

Research article

Open Access

## The coevolution of cooperation and dispersal in social groups and its implications for the emergence of multicellularity

Michael E Hochberg\*<sup>1,2,3</sup>, Daniel J Rankin<sup>4</sup> and Michael Taborsky<sup>4</sup>

Address: <sup>1</sup>Institut des Sciences de l'Evolution, Centre National de la Recherche Scientifique, UMR 5554, Université Montpellier II, 34095 Montpellier, France, <sup>2</sup>Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA, <sup>3</sup>National Centre for Ecological Analysis and Synthesis, 435 State Street, Suite 300, Santa Barbara, CA 93101-3351, USA and <sup>4</sup>Department of Behavioural Ecology, University of Bern, Wohlenstr. 50a, 3032 Hinterkappelen, Switzerland

Email: Michael E Hochberg\* - mhochber@univ-montp2.fr; Daniel J Rankin - daniel.rankin@esh.unibe.ch; Michael Taborsky - michael.taborsky@esh.unibe.ch

\* Corresponding author

Published: 19 August 2008

Received: 4 March 2008

*BMC Evolutionary Biology* 2008, **8**:238 doi:10.1186/1471-2148-8-238

Accepted: 19 August 2008

This article is available from: <http://www.biomedcentral.com/1471-2148/8/238>

© 2008 Hochberg et al; licensee BioMed Central Ltd.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/2.0>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

### Abstract

**Background:** Recent work on the complexity of life highlights the roles played by evolutionary forces at different levels of individuality. One of the central puzzles in explaining transitions in individuality for entities ranging from complex cells, to multicellular organisms and societies, is how different autonomous units relinquish control over their functions to others in the group. In addition to the necessity of reducing conflict over effecting specialized tasks, differentiating groups must control the exploitation of the commons, or else be out-competed by more fit groups.

**Results:** We propose that two forms of conflict – access to resources within groups and representation in germ line – may be resolved in tandem through individual and group-level selective effects. Specifically, we employ an optimization model to show the conditions under which different within-group social behaviors (cooperators producing a public good or cheaters exploiting the public good) may be selected to disperse, thereby not affecting the commons and functioning as germ line. We find that partial or complete dispersal specialization of cheaters is a general outcome. The propensity for cheaters to disperse is highest with intermediate benefit:cost ratios of cooperative acts and with high relatedness. An examination of a range of real biological systems tends to support our theory, although additional study is required to provide robust tests.

**Conclusion:** We suggest that trait linkage between dispersal and cheating should be operative regardless of whether groups ever achieve higher levels of individuality, because individual selection will always tend to increase exploitation, and stronger group structure will tend to increase overall cooperation through kin selected benefits. Cheater specialization as dispersers offers simultaneous solutions to the evolution of cooperation in social groups and the origin of specialization of germ and soma in multicellular organisms.

### Background

Cooperation is central to transitions in individuality [1-4]. Full individuality is achieved when components coop-

erate and relinquish their autonomy to the larger whole. Depending on the type of transition, this may necessitate the division of labor in growth, reproduction, develop-

ment, feeding, movement, and protection against external aggression and internal conflict [5,6]. In the evolution of multicellularity, the chain of events from autonomous individuals at one level to the incorporation of these individuals into a more complex entity remains unclear [5]. However, some of the putative forces are likely to be general, since multicellularity has arisen many different times in evolutionary history [7,8]. Moreover, that many groupings do not show sophisticated specialization and are characterized by substantial levels of internal conflict [9,10], suggests that incomplete multicellularity may be a frequent outcome. What mechanisms are essential to generate individuality? We believe that a general theory needs to explain both full and incomplete transitions towards multicellular individuals.

Previous work highlights group and kin selection [5,10,11], organism size [12,13], and the reorganization of fitness and specialization tradeoffs [14] as playing roles in the evolution of multicellularity. A feature common to these mechanisms is the establishment and maintenance of cooperative behaviors amongst subunits through, for example, conflict mediation (e.g. [15,16]). Based on a recent literature review, Grosberg and Strathmann [8] argued that for cooperation to emerge and favor the specialization of subunits, groups of cells need to reduce genetic conflicts arising in cell lineages [10]. They conclude that several mechanisms can limit such conflicts, perhaps the most important being development from a single cell (e.g., [5,16]).

