

EVOLUTIONARY BIOLOGY

Kin selection promotes female productivity and cooperation between the sexes

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Hamilton's theory of kin selection explains the evolution of costly traits that benefit other individuals by highlighting the fact that passing genes to offspring is not the only way of increasing the representation of those genes in subsequent generations: Genes are also shared with other classes of relatives. Consequently, any heritable trait that affects fitness of relatives should respond to kin selection. We tested this core prediction of kin selection theory by letting bulb mites (*Rhizoglyphus robini*) evolve in populations structured into groups of relatives or nonrelatives during the reproductive phase of the life cycle. In accordance with predictions derived from kin selection theory, we found that evolution in groups of relatives resulted in increased female reproductive output. This increase at least partly results from the evolution of male traits that elevate their partners' fecundity. Our results highlight the power and universality of kin selection.

INTRODUCTION

Kin selection theory (1) has been widely accepted as an explanation for the evolution of altruistic traits (2). However, the role of relatedness in the evolution of altruistic traits has recently been questioned, with ecological factors that favor group living highlighted as an alternative hypothesis (3, 4). Although this call for a paradigm shift has drawn criticism (5), discrimination between genetic and ecological factors that could lead to the evolution of altruistic traits in contemporary social groups is difficult because ecological factors favoring group living also increase relatedness. However, if kin selection is a universal force shaping phenotypic evolution, the effects of relatedness should be readily observable on the evolution of any heritable trait if that trait affects the fitness of relatives. Thus, experimental evolution is an ideal tool to test the generality of kin selection theory. Here, we use this tool to investigate how relatedness affects female reproductive success, a crucial fitness component.

We focused on female reproductive output because it is likely to be compromised by the "tragedy of the commons" (6) and, as such, is likely to be modulated by kin selection. The tragedy of the commons occurs when individual competition reduces the resource over which individuals compete, resulting in lower overall fitness for all members of a group (6). In the case of female reproductive output, the tragedy of commons may be a consequence of selfish, wasteful utilization of resources (for example, food), leading to overexploitation. Furthermore, investment in traits that aid in competition is likely to come at the cost of productivity (6). Finally, female reproductive output may be compromised by sexual conflict. Reproduction is far from being a collaborative endeavor, and conflicts abound not only within sexes competing for reproductive opportunities but also between the two sexes. Such intersexual conflicts are widespread because reproductive interests of males and females rarely overlap perfectly, except for strict lifetime monogamy (7, 8). For example, males typically benefit from copulations with many females, but copulations may decrease female fitness (9, 10).

Kin selection is expected to modulate the tragedy of the commons when groups of self-restraining relatives are able to "export" more offspring into a global population of unrelated individuals (11). If all

competition in a structured population takes place locally, competition between relatives may cancel out any inclusive fitness benefits of self-restraint (12, 13). However, under a range of scenarios, including limited dispersal and hard selection (that is, selection which does not equalize reproductive output of local populations), kin selection should affect the evolution of social traits [reviewed by West *et al.* (11)]. Recently, it has been argued that kin selection may be important in the modulation of sexual conflict because harm inflicted on females decreases the fitness of female and/or male relatives of harmful males (14–16). This reasoning is supported by a number of recent theoretical models (14, 17, 18). Most of these models have focused on the inclusive fitness effects of competition between related males. If mating takes place between relatives, kin selection for decreased harm inflicted by males on their female relatives could also play a role (14), although its importance remains to be explored, and evolution of inbreeding avoidance mechanisms (19, 20) may complicate predictions.

To test the effect of relatedness on the evolution of the female reproductive output, we established three replicate kin selection lines, in which individuals matured and mated in 100 groups of sibs. Three replicate control lines consisted of otherwise identical but unrelated groups. After mating, all females in a replicate line were pooled and allowed to oviposit. Thus, reproductive competition between females took place in a global population, but female reproduction could have been affected by all inter- and intrasexual interactions taking place in their social groups before pooling.

RESULTS AND DISCUSSION

Experimental evolution was carried out for nine generations, followed by two generations of monogamous mating with unrelated individuals, with each female contributing two offspring to the next generation. The same treatment of kin selection and control lines allowed us to minimize any maternal effects, whereas the minimal possibility of selection in these two additional generations prevented back-evolution (13).

