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LETTER

Experimental evidence that local interactions select against selfish behaviour

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 Volker Rudolf⁵

Abstract

How social behaviours evolve remains one of the most debated questions in evolutionary biology. An important theoretical prediction is that when organisms interact locally due to limited dispersal or strong social ties, the population structure that emerges may favour cooperation over antagonism. We carry out an experimental test of this theory by directly manipulating population spatial structure in an insect laboratory model system and measuring the impact on the evolution of the extreme selfish behaviour of cannibalism. We show that, as predicted by the theory, Indian meal moth larvae that evolved in environments with more limited dispersal are selected for lower rates of cannibalism. This is important because it demonstrates that local interactions select against selfish behaviour. Therefore, the ubiquitous variation in population structure that we see in nature is a simple mechanism that can help to explain the variation in selfish and cooperative behaviours that we see in nature.

Keywords

Cannibalism, experimental evolution, inclusive fitness, *Plodia interpunctella*, social evolution, space.

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INTRODUCTION

Social behaviour is clearly on a continuum from co-operation and altruism to extreme selfish behaviour such as cannibalism. How natural selection can result in such a broad range of behaviours both across and within species continues to fascinate evolutionary biologists (Hamilton 1963, 1964; Axelrod & Hamilton 1981; West *et al.*, 2002; Griffin *et al.*, 2004; Kummerli *et al.*, 2009; Nowak *et al.*, 2010). This challenge has led to the development of a large body of theory using inclusive fitness and other approaches (Hamilton 1963, 1964; Axelrod & Hamilton 1981; West *et al.*, 2002; Nowak *et al.*, 2010), which has surprisingly led to only a few direct experimental tests of this theory (Griffin *et al.*, 2004; Diggle *et al.*, 2007; Kummerli *et al.*, 2009; Schrader *et al.*, 2015). Furthermore, many existing tests examine relatively simple cooperative social traits in microbial systems (Griffin *et al.*, 2004; Diggle *et al.*, 2007; Kummerli *et al.*, 2009) rather than the complex animal social and antagonistic behaviours where the theory is typically applied (Schrader *et al.*, 2015). Empirical tests of the theory that examine complex social behaviours in a wider range of organisms are therefore needed in order to understand the drivers of the wide spectrum of social behaviours in nature from altruism to extreme selfish behaviours such as cannibalism.

Biologists' views on social interactions radically changed 50 years ago when Hamilton's famous inequality suggested that although natural selection is intrinsically selfish,

cooperation can be favoured under some limited conditions (Hamilton 1963, 1964; Axelrod & Hamilton 1981). Evolutionary theory has often explained selection against selfish behaviour through behavioural games with direct and indirect reciprocity (e.g. tit-for-tat and the prisoners dilemma) (Axelrod & Hamilton 1981; Nowak & Sigmund 1992; Nowak *et al.* 1993; Riolo *et al.*, 2001). However, it is now increasingly recognised that population structure generated by social or spatial relationships within a population may play a central role in selecting for cooperation or antagonism (Lion *et al.*; Hauert & Doebeli 2004; Lion & van Baalen 2007; Lion & Boots 2010; Rudolf *et al.*, 2010). Population structure has important impacts on selection due to the emergence of both ecological and genetic correlations (Lion *et al.*; Hauert & Doebeli 2004; Lion & van Baalen 2007; Lion & Boots 2010) (Figure 1). The potential for spatial structure to increase interactions between kin was intuitive driver of the idea that it would select against selfish behaviour, but early models that assume complete local density regulation found no effect of population structure on the evolution of altruism since increased competition between kin exactly countered the benefits of helping kin (Taylor 1992a,b). However if there is 'elasticity' in populations that allows overproduction nearby due to for example empty space and local density-dependent processes, then local interactions can select against behaviours (Lion & van Baalen 2007; Alison & Taylor 2008). In general, theory predicts that the direction of selection on selfish vs. altruistic behaviour and therefore the evolutionary outcome