A key type of subunit specialization in multicellular organisms is the separation of germ and soma [1,5,10,17,18]. Separating germ and somatic functions amongst individual cells or cell lineages requires that each sacrifice autonomy. Theory predicts that such specialization is promoted by non-mutually exclusive mechanisms such as cooperation and relatedness amongst cell lineages [10], cheater control [1,19,20] and adaptive responses to tradeoffs between survival and reproductive functions, i.e. a covariance effect augmenting the fitness of the group over the average fitness of its members [14]. It is not known whether the alignment of fitness interests in emerging soma and germ lines tends to occur before, during or after other types of specialization characteristic of multicellular organisms [12].

A pervasive feature in a diverse array of social systems is that individuals not contributing to the common good either act as dispersers, or are either rewarded for, or coerced into, cooperating. Examples range from bacteria (e.g. *Pseudomonas fluorescens*) through protozoa (e.g. *Volvox carterii*) to metazoans, like eusocial insects and mammals (see Additional file 1). For example, in naturally occurring *Dictyostelium* slime molds prespores secrete a

chlorinated hexaphenone (DIF-1) inhibiting redifferentiation of prestalk cells into prespores, which would transpose them from "cooperative" stalk building to "cheating" spore production (i.e. a transition into the dispersing and perennial germ line; [21,22]). Cheating is further curtailed by pleiotropic effects of a gene required to permit receipt of this signal, which affects also the probability of spore formation [23]. In tunicates such as *Botryllus schlosseri*, natural chimeras consisting of genetically nonhomogenous organisms often show reproducible germ cell parasitism that is sexually inherited, with "parasitic forms" being expressed only in the germ line, i.e. in the dispersing entities [24]. In the cooperatively breeding cichlid fish *Neolamprologus pulcher*, brood care helpers of both sexes are forced to pay rent for being tolerated in a safe territory [25,26]. To avoid being punished they preemptively appease dominants by cooperative and submissive behavior [27]. Typically, in these cichlids and in cooperatively breeding meerkats *Suricata suricatta*, subordinates preparing for dispersal reduce helping [28,29], which might be explained by reduced costs of potential punishment by eviction [30,31]. In eusocial mole rats (*Heterocephalus glaber* and *Cryptomys damarensis*) non-reproductive helpers and hardly helping dispersers coexist [32-34]. Policing of subordinates by dominant breeders may simultaneously maintain social order and stimulate cooperative behaviors [35,36]. This distinction of roles between individuals is particularly obvious in the separation between soma and germ that has apparently evolved many times independently [7]. Nevertheless, there are examples where cooperative behaviors are associated with enhanced group dispersal (see Additional file 1). For example, in the soil-dwelling social bacterium *Myxococcus xanthus*, individualistic cell movement ('A-motility') promotes swarming on hard surfaces, whereas swarming on soft surfaces is a group function driven primarily by individually costly S-motility [37].

These empirical patterns merit explanation, and we take a first step by employing optimization techniques to evaluate the conditions leading to associations between dispersal and social strategy. Sociality in our models takes the form of cooperation in the production of a public good. Previous study of public goods has shown how cheating, if left unchecked, potentially leads to a "tragedy of the commons" [38,39], whereby individual selection tends to favor exploitation of the public good at some concurrent or future detriment of the group. Several non-mutually exclusive mechanisms may promote cooperation and group persistence, including kin selection (e.g., [40-42]), rewards and sanctions (e.g., [43,44]), spatial and network structure (e.g., [45-47]), and signals involving kin or non-kin (e.g., [48-50]). Recent reviews and perspectives can be found in Crespi [51], Sachs and colleagues [52], Lehmann and Keller [53], and West and coworkers [54].