The crucial prediction of kin selection theory is that evolution of group-benefit traits is more likely if group members are genetically related. Thus, we predicted that lines evolving under kin selection will have higher reproductive output. We tested this prediction under conditions similar to those under which our lines evolved (that is, female fecundity was measured for 2 days, after a 5-day interaction period). However, to control the direct effect of relatedness of group

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members on female fecundity (as opposed to the effect of relatedness during experimental evolution), the interacting group consisted of unrelated individuals in both treatments. We found that reproductive output of females from kin selection lines was higher (Fig. 1).

Furthermore, we investigated whether male-female interactions significantly contribute to this increased reproductive output of females evolving under kin selection. Mating is costly to female bulb mites and depresses their fecundity (10), but experimental evolution under relaxed sexual conflict (achieved by enforced monogamy) significantly reduced these detrimental effects of males on female fitness (16). Here, we asked whether similar effects can be observed if the overlap between male and female reproductive interests, and between interests of competing males, results from their relatedness. We have found that this is indeed the case: Females from stock population mated to males from kin selection lines had higher fecundity than those mated with males from control lines (Fig. 2). This shows that kin selection can mitigate sexual conflict, as predicted by theory (14).

In response to the evolution of decreased male harm to females, females have been reported to evolve decreased resistance to this harm (21, 22). This suggests that selection pressure against female resistance arises because resistance is costly. Consequently, removing or reducing these costs may contribute to increased productivity of populations (21). If females from kin selection lines evolved decreased resistance to male harm, they should show lower fecundity when mated with males from the stock population (because these males still express traits that make copulation costly to females). We observed the opposite: Females from kin selection lines showed higher fecundity (Fig. 3).

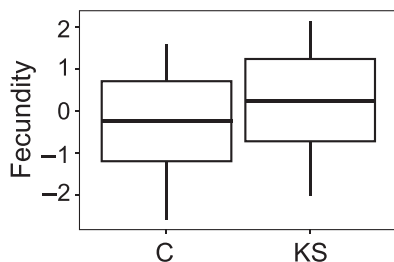


Fig. 1. The effect of nine generations of evolution under kin selection on female fecundity. After mating in groups of unrelated individual (males and females coming from the same experimental line), females from kin selection lines laid more eggs ($t_{174} = 3.34$, $P = 0.001$; see Supplementary Materials for details). Mean of the z-transformed number of eggs is shown and the box represents ± 1 SD and the whiskers represent minimum and maximum. C, control lines; KS, kin selection lines.

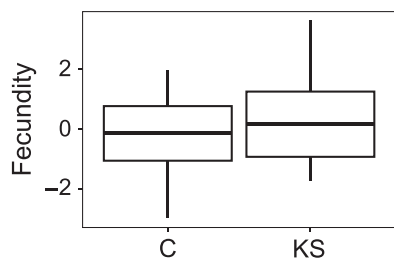


Fig. 2. The effect of male evolutionary history on female fecundity. Females from the stock population were more fecund after being paired for 5 days with males from kin selection lines compared to males from control lines ($t_{174} = 2.05$, $P = 0.041$; see Supplementary Materials for details). Mean of the z-transformed number of eggs is shown and the box represents ± 1 SD and the whiskers represent minimum and maximum.

This suggests that decreased resistance may have not evolved as fast in response to kin selection as in response to evolution under monogamy, which directly selected for decreased sexual conflict. Nevertheless, this result points to positive effects of kin selection on female fitness, which is independent of the effect that males have on their mating partners. These positive effects of kin selection might have arisen, for example, due to converting resources spent on larval competition and/or resource competition between females on reproduction.

Evolution of sex ratio is a common consequence of kin selection (23) because female-biased sex ratio increases representation of the offspring-producing sex in the global population. Furthermore, female-biased sex ratios should reduce any harmful effects of males on females within the group. However, in a system with chromosomal sex determination (XO in the bulb mite), any evolution of sex ratio would require genetic variation at modifier loci that would bias sex ratio. Nevertheless, kin selection lines tended to show more female-biased sex ratios (mean proportion of females, 0.580; range, 0.57 to 0.60) than control lines (mean, 0.544; range, 0.52 to 0.57), but this difference was not significant ($P = 0.109$).

Two male morphs occur in *Rhizoglyphus robini*: armored, aggressive fighter males and unarmored, benign scramblers (24). Fighters can sometimes kill rival males, and fighter-induced mortality could bias sex ratio and thus reduce overall male harm to females. Alternatively, presence of aggressive fighters might cause female mortality as a side effect, as reported for other acarids (20). However, mortality in all lines was low during the 5-day interaction period (males, 9.3%; females, 1%), suggesting that kin selection on male morph must have been weak. We observed no significant difference between treatments in proportions of morphs (kin selection lines: mean, 0.770; range, 0.57 to 0.91; and control lines: mean, 0.812; range, 0.70 to 0.88; $P = 0.200$).