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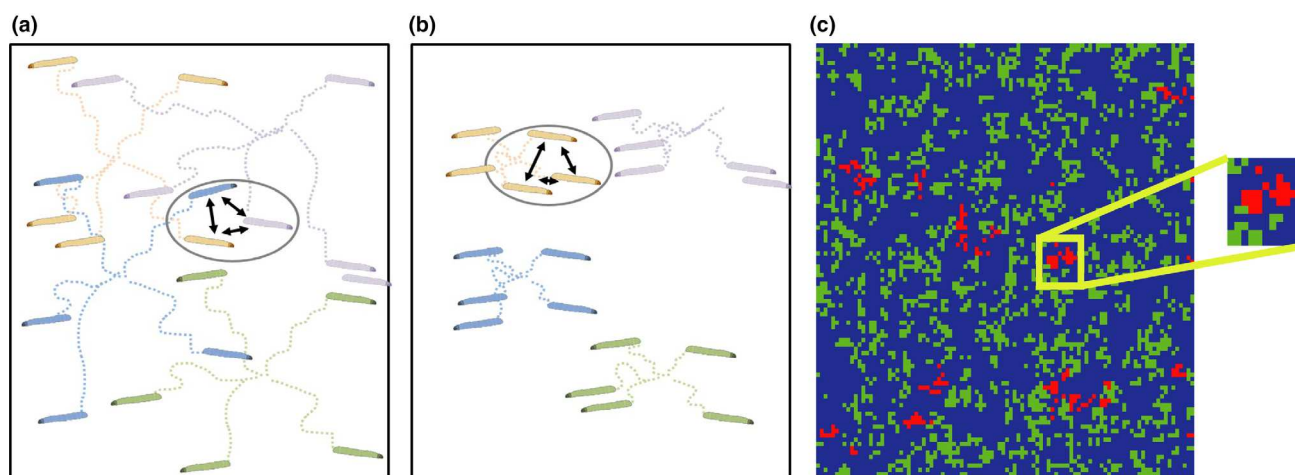


Figure 1 (a and b) show a schematic of populations with high (low viscosity) and low (high viscosity) movement rates of individuals respectively. Different colours indicate different kin (genotype) groups, larvae indicate current positions, and dots indicate past random movements, with the length representing movement rates. Lower movement rates result in spatial clumping of genotypes within populations, increasing the probability that local cannibalistic interactions (example indicated by circles) occur among closely related individuals. (c) shows the output from a typical spatial model where green and red dots represent two classes of organisms – cannibals and victims – and blue empty space. Spatial structure results in clustering of the particular classes – ecological correlations while genetic correlations arise from clustering of the same and related genotypes. It is these patterns that generate selection on the traits

depends crucially on the interplay between the effects of this ecological and genetic spatial structuring (Lion & van Baalen 2007; Lion & Boots 2010). Local interactions typically select behaviours to become more co-operative and less antagonistic (Lion & van Baalen 2007). A particularly well-studied example of this general phenomenon is that theory predicts that as interactions become more local parasites are selected for lower transmission and virulence, a prediction that has received empirical support (Boots & Sasaki 1999, 2000; Boots & Meador 2007; Lion & Boots 2010). Recent theory has predicted that lower rates of cannibalism are predicted as interactions become more local but there are currently no empirical tests of this prediction (Lion & van Baalen 2007; Rudolf *et al.*, 2010).

While originally considered as an abnormal behaviour in only a few species, cannibalism has now been recorded in more than 1,300 species across a diverse group of taxa, ranging from protists and invertebrates to humans (Polis 1981). Cannibalism is ubiquitous in nature and frequently acts as an important factor regulating the dynamics of populations (De Roos & Persson 2002; Rudolf 2007), communities (Miller & Rudolf 2011), through to entire ecosystems (Miller & Rudolf 2011). The commonness of cannibalistic behaviour is not surprising given that it provides many clear fitness benefits, such as the ingestion of a particularly high-quality resource (in the perfect stoichiometric ratios) and the removal of potential competitors. However, the propensity for cannibalistic behaviour varies substantially across species and within species and it is clear that much of this variation has a genetic component (Stevens 1989). Recent theory suggests that this variation could be driven by differences in the dispersal behaviour of individuals within populations and the concurrent change in the spatial structure of genotypes within population (Lion & van Baalen 2007; Rudolf *et al.*, 2010). Specifically, the theory predicts that limiting

dispersal should select against cannibalism because it increases the risk of encountering and thus cannibalising kin (Lion & van Baalen 2007; Rudolf *et al.*, 2010), but this theory is untested.