We develop a model based on kin selection that incorporates dispersal specialization, as suggested by the case studies in Table S1 (see Additional file 1). We employ the terms "soma" and "germ" to represent the functions of within-group growth and dispersal leading to the founding of new groups, respectively. Our use of the terms "cooperators" and "cheaters" refers to social behaviors within the commons (e.g., soma), and this should be distinguished from the frequent usage of "cheaters" as cooperative somatic lineages trying to gain access to germ line (e.g., [1,5,8,10,22]). Specifically, cooperators contribute to the public good within a distinct group at an individual cost, and cheaters exploit the public good. Cooperators and/or cheaters may be selected to either remain in a group, or to disperse (potentially founding new groups). Our theory proposes a mechanism leading to high overall cooperation, based on dispersal specialization. In addition to increasing our understanding of cooperative and dispersal behaviors, it could apply to the evolution of multicellularity in a range of contexts, including physiologically integrated organisms [55,56], organisms with both solitary and integrated life-styles (e.g., [57]), and complex societies [58].

**Methods**

We formalize our verbal arguments given above by developing and analyzing a model of coevolution between exploitation of the commons and dispersal. From the outset, we stress that our model is a highly simplified representation of this process, and not aimed to make quantitative predictions for any given system. Rather, our goal is to identify the qualitatively important drivers in the coevolution of individual strategies and the evolution of multicellularity.

In our model the focal units of selection are individuals themselves, rather than the higher-level unit. A transition to multicellularity is favored when the interests of the individual and the higher-level (the group) are aligned [5,8,15]. Previous models investigating the transition to multicellularity invoke a framework where the group is the focal unit of selection (see, for example [15]). However, focusing on the higher-level as the focal unit does not easily allow the investigation of optimization at the lower level [59], and the individually-selected conditions leading to a major transition [60]. Grosberg and Strathmann [8] have argued that many of the requirements for transitions to multicellularity exist in unicellular organisms (for social groups, see [61]). Once a transition is in progress, and the "group" begins to behave as an individual entity, one can begin to treat this unit as an evolving individual in itself.

We analyze an optimization model that takes into account the effect of both the phenotype of the focal indi-

vidual and the average phenotype of the group in which it lives, on the fitness of the focal individual (see Table 1 for descriptions of parameters and variables). The approach is based on the direct fitness method [42,62] in that, by considering the effects of both individual and average group phenotypes on the fitness of a focal individual, we can apply the Price Equation to partition these effects as weighted by the relatedness of the focal individual to other members of the group [42]. We can then assess the relative impacts of (1) costs and benefits of individual behaviors and (2) kin structure, on associations between exploitative strategy within a group, and dispersal to found new groups. Nevertheless, our model oversimplifies the complexity of social behavior and dispersal decisions (for review, see [63]), and should thus be viewed as a preliminary attempt to identify patterns.

Our model makes several assumptions. First, we do not explicitly consider dynamics, such as group founding, group numbers, individual emigration and immigration, and competition for limiting resources within or between groups. Rather, we assume negligible variation in intergroup competition. Second, our model does not explicitly incorporate genetic polymorphisms, meaning that the heritable traits are probabilities to adopt alternatives of each strategy (disperse or stay; cooperate or cheat) depending on environmental and/or social conditions [1,10,32,64-66]. Third, there is a simple direct tradeoff between an individual's viability (growth, survival and reproduction) within the group and its ability to disperse and found new groups. This is based on the well established life-history trade-off between reproduction and dispersal (see [67]), probably best studied in insects (on the physiological scale e.g. [68-70]; on the ecological scale e.g. [71,72]). Whereas growth and reproduction within the

