrated that a form of spite can evolve via hitchhiking in a spatial context with recombination among loci, which suggests that the Hawkshaw effect may indeed function in the presence of recombination. Finally, it would be interesting to consider the evolution of alleles that affect how organisms collect into groups. In an intriguing study, Powers et al. (2011) showed how cooperative alleles can become linked to alleles that favor small initial group sizes, allowing the coevolution of both. Incorporating group size evolution into our framework would be a promising future direction.

In summary, we have explored a scenario where an allele improves its own prospects for hitchhiking. While the most straightforward case involves direct effects of the allele on its owner (e.g., a mutator allele), here we have explored a more subtle case. Specifically, the increased probability of hitchhiking of our focal allele occurs due to its social impact within a structured population. In the process, the social behavior increases in proportion despite its costs. Common explanations for the evolution of costly social traits, specifically genetic hitchhiking and positive assortment, are elements of our model. Our theoretical results reveal this unification to be synergistic. Given the biological plausibility of our theoretical assumptions, the Hawkshaw effect will be an important consideration in future studies of social evolution.

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DATA ARCHIVING

The doi for our data is 10.6084/m9.figshare.2056563.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

- Figure S1.** Cooperator presence as a function of various model parameters.
- Figure S2.** Decomposition of the effect of mutation rate on cooperator success.
- Figure S3.** The evolution of cooperators without mutation at the cooperation locus.
- Figure S4.** Cooperator success in environments changing at different rates.
- Figure S5.** Cooperator success in changing environments with a subset of adaptive loci affected by environmental change.
- Figure S6.** The Hankshaw effect without stress-induced thinning.
- Figure S7.** The effect of migration topology within the network of subpopulations.
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- Figure S9.** The effect of non-linear productivity functions.
- Figure S10.** The effect of non-linear fitness functions.
- Figure S11.** Stable polymorphism of cooperators and defectors.
- Figure S12.** The effect of initial cooperator proportion.
- Figure S13.** The evolution of spite by the Hankshaw effect.