Here, we test the specific theoretical prediction that dispersal limitation and the concurrent increase in local interactions select against cannibalism. More generally we are testing how variation in spatial structure within populations impacts where behaviours lie on the selfish to altruistic continuum. We establish replicate populations of the cannibalistic phycitid moth species *Plodia interpunctella* for 10 generations across a gradient of selective regimes where the average movement rates and thus proportion of local interactions varies across treatments and acts on any standing variation for cannibalism within our moth populations. We found that, as predicted by theory, higher population viscosity favoured less cannibalism.

METHODS

Experimental design

We use an experimental evolution approach with replicated populations of the phycitid moth species *P. interpunctella*, in which cannibalism is common. Each population is maintained at one of the five different food viscosities leading to different rates of movement within the food. Larvae of *P. interpunctella* remain within their food medium, and therefore, an increase in the viscosity of the food medium leads to lower individual movement rates and as a consequence more local interactions within the population on average (Figure 2). We used established methods to manipulate the viscosity of the food medium in order to alter dispersal distances of the individuals without altering the calorific content of the food media (Boots & Begon 1994; Boots & Roberts 2012).

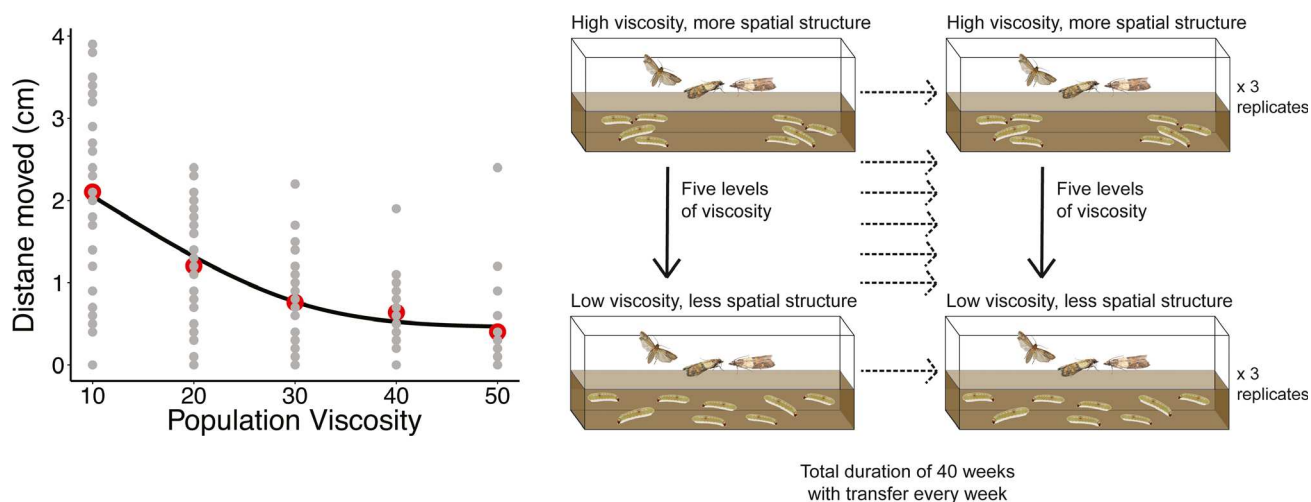


Figure 2 A schematic of the experimental evolution experiment. The impact of the viscosity manipulation on the rate of movement of larvae (The red dots are the mean values and the line represents the model fit) showing lower movement in the more viscous food media

We established three replicate populations at each of five levels of population viscosity resulting in a total of 15 microcosms that were maintained under constant conditions for 10 generations. This design allowed us to create a range of selective regimes where the average proportion of local interactions across the treatments varies and this acts on any standing variation for cannibalism within our moth populations. After approximately 10 generations, we performed a series of standardised cannibalism assays to compare the propensity for cannibalism in individuals derived from those (F2 in a common environment) selected on the different environments.