Overall, our results demonstrate and reinforce that kin selection is a powerful mechanism capable of shaping phenotypic evolution. This selection includes evolution of male traits, which have an effect on female fitness. Plastic expression of female harm traits in response to relatedness between competing males has been implicated by Carazo *et al.* (25), in the modulation of sexual conflict in *Drosophila melanogaster*: Females exposed to groups of three brothers were more fit than females exposed to groups of three unrelated males with the difference even reported to carry over to the next generation (26). However, these results remain open to interpretation (26–28). For example, Hollis *et al.* (27) showed that familiarity between related males is necessary to reproduce the results of Carazo *et al.* (25). However, although Hollis *et al.* (27) argued that familiarity may have effects independent of kin selection

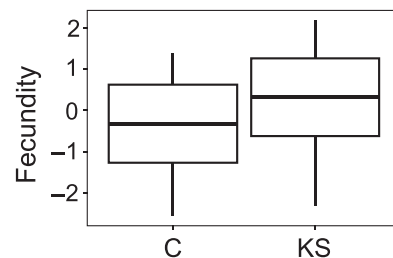


Fig. 3. Fecundity of kin-selected and control females when paired with stock population males. Females from kin selection lines were more fecund compared to females from control lines after being paired for 5 days with males from the stock population ($t_{176} = 4.54$, $P < 0.001$; see Supplementary Materials for details). Mean of the z-transformed number of eggs is shown and the box represents ± 1 SD and the whiskers represent minimum and maximum.

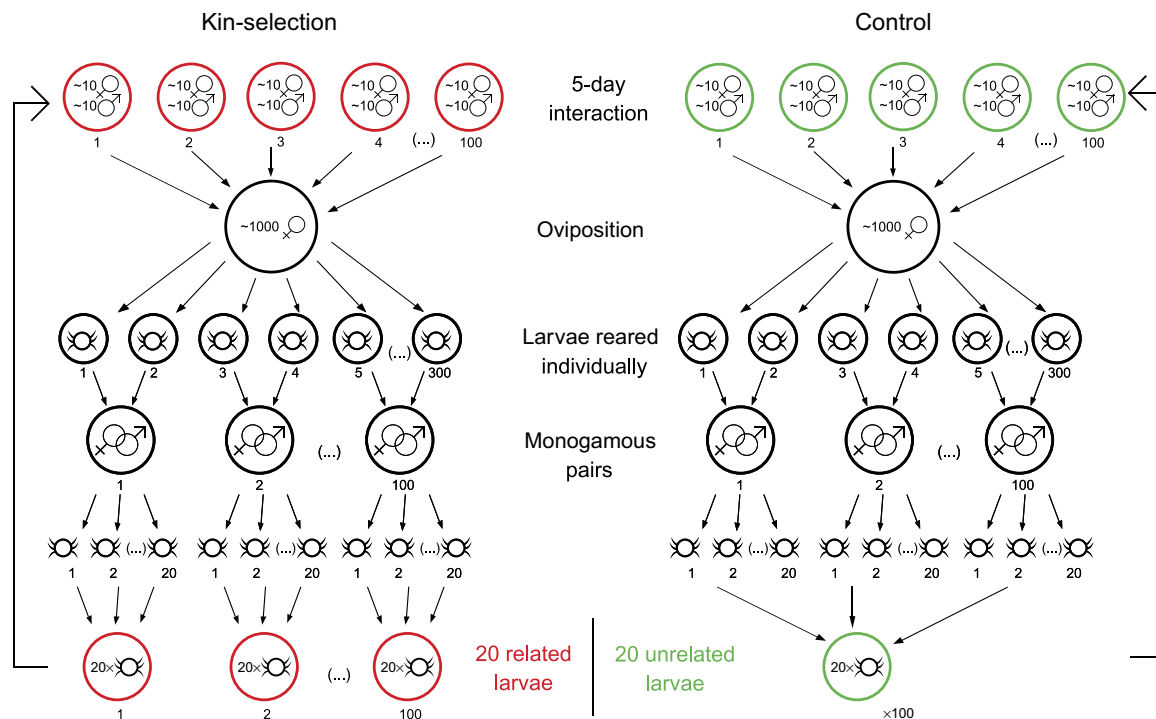


Fig. 4. Schematic representation of experimental evolution protocol for kin selection and control lines. Reproductive competition took place during a 5-day interaction between full sibs (kin selection) or unrelated individuals (control). After the interaction period, inseminated females were pooled and allowed to lay eggs, and larvae produced in the resulting global populations were selected randomly to start the next generation. Experimental evolution generations, in which kin selection and control treatments were implemented, were interspaced with relaxed selection monogamy generations, which served to obtain full-sib families and prevented inbreeding in kin selection lines. There were three independent replicates for both kin selection and control lines. See Materials and Methods for more details.