**Table 1: Parameters and variables used in this study.**

w	Individual fitness
r	Relatedness between any two randomly selected individuals in the group
s	Individual cost to cooperator growth in the group
k	Number of individuals in a group (an inverse measure of kin selection)
c	Individual cost to cooperator dispersal
e	Individual cost to cheater dispersal
Q	Impact of sedentary cheaters on the individual fitness of group members (via consumption of the public good)
P	Impact of sedentary cooperators on the individual fitness of group members (via production of the public good)
n	Relative frequency of cooperators in the group (1-n is the proportion of cheaters)
z	Relative frequency of cheaters dispersing
y	Relative frequency of cooperators dispersing
d	Overall investment in dispersal. $d = yn + z(1-n)$
$\Phi$	Overall cooperation with respect to the public good. $\Phi = n*(1-y^*) + (1-n)*z^*$
$\sigma$	Association between dispersal and cooperation. $\sigma = y/(y+z)$

group impacts the production and consumption of the public good, the tendency to disperse reduces these impacts because of the limited presence of dispersers in the source group.

**Life cycle and fitness equations**

We assume that a group's life-cycle has three sequential stages: colonization, growth, reproduction and survival of individuals within the group; exhaustion of resources; and the dispersal of survivors. Some of the survivors may stay at the same site of the source group, and others disperse as colonists to other sites.

The model tracks the fitness contribution of a mutant individual *i*, within group *j* [42,62]. Fitness effects are partitioned between cooperators and cheats—who have positive and negative impacts on the public good, respectively—and amongst dispersal strategies. Thus four strategies are possible: (1) cooperate and remain in group, (2) cooperate and disperse, (3) cheat and remain in group, and (4) cheat and disperse. Only the first and third strategies affect the public good.

The proportion of cooperators in the group is *n<sub>i</sub>* (for simplicity, hereafter we denote individual *i* within group *j* using the subscript *i* only), which can take continuous values between 0 and 1. Moreover, our model incorporates two dispersal strategies based on whether the dispersing individual is a cooperator or a cheater. We define *γ<sub>i</sub>* as the investment of a cooperator in dispersal and *z<sub>i</sub>* as the investment of a given cheater in dispersal. Both of these quantities take on continuous values between zero and one. The mean proportions of dispersing cooperators and cheaters in group *j* are *γ<sub>j</sub>n<sub>j</sub>* and *z<sub>j</sub>(1-n<sub>j</sub>)*, respectively and overall investment in dispersal is *d<sub>j</sub> = γ<sub>j</sub>n<sub>j</sub> + z<sub>j</sub>(1-n<sub>j</sub>)*.

The fitness equation takes the form

$$w_i = D(n_i, \gamma_i, z_i) E(n_i, \gamma_i, z_i) G(n_i, \gamma_i, z_i), \tag{1}$$

where the functions *D* and *E*, respectively, represent the contribution of selection on dispersal and the exploitation of the public good of individual *i* in group *j* to its own fitness. Function *G* is the overall investment in the public good in group *j*.

Dispersal is modeled by considering the fitness contributions of both individuals that stay at the site previously occupied by the group and others that disperse [73]. We assume that the costs of dispersal may differ between cooperators (*c*) and cheaters (*e*). Small costs would indicate abundant new sites for group establishment and high disperser survival. Although we consider different cases in the analysis, our general expectation is that the costs of cooperation will extend to dispersal, such that *c* > *e*.

The function, *D*, takes the form

$$D(n_i, \gamma_i, z_i) = \left[ \frac{(1 - z_i(1-n_i) - \gamma_i n_i)}{(1 - z_j(1-n_j) - \gamma_j n_j + (1-e)z(1-n) + (1-c)\gamma n)} \right] + \left[ \frac{((1-e)z_i(1-n_i) + (1-c)\gamma_i n_i)}{(1 - e z(1-n) - c \gamma n)} \right]. \tag{2}$$

The first term in square brackets describes the fitness of a non-disperser ( $1 - z_i(1-n_i) - \gamma_i n_i$ ) relative to the average non-disperser ( $1 - z_j(1-n_j) - \gamma_j n_j$ ) and immigrants  $((1-e)z(1-n) + (1-c)\gamma n)$ . The second term describes the fitness of a disperser  $((1-e)z_i(1-n_i) + (1-c)\gamma_i n_i)$  given the competition it faces with residents  $(1 - z(1-n) - \gamma n)$  and migrants  $((1-e)z(1-n) + (1-c)\gamma n)$  in another group. The terms *n*, *z* and *γ* (i.e., without subscripts) are population-wide means. The denominator in both terms represents the amount of competition faced either in the original group, in the case of a non-disperser, or in a new group, in the case of the disperser. Note that in the limit of no dispersal, individual fitness can still be positive under the assumption that groups survive indefinitely.