Viscosity treatment

Fundamental to our experimental design is that the *P. interpunctella* larvae live within the food media. Therefore, by altering the viscosity of this media, we can change the amount of movement that on average occurs within the microcosms. The larvae remain within the food and do not typically move over the top of the media until the fifth instar when they are not feeding. Standard food medium is made by mixing HiPP 7-Korn organic harvest breakfast cereal (100 g), brewer's yeast (20 g), glycerol (40 ml, 50 ml, 60 ml, 70 ml or 80 ml), sorbic acid (0.2 g) and methyl paraben (0.2 g). Our aim was to alter the viscosity of the media without significantly impacting the life-history characteristics of the larvae. Thus, in our viscosity manipulation, all of the key nutritional components of the standard food are maintained, but the amount of glycerol that is added is changed and this alters the viscosity of the media without impacting significantly the nutritional characteristics. To confirm this, we tested the impact of different proportions of glycerol (our viscosity manipulation) on the key life-history characteristics of pupal weight and development time by placing single individual second instar larvae into individual pots and measuring their time to pupation for each of the five food media with a minimum of 50 replicates. Two days after pupation – when the pupae have hardened

and are able to be manipulated – the pupae were weighed. For the experiments, we chose five food types over a range of different levels of glycerol food – 40 ml, 50 ml, 60 ml, 70 ml, 80 ml per 100 g of HiPP cereal – where we had found no significant effect on either pupal weight ($\chi^2 = 2.26$, $DF = 2$, $P = 0.32$) or development time ($\chi^2 = 1.14$, $DF = 2$, $p = 0.56$) in preliminary experiments across a wide range of viscosities.

In preliminary experiments using the stock insects, we quantified the effects of this manipulation of the food viscosity on the movement of larvae using 15 cm × 1 cm × 1 cm lanes of the food medium. First instar larvae from stock cultures were placed at the start of a lane for 12 days until larvae matured to third instar. Lanes were kept within ventilated plastic boxes in incubators at $27 \pm 2^\circ\text{C}$, $35 \pm 5\%$ humidity and 16:8 light dark cycle. The distance travelled to the nearest centimetre, was measured by removing food from lanes in 1-cm chunks and searching for third instar larvae. We carried out 4 blocks in which there were initially 10 replicates for each food viscosity.

Cannibalism evolution experiment

The experimental populations were initiated by placing 15 fifth instar male larvae and 15 fifth instar female larvae onto 170 g of food medium in 20 cm × 20 cm plastic containers with ventilation holes. The larvae were taken at random from a large outbred population maintained in our laboratory over a number of years. Three replicates were established for each food viscosity (15 replicate populations in total). Populations were maintained for 40 weeks in incubators at $27 \pm 2^\circ\text{C}$, $35 \pm 5\%$ humidity and 16:8 light dark cycle. The food medium in each replicate was divided into six equal sections. Across all treatments one section of food medium was removed every 7 days and replaced with fresh food medium. Dead adults were removed weekly and counted. The dynamics show generational cycles with the average population densities across the four lowest viscosities were similar (Tukey's range

tests: $P > 0.536$) although there was a significantly lower average density in the most viscous treatment (Tukey's range test: $P < 0.022$).

Cannibalism trials

At the end of the experiment, the rates of cannibalism were compared across the treatments by using F2 (raised on standard food media across all treatments to avoid maternal effects) larvae. Specifically, adults from each population were allowed to lay onto standard food media and 30 newly emerged adults were then allowed to lay eggs onto food media. For the specific trials, 25 pairs of third instar larvae of the same age were then taken from these pots and placed together in small dishes. Each trial was then checked for cannibalism after a 4-hour period. Cannibalism rates were then calculated as the proportion of the 25 trials that showed cannibalism in the F2 from each selected line.