[but see (26) for counterarguments], the design of their study was not fully factorial and they did not demonstrate that familiarity can explain the results of Carazo *et al.* (25) in the absence of kinship. Because familiarity is a common way to discriminate kin from nonkin in many animals (29), the results of Hollis *et al.* (27) do not contradict a kin selection interpretation of Carazo *et al.* (25). Nevertheless, the effect of relatedness (and/or familiarity) between males on female fitness has not been confirmed in other *D. melanogaster* populations (28, 30), so the generality of the findings of Carazo *et al.* (25) remains unclear.

Our design allowed us to control factors that make inferences of the role of kin selection in evolution of prosocial traits difficult. Familiarity did not confound our results, because during all fecundity assays, the interacting individuals were unrelated and unfamiliar in both kin selection and control treatments. The differences between treatments in familiarity were also minimized during experimental evolution because unrelated larvae in control treatment were assembled in groups soon after emergence. Furthermore, unlike earlier work (31) that also used experimental evolution, our results indicate that increased genetic differentiation among groups achieved by inbreeding within groups is not necessary for the evolution of traits beneficial to relatives. We were able to decouple relatedness from inbreeding by alternating inbreeding and outbreeding generations (Fig. 4), but the effects we report are only likely to be enhanced when inbreeding increases genetic differentiation between groups of relatives (31, 32). Under natural conditions, evolution of decreased competition between relatives, and of reduced harm males inflict on females, requires that a significant part of competition occurs outside the group of relatives (11). Possible scenarios would include sex-biased migration (14, 17, 18) or migration of locally inseminated females

to lay eggs in a global population, as observed, for example, in some species of parasitoid wasps (33). Metapopulation dynamics similar to those observed in bulb mite (34), characterized by fast population growth and colonization of new patches when the resource is fully exploited, could also be conducive to kin-selected evolution of self-restraint. Under these dynamics, new patches (such as bulbs or roots in the case of the bulb mite) are likely to be invaded by a few pairs of adults, or a few inseminated females. The progeny of each colonist would initially mate locally, but, with fast population expansion, the next generation would see global competition between the offspring of different colonists, both within a patch (bulb) or for colonization of new patches. Alternatively, effects similar to the ones we report could evolve in a natural context as facultative response to the presence or absence of relatives in a reproductive group (25). Tracing the evolution of the effect of males on their mates under various scenarios mimicking those observed in nature would be an important target for future experimental evolution work. Generally, our results thus attest that kin selection is a pervasive and powerful evolutionary force, as envisaged by Hamilton (1).

MATERIALS AND METHODS

Base population

Mites used in the experiment came from a laboratory stock culture, which was established from five collections around Krakow, Poland, made in years 2008 to 2012. Each collection consisted of >50 individuals. The large stock culture (>1000 individuals, subdivided into periodically mixed subpopulations) was maintained at 25°C with >90% humidity and fed with dried yeast. The same temperature, humidity,

and feeding were maintained throughout all experimental protocols described below. In all experiments, mites were maintained in glass vials with a plaster of Paris bottom soaked with water to maintain high humidity. Virgin males and females for all protocols described below were obtained by rearing larvae individually in a 0.8-cm-diameter vials until adulthood.

Experimental evolution

We maintained three “kin selection” lines and three “control” lines. Kin selection and control treatments were implemented in odd-numbered experimental evolution generations, which were interspaced with relaxed selection monogamy generations necessary to obtain full-sib families (Fig. 4). Furthermore, the monogamous generation also prevented accumulation of inbreeding in kin selection lines.

At the beginning of each experimental evolution generation, we placed 20 larvae in a 0.8-cm-diameter interaction vial. The food was provided in a marginal excess, that is, some food was always present, but between subsequent feedings, its quality deteriorated due to increasing content of feces. This ensured some competition for high-quality fresh food, but prevented starvation, which would slow down larval development. Specifically, the vial contained about 20 grains of yeast when larvae were placed in it. The same amount was added 3 days later (after nymphs emerged). After adults emerged, 40 to 50 grains were added. There were 100 interaction groups per line. After adults emerged, they were maintained in the interaction vials for five more days, during which time mating took place. In kin selection lines, all larvae placed in an interaction vial were full siblings, such that larvae and adults competed with their relatives for resources, and males competed with their brothers for access to their sisters, whereas in control procedure, all larvae (and then individuals in a mating group) were unrelated. Bulb mites started mating immediately after the final molt and mated several times a day, so this period involved intense reproductive activity and reproductive competition among males. After the 5-day mating period, females from all mating groups in each line (~1000 females) were pooled in a 9-cm-diameter oviposition vials provided with food available ad libitum for 2 days to lay eggs and then removed.

