Fitness Trade-offs Result in the Illusion of Social Success

Graphical Abstract

Highlights
- *D. discoideum* “cheater” genotypes produce smaller spores with reduced viability
- *D. discoideum* “losers” invest in larger spores with higher viability
- A number/viability trade-off means different social strategies have similar fitness
- Cheating may be illusory unless viewed in the context of multidimensional fitness

Authors
Jason B. Wolf, Jennifer A. Howie, ..., Daniel Rozen, Christopher R.L. Thompson

Correspondence
jason@evolutionarygenetics.org (J.B.W.), christopher.thompson@manchester.ac.uk (C.R.L.T.)

In Brief
If exploitation of social partners increases fitness, then selection should favor one optimal winning strategy. However, cheaters and losers often coexist. Here, Wolf et al. show that different social strategies can coexist in the social amoeba *D. discoideum* due to trade-offs between social traits, meaning that simple views of cheating may be illusory.
Fitness Trade-offs Result in the Illusion of Social Success

Jason B. Wolf,1,* Jennifer A. Howie,2 Katie Parkinson,2 Nicole Gruenheit,2 Diogo Melo,3 Daniel Rozen,4 and Christopher R.L. Thompson2,*

1Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath BA2 7AY, UK
2Faculty of Life Sciences, Michael Smith Building, University of Manchester, Oxford Road, Manchester M13 9PT, UK
3Departamento de Genética e Biologia Evolutiva, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil
4Institute of Biology, Leiden University, Sylvius Laboratory, Sylviusweg 72, PO Box 9505, 2300 RA Leiden, the Netherlands
*Correspondence: jason@evolutionarygenetics.org (J.B.W.), christopher.thompson@manchester.ac.uk (C.R.L.T.)

RESULTS AND DISCUSSION

Social Success in D. discoideum

D. discoideum live as single-celled amoebae in terrestrial habitats, but when their food is depleted, large numbers (~10^9) of individuals aggregate to form a multicellular fruiting body [13, 14]. The fruiting body is comprised of dead stalk cells that sacrifice themselves to hold aloft a ball of viable spores. Importantly, because fruiting bodies can contain a mixture of different genotypes, this is expected to lead to selection for exploitative social “cheaters,” which in D. discoideum have historically been defined simply as those strains that are overrepresented in the spore population of chimeric fruiting bodies [12, 15–20]. Consistent with earlier experiments [21, 22], we found that a set of genotypes isolated from a small geographic area in North Carolina [23] showed highly significant quantitative genetic variation (i.e., among-strain variation, H^2) in the relative number of spores produced by each strain after amoebae were mixed in a 50:50 ratio and allowed to undergo chimeric development (H^2 = 0.35, credible interval (CI) = [0.16, 0.62]; see Figure S1). This resulted in a linear (transitive) dominance hierarchy (H^2 = 0.73, p < 0.001; see [24]) with clear cheaters and “losers” when defined solely in terms of spore numbers. These observations thus raise a critical question: what processes maintain such variation in apparent social success in this species?

Trade-offs Exist between Spore Size, Number, and Viability

One mechanism by which variation in social success could persist is if fitness gains during social competition are offset by inherent costs in another context (e.g., social traits expressed in a non-social context or through pleiotropic links between different social traits or social and non-social traits). Such trade-offs could potentially lead to the coexistence of diverse social behaviors, where different strategies have similar overall fitness, and hence the variation is nearly neutral and persists at mutation-selection balance [25]. It is also possible that the traits mediating social interactions are shaped primarily by selection in a non-social context, which incidentally gives rise to variation in social fitness, but only as a neutral byproduct.
Fitness trade-offs for non-social traits are known to be widespread [26]. For example, genotypes that produce greater numbers of offspring often compromise their investment into each individual offspring [27]. These quality-versus-quantity trade-offs (often stated in terms of a size/number trade-off) are ubiquitous in nature [28], with the optimum balance depending on the organism and the environment [29]. However, in the D. discoideum social system, where spores can be thought of as “offspring,” studies have used only the relative number of spores produced by different genotypes during social encounters as a measure of relative social success and thus social fitness, without consideration of the quality of those spores. Therefore, this interpretation relies on the implied and untested assumption that all offspring are created equal. Here we challenge this assumption, reasoning that D. discoideum genotypes could potentially produce large numbers of small, low-quality progeny (i.e., small spores with relatively low viability) or invest in smaller numbers of larger but higher-quality progeny (i.e., larger spores with higher viability). As the two strategies could result in the same overall fitness return, such a trade-off could result in the persistence of variation in spore investment strategies, which are in turn manifested as variation in social strategies when the relative numbers of spores produced in chimeras is considered as the sole measure of “success.”