Statistical analysis

We analysed dispersal distance using a general linear mixed model (lmer function in 'lme4' package), in which food treatment was entered as a continuous predictor and block as a random effect. Dispersal distance was $\log(+0.01)$ transformed to account for the non-linear relationship between food treatment and dispersal and remove heteroscedasticity. To examine the relationship between cannibalism and dispersal, we conducted two separate general linear model (GLM) analyses. In the first, we modelled the proportion of cannibalized conspecifics as a function of food treatment and in the second as a function of dispersal distance, with food treatment or average dispersal distance as continuous fixed effect, and binomial error structure using the base 'glm' function in R. All p-values were obtained with the 'Anova' function in the 'car' package based on Wald chi-square statistics.

RESULTS

Individuals in more viscous treatments moved on average less than half the distance than those in low viscosity treatments and there was a significant non-linear negative relationship ($\chi^2 = 53.04$, $P < 0.00001$) between viscosity and dispersal distance (Figure 2). Since adults lay clutches of multiple eggs in

this species, increasing viscosity also results in more spatial 'clumping' of, and hence more interactions between, siblings, thereby altering the social and genetic spatial structure of populations in our system.

Our key result is that the average cannibalism rate significantly ($\chi^2 = 6.53$, $P = 0.0106$) declined in more viscous populations (Figure 3) and increased with average dispersal rates within a treatment ($\chi^2 = 6.05$, $P = 0.0139$) (Figure 3). This relationship is consistent with the theoretical predictions and thus provides clear experimental evidence demonstrating that changes in dispersal select against extreme selfish behaviour and emphasises the importance of social and genetic structure of populations in driving the evolution of social behaviour. Removing any of the treatments from the analysis reduces the power of the experiment resulting in an insignificant relationship, but the slope of the relationship remains similar and within one standard error. The relationship is therefore not strongly driven by a particular treatment.

DISCUSSION

Recent theory and empirical work have emphasised that social and spatial structuring within populations may be a key factor that may explain the wide range of social behaviour that have evolved in nature. Social behaviour in the wild has been linked to genetic relatedness (Sharp *et al.*, 2005) and experiments in microbial laboratory systems have demonstrated that higher relatedness can select for co-operative rather than cheating behaviour (Kuemmerli *et al.*, 2009). Here we directly manipulate spatial structure, which is ubiquitous in nature, and show that local interactions select against the extreme selfish behaviour of cannibalism. It is clear from the theory (Lion & van Baalen 2007; Rudolf *et al.*, 2010) that a major driver of this effect is that local interactions lead to a higher chance of cannibalisms of kin. It is important to note that this kin selection is an emergent property that is the result of local clustering of related individuals.

In general, evolutionary biology has focussed on the determinants of altruistic behaviour, with less direct discussion of the limits of selfish behaviour, including cannibalism. Our study provides clear empirical evidence demonstrating that variation in the spatial structure of interactions within a population can strongly select against a extreme selfish behaviour (cannibalism) that otherwise would be adaptive. Intuitively

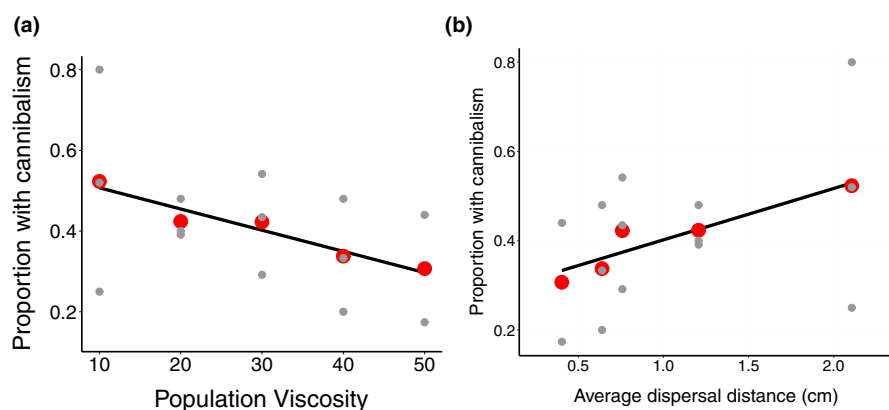


Figure 3 The rates of cannibalism for the different viscosity treatments and the average distance moved (estimated independently for each of the different viscosity treatments) against the rate of cannibalism in the selected lines. The red dots are the mean values and the line represents the model fit