After larvae emerged, ~300 of them were selected at random for the next (monogamous) generation and reared individually to obtain virgin adults. Thus, representation of female offspring in the next generation was proportional to their productivity in a global population, but this productivity should have been affected by social interactions, including any sexual conflict, in interaction groups. The adults were sexed, and 100 monogamous pairs were created at random. Thus, in both the kin selection and control treatment groups, monogamous pairs were unrelated. As a result, genome heterozygosity with respect to alleles identical by descent was restored in kin selection lines at each monogamous generation, thus preventing accumulation of inbreeding. Then, 20 larvae from each resulting family were randomly selected to establish the next experimental evolution generation. Monogamy and equal contribution of each female from monogamy generation to the next (experimental evolution) generation ensured little opportunity for selection. Experimental evolution lines were maintained for 18 generations (that is, they experienced 9 generations of experimental evolution in kin selection and control treatments).

Measurements

The effect of experimental evolution on female reproductive potential, the contribution of males to this potential, sex ratios, and proportions

of morphs were measured after 18 generations of experimental evolution. Before measuring, lines from both treatments underwent “standardization,” that is, two generations of monogamous mating with unrelated individuals. Two larvae from each monogamous pair were collected at random to start the next generation. The larvae were reared individually, and virgin adults were paired upon emergence. Proportions of morphs and proportions of fighters were determined at the second monogamous generation. Virgin individuals were taken to measure the reproductive output 1 to 2 days after emergence. Because of logistic constraints, we conducted experimental evolution in three blocks. Each block contained one kin selection line and one control line. The measurements of reproductive output were performed blindly with respect to the treatment.

Experiment 1: Overall effect of evolution under kin selection on female reproductive output.

The purpose of this experiment was to compare female productivity between kin selection and control treatments under conditions similar to those under which these lines evolved. Thus, the experiment started by placing five virgin males and five virgin females in the interaction vials, containing about 30 grains of food for 5 days. To control for the direct effect of relatedness of group members on female fecundity, the interacting group consisted of unrelated individuals in both kin selection and control treatments. One female from each vial was then randomly selected, and the number of eggs laid during the next 2 days (that is, at the time when reproductive competition between females took place during experimental evolution) was counted.

Experiment 2: Male effect on female reproductive output.

To assess how kin selection shapes the way males affect female reproductive output, we paired virgin males from kin selection and control lines with virgin females from the stock population (that is, females whose ancestors did not experience experimental evolution). There were 25 to 33 pairs per line. The pairs were kept together in a 0.8-cm-diameter vial, containing five grains of yeast, for 5 days. After this period, a female from each pair was placed in a fresh vial, containing food available ad libitum, to lay eggs for 2 days. On day 3, the laid eggs were counted.

Experiment 3: Female resistance to male harm.

To investigate whether females from kin selection lines evolved reduced resistance to male harm, we paired virgin females from experimental evolution lines with virgin males from the stock population. Twenty-seven to 32 females per line were tested. The pairs were kept together in a 0.8-cm diameter vial, containing five grains of yeast, for 5 days. After 5 days of interaction, males were removed and females were transferred to new vials provided with food available ad libitum. After 3 days of oviposition, the eggs were counted.

Statistical analyses

All analyses were carried out using R-3.3.0 (35). For fecundity data from experiments 1 to 3, we selected the optimal model following Zuur *et al.* (36) by comparing the fit of a linear mixed-effect model containing a random effect line [implemented in `lme` function in `nlme` package (37)] with a fit of a model without the random effect (implemented in `gls` function). The data were z -transformed within blocks before analyses. Model assumptions were checked using diagnostic plots. The optimal model was selected on the basis of likelihood ratio test (with restricted maximum likelihood used as a measure of fit) implemented by the `anova` function in R, but P values were conservatively divided by two to deal with the boundary effect (tables S1 to S3) (36).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/3/e1602262/DC1>

table S1. Model selection results.

table S2. Optimal general linear models.

table S3. Results of full general linear mixed models.

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