To investigate the hypothesis that non-social trade-offs might explain the persistence of variation in social traits by permitting the coexistence of diverse social strategies, we quantified the total number, size, and viability of spores produced by each strain. We identified significant quantitative genetic variation for the total number of spores produced ($H^2 = 0.25, CI = [0.12, 0.41]$), spore size ($H^2 = 0.59, CI = [0.20, 1.12]$), and spore viability ($H^2 = 0.62, CI = [0.19, 1.12]$) (Figure S1). Moreover, we identified significant genetic correlations between all three measures (Figure 1). First, the total number of spores produced was found to be significantly negatively genetically correlated with spore size ($r = -0.72, 95\%$ credible interval, CI = [-0.95, -0.43]; Figure 1A), demonstrating that strains producing more spores do so at least in part by making smaller spores. Second, variation in spore size was significantly positively genetically correlated with differences in spore viability ($r = 0.86, CI = [0.65, 0.99]$; Figure 1B), indicating that larger spores hatch and survive better than smaller spores. Third, the variation in spore viability was significantly negatively genetically correlated with variation in the number of spores produced ($r = -0.54, CI = [-0.88, -0.22]$; Figure 1C), revealing that genotypes producing more, smaller spores also produce spores with reduced viability.

**Social Success Comes at the Cost of Decreased Spore Viability**

Having identified significant variation in traits associated with apparent social success and spore traits, we next asked how these traits translate into the total realized social fitness of each genotype (where “social fitness” refers to the relative fitness of different genotypes resulting from social interactions). We found that the relative representation of spores of each genotype after chimeric development (chimeric representation) was positively genetically correlated with total number of spores produced ($r = 0.50, CI = [0.13, 0.79]$; Figure 1D) and negatively genetically correlated with spore size ($r = -0.55, CI = [-0.85, -0.18]$; Figure 1E), suggesting that genotypes that produce more spores consequently have higher representation in the chimeric sporehead but do so by producing more but smaller spores. However, because spore viability scales negatively with spore size, this leads to a negative genetic correlation between viability and chimeric representation ($r = -0.69, CI = [-0.95, -0.40]$; Figure 1F). Together, these results lead to the conclusion that genotypes that achieve higher representation of spores in chimeric fruiting bodies do so by producing greater numbers of lower-viability spores.

**Trade-offs Negate Fitness Gained through Sporehead Representation**

By accounting for these correlations between traits (summarized in Figure 2), we estimated a realized social fitness value that discounts representation of spores during chimeric development.
likely that both trade-offs arise from differences in the number or viability of resulting spores. We therefore believe it is more likely that both trade-offs arise from differences in the number and viability of resulting spores. This analysis clearly demonstrates that, due to trade-offs between traits, the relationship between spore size (Figure 3A) or spore number (Figure 3B) and realized social fitness is essentially flat. Therefore, despite significant variation in both of these underlying traits, which ultimately determine components of fitness, this variation appears to be effectively neutral in terms of realized social fitness.

Trade-offs Help Explain the Coexistence of Cheaters and Losers

Social systems and measurements of social success are often viewed from the perspective of a single fitness-related trait (e.g., [12, 22]), which is then used as a proxy for total fitness. Although this narrow consideration is sometimes unavoidable given the challenge of measuring overall fitness in a relevant environmental context, our results reveal that this narrow perspective may produce misleading conclusions because it ignores the fact that organisms are inherently “multidimensional,” being composed of suites of traits that together determine their fitness. Realized fitness of any genotype will therefore be the product of different, potentially conflicting components. Moreover, examining fitness through this multidimensional lens highlights the fact that traits affecting different aspects of life history not clearly associated with social interactions could have indirect effects on social success [31]. As a consequence, although each individual trait may appear to confer a fitness advantage (and therefore be under directional selection), the multidimensional system of traits is constrained by trade-offs, resulting in no net selection on the set of traits when viewed as a whole [32].

The label of “cheater” has often been applied to *D. discoideum* genotypes that have a higher representation of spores than some of their competitors during chimeric fruiting body development. One way this could occur is if genotypes exhibit differences in developmental signaling that lead to different ratios of spore or stalk cells [33]. Although this mechanism is possible, it is hard to envisage how it could lead to differences in total spore number, as well as affecting the size or viability of resulting spores. We therefore believe it is more likely that both trade-offs arise from differences in the number of reductive cell divisions that occur during the multicellular stages of the life cycle. Indeed, there is widespread evidence supporting the idea that some cells, and especially those destined to become spores, do indeed undergo division during the migratory slug phase [34, 35]. If resources and biomass were limiting and unequally partitioned in the multicellular slug, such reductive division would result in smaller cells, thus providing a plausible explanation for the resulting smaller spores observed. This latter pattern appears to explain much of the variation observed, given that different spore production strategies appear to result in similar social fitness as a result of trade-offs. Under this scenario, different spore production strategies are nearly neutral in terms of their influence on social fitness (Figure 3), and hence the continuum of social behavioral strategies seen in these genotypes may simply reflect low selection pressure on social traits.