this result can be understood because cannibals pay a higher inclusive fitness cost in local populations that outweighs the benefits of cannibalism that includes reduced competition in addition to the increased reproduction that the excellent resource that cannibalism provide. Given that some degree of population structure caused by processes such as limited dispersal and social interactions is likely in most if not all systems, this simple ubiquitous process may help explain the variation that we see in nature in social behaviours such as cannibalism (Miller & Rudolf 2011). There is little data on the relationship between spatial structure and cannibalism rates in natural systems, although gregarious Ascidian species reject conspecific eggs and larvae, while non-gregarious species typically consume both suggesting that the spatial clumping of individuals may have selected against cannibalism in this system (Young 1988). It also follows that higher cannibalism may select for increased dispersal as seen in a number of species (Rudolf 2006, 2008) and therefore reducing population viscosity. Future studies could assess any selection on dispersal in the presence and absence of cannibalism.

Given that early models that assume complete local density regulation find no effect of population structure on altruism (Taylor 1992a,b), our results emphasise the importance of the way that local demography and ecology interact with spatial structure in determining the evolutionary outcomes. At the ecological level, the distribution of individuals (e.g. susceptible and infected hosts, co-operators and defectors, predators and prey, cannibals and prey) is impacted by the proportion of interactions (reproduction, infection, predation) that occur locally, that is among neighbours in close spatial proximity. With local interactions, particular types of individuals such as cannibals or co-operators become increasingly clustered into groups and therefore interact more with each other (Figure 1). The impact of these local demographic processes in addition to the spatial distribution of alleles and the propensity for related individuals (kin) to interact with each other are critical to the outcomes (Lion & van Baalen 2007; Lion & Boots 2010). Furthermore, in addition to spatial structure, it is increasing apparent that the population structure due to social interactions can also impact the evolution of social traits. For example, social behaviour is promoted in evolutionary games on graphs ranging from the random regular, random and scale free networks where an equivalence of Hamilton's rule is found with the average degree of a graph as an inverse measure of relatedness (Ohtsuki *et al.*, 2006). Taken as a whole, it is clear that both the nature of the population structure, resulting from spatial or social interactions and the impact of local density depending is critical in determining the outcome, but population structure is likely to be an important determinant of social behaviour.

Spatial structure itself has previously been shown to select for co-operative behaviour in yeast and bacterial model systems (Kummerli *et al.*, 2009), and there are experimental demonstrations that limited dispersal can select parasites to be prudent in both microbial (Kerr *et al.*, 2006) and insect hosts (Boots & Meador 2007). However, there remain relatively few microevolutionary experiments that manipulate spatial structure in order to test the theory. One challenge with these experiments, including the current study, is that it is not always possible to completely control for all possible confounding factors. In our case, we are selecting

on standing variation and although we saw no impact on individuals of the food medium, there were on average lower population densities at the highest resource level. Given the consistency of densities across the other food media, it is unlikely that this difference explains our results, but it is very difficult to carry out a perfect experiment where selection is tightly controlled in this context. Overall, our results imply that there is considerable potential for selection against selfishness in nature given that some degree of population structure and limited dispersal is common in most if not all populations. More broadly, variation in population structure provides a very simple source of variation in co-operation and selfishness within and across species in nature.

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AUTHOR CONTRIBUTIONS

MB and VR conceived the study, which was carried out DC, JC and HT under the supervision of MB. DC, MB and VR analysed the data and wrote the paper.

AUTHORSHIP

MB and VR conceived the study, which was carried out DC, JC and HT under the supervision of MB. DC, MB and VR analysed the data and wrote the paper.

DATA ACCESSIBILITY STATEMENT

The data supporting the results will be archived in Dryad, and the data DOI will be included at the end of the article <https://doi.org/10.6078/D14Q48>.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13734>.

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