It is important to note, however, that although we have shown that relative representation in the sporehead is a poor measure of true social success, when interactions are viewed from the perspective of realized social fitness (which includes both spore number and viability) we find that there remains variation in social fitness that should reflect the true nature of cheaters and losers in this system (Figure 3). Similarly, in other microbial systems such as *Myxococcus* and *Pseudomonas*, cheater genotypes that exploitatively outcompete cooperators in mixed groups have been described when social fitness is measured in terms of the relative production of viable spores or cells, respectively [5, 10]. This is almost certainly due to the fact that microbes have complex life cycles and live in heterogeneously structured environments where diverse intra- and interspecific dynamics will interact to affect fitness. Other life history traits that we have not examined are no doubt manifest...
in these ecologically relevant scenarios, and these in turn may directly or indirectly influence the coexistence of apparent social traits [36].

Our study therefore has clear implications for understanding the evolution of social traits in terms of cheater or cooperator strategies. Most notably, our results illustrate the importance of considering life history trade-offs when assessing social fitness: although many social systems, such as *D. discoideum*, may appear unbalanced with individuals that appear to “win,” these individuals are really no better off in terms of fitness than individuals that appear to “lose.” These observations may thus explain the paradoxical coexistence of substantial genetic variation in apparent social success in this and potentially other social organisms.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure, one table, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.02.061.

AUTHOR CONTRIBUTIONS

C.R.L.T., D.R., and J.B.W. conceived and designed the project and wrote the manuscript. J.A.H. performed the measurements of social success and spore numbers. K.P. and N.G. performed the measurements of spore size and viability. D.M. and J.B.W. designed the data analyses. D.M. performed all analyses.

ACKNOWLEDGMENTS

We thank Daizaburo Shizuka for assistance with the analysis of social dominance. This work was supported by funding from the Natural Environment Research Council (UK) to C.R.L.T., D.R., and J.B.W.; the Biotechnology and Biological Research Council to J.B.W.; a Wellcome Trust Investigator Award to C.R.L.T.; and FAPESP grant numbers 2011/14295-7 and 2014/01694-9 and a Visiting Postgraduate Scholar grant from the University of Bath to D.M.

Received: November 5, 2014
Revised: January 20, 2015
Accepted: February 20, 2015
Published: March 26, 2015

REFERENCES

1. Strassmann, J.E., Queller, D.C., Avise, J.C., and Ayala, F.J., eds. (2012). In In the Light of Evolution, Volume V: Cooperation and Conflict (The National Academies Press).
2. Sachs, J.L., Mueller, U.G., Wilcox, T.P., and Bull, J.J. (2004). The evolution of cooperation. Q. Rev. Biol. 79, 135–160.
3. Ghoul, M., Griffin, A.S., and West, S.A. (2014). Toward an evolutionary definition of cheating. Evolution 68, 318–331.
4. Popat, R., Crusz, S.A., Messina, M., Williams, P., West, S.A., and Diggle, S.P. (2012). Quorum-sensing and cheating in bacterial biofilms. Proc. Biol. Sci. 279, 4765–4771.
5. Velicer, G.J., Kroos, L., and Lenski, R.E. (2000). Developmental cheating in the social bacterium *Myxococcus xanthus*. Nature 404, 598–601.
6. Zhang, Q.G., Buckling, A., Ellis, R.J., and Godfray, H.C. (2009). Coevolution of cooperators and cheaters in a microbial system. Evolution 63, 2248–2256.
7. MacLean, R.C., Fuentes-Hernandez, A., Greig, D., Hurst, L.D., and Gudelj, I. (2010). A mixture of “cheaters” and “co-operators” can enable maximal group benefit. PLoS Biol. 8, e1000486.
8. West, S.A., Griffin, A.S., Gardner, A., and Diggle, S.P. (2006). Social evolution theory for microorganisms. Nat. Rev. Microbiol. 4, 597–607.
9. West, S.A., Diggle, S.P., Buckling, A., Gardner, A., and Griffin, A.S. (2007). The social lives of microbes. Annu. Rev. Ecol. Evol. Syst. 38, 53–77.
10. Sandoz, K.M., Mitzimberg, S.M., and Schuster, M. (2007). Social cheating in *Pseudomonas aerugionsa* quorum sensing. Proc. Natl. Acad. Sci. USA 104, 15876–15881.
11. Vos, M., and Velicer, G.J. (2009). Social conflict in centimeter-and global-scale populations of the bacterium *Myxococcus xanthus*. Curr. Biol. 19, 1763–1767.
12. Strassmann, J.E., Zhu, Y., and Queller, D.C. (2000). Altruism and social cheating in the social amoeba *Dictyostelium discoideum*. Nature 408, 965–967.
13. Li, S.J., and Purugganan, M.D. (2011). The cooperative amoeba: *Dictyostelium* as a model for social evolution. Trends Genet. 27, 48–54.
14. Shaulsky, G., and Kessin, R.H. (2007). The cold war of the social amoebae. Curr. Biol. 17, R684–R692.
15. Strassmann, J.E., and Queller, D.C. (2011). Evolution of cooperation and control of cheating in a social microbe. Proc. Natl. Acad. Sci. USA 108 (2), 10855–10862.
16. Gilbert, O.M., Foster, K.R., Mehlisadi, N.J., Strassmann, J.E., and Queller, D.C. (2007). High relatedness maintains multicellular cooperation in a social amoeba by controlling cheater mutants. Proc. Natl. Acad. Sci. USA 104, 8913–8917.
17. Santorelli, L.A., Thompson, C.R., Villegas, E., Svetz, J., Dinh, C., Parikh, A., Suggang, R., Kuspa, A., Strassmann, J.E., Queller, D.C., and Shaulsky, G. (2008). Facultative cheater mutants reveal the genetic complexity of cooperation in social amoebae. Nature 451, 1107–1110.
18. Khare, A., Santorelli, L.A., Strassmann, J.E., Queller, D.C., Kuspa, A., and Shaulsky, G. (2009). Cheater-resistance is not futile. Nature 456, 980–982.
19. Santorelli, L.A., Kuspa, A., Shaulsky, G., Queller, D.C., and Strassmann, J.E. (2013). A new social gene in *Dictyostelium discoideum*, *chtB*. BMC Evol. Biol. 13, 4.
20. Fortunato, A., Queller, D.C., and Strassmann, J.E. (2003). A linear dominance hierarchy among clones in chimeras of the social amoeba *Dictyostelium discoideum*. J. Evol. Biol. 16, 438–445.
21. Buttery, N.J., Thompson, C.R., and Wolf, J.B. (2010). Complex genotype interactions influence social fitness during the developmental phase of the social amoeba *Dictyostelium discoideum*. J. Evol. Biol. 23, 1664–1671.
22. Buttery, N.J., Rozen, D.E., Wolf, J.B., and Thompson, C.R. (2009). Quantification of social behavior in *D. discoideum* reveals complex fixed and facultative strategies. Curr. Biol. 19, 1373–1377.
23. Francis, D., and Eisenberg, R. (1993). Genetic structure of a natural population of *Dictyostelium discoideum*, a cellular slime mould. Mol. Ecol. 2, 385–391.
24. Shizuka, D., and McDonald, D.B. (2012). A social network perspective on measurements of dominance hierarchies. Anim. Behav. 83, 925–934.
25. Van Dyken, J.D., Linksveyer, T.A., and Wade, M.J. (2011). Kin selection-mutation balance: a model for the origin, maintenance, and consequences of social cheating. Am. Nat. 177, 288–300.
26. Roff, D.A. (1992). The Evolution of Life Histories: Theory and Analyses. (Chapman & Hall).
27. Stearns, S. (1992). The Evolution of Life Histories. (Oxford University Press).
28. Morris, D.W. (1987). Optimal allocation of parental investment. Oikos 49, 332–339.
29. Parker, G.A., and Begon, M. (1986). Optimal egg size and clutch size: effects on environment and maternal phenotype. Am. Nat. 128, 573–592.
30. Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. J. Stat. Softw. 33, 1–22. http://www.jstatsoft.org/v33/i02/paper/.
31. Zhang, X.-X., and Rainey, P.B. (2013). Exploring the sociobiology of pycovarid-producing *Pseudomonas*. Evolution 67, 3161–3174.
32. Walsh, B., and Blows, M.W. (2009). Abundant genetic variation + strong selection = multivariate genetic constraints: a geometric view of adaptation. Annu. Rev. Ecol. Evol. Syst. 40, 41–59.
33. Parkinson, K., Buttery, N.J., Wolf, J.B., and Thompson, C.R. (2011). A simple mechanism for complex social behavior. PLoS Biol. 9, e1001039.
34. Muramoto, T., and Chubb, J.R. (2008). Live imaging of the Dictyostelium cell cycle reveals widespread S phase during development, a G2 bias in spore differentiation and a premitotic checkpoint. Development 135, 1647–1657.
35. Zimmerman, W., and Weijer, C.J. (1993). Analysis of cell cycle progression during the development of Dictyostelium and its relationship to differentiation. Dev. Biol. 160, 178–185.
36. Sathe, S., Khetan, N., and Nanjundiah, V. (2014). Interspecies and intra-species interactions in social amoebae. J. Evol. Biol. 27, 349–362.