All non-dispersing individuals are selected to exploit, but given our assumption that there is a cost of cooperation (*s*), this will weight selection to favoring cheaters, all else being equal. The function, *E*, describes the contribution of individual *i* to its own fitness through exploitation of the public good and is given by

$$E(n_i, \gamma_i, z_i) = \frac{[(1-z_i)(1-n_i) + (1-s)(1-\gamma_i)n_i]}{[(1-z_j)(1-n_j) + (1-s)(1-\gamma_j)n_j]}, \tag{3}$$

where the subscript *j* indicates mean group levels, and the constant *s* measures the cost to individual cooperators in producing the public good.

The overall effect of group investment in the public good on individual fitness is described by

$$G(n_i, \gamma_i, z_i) = 1 + P(1-\gamma_j)n_j - Q(1-z_j)(1-n_j), \tag{4}$$

where it is assumed that non-dispersing cooperators have a positive effect on the public good (scaled by *P*) as their frequency, *n<sub>j</sub>*, increases [74,75], whereas cheaters have a net negative effect on the public good (scaled by *Q*) as their frequency,  $1-n_j$ , increases. Note that in the absence of cooperators, cheats can persist as long as their impact on the commons is sufficiently low ( $z Q < 1$ ). Alternatively, when group effects are nil (i.e. *P* = *Q* = 0), the notion of a group is a collection of autonomous individuals.

**Relatedness and numerical simulation methods**

We analyze the model by employing the Price Equation, which enables us to express possible fitness maxima as a function of constant parameters and variables, and the relatedness, *r*, between individuals. Taylor and Frank [62]

give methods for finding the equilibrium, such that for any trait  $v$  we have

$$dw_i/dv_i = \partial w_i/\partial v_i + r \partial w_i/\partial v_j \quad (5)$$

from which we can find a steady state(s) when  $dw_i/dv_i = 0$  to find any or all  $v^* = \gamma^*, z^*, n^*$ .

In our model,  $r$  can either be a parameter (referred to as an "open model" by Gardner and West [76]) or can emerge from the underlying structure of the population (referred to as a "closed" model in [76]). In the latter case, we may derive  $r$  from the dispersal of individuals in the population with the recursion relation (e.g., [39,76])

$$r(t+1) = 1/k + (k - 1)/k (1 - d)^2 r(t). \quad (6)$$

This recursion tracks the probability that a given focal individual is identical by descent to another randomly picked individual at time  $t$ . The parameter  $k$  is the effective number of individuals in the group, and can be viewed as a measure of genetic diversity due to individual aggregation in group founding and habitat structure. [Note however that our model does not explicitly track the actual number of individuals in the group]. Low  $k$  is indicative of group founding by single individuals, group resistance to immigration, and abundant open sites for group founding [10,77].

In the recursion above, the term  $1/k$  represents the probability that the randomly picked individual is the focal individual itself. The second term represents the probability that the randomly picked individual is different to the focal individual, and that neither have dispersed (represented by  $(1-d)^2$ ). This is multiplied by the relatedness from the previous round. Solving this recursion relation yields the equilibrium relatedness, which is

$$r = 1/(k - (k - 1) (1 - d)^2). \quad (7)$$

As we assume weak selection, the probability that a given individual disperses depends on the probability that it is a cooperator and disperses, plus the probability that it is a cheater and disperses, so  $d = \gamma n + z(1-n)$  in this case. Under the assumptions of weak selection, we evaluate this recursion for the case when  $v_i = v_j = v$ , where  $v$  is the trait in question.

Optimal strategies were solved numerically. This consisted of iterating equation (5) with steps of 0.05 or smaller for a total of 100,000 steps, which was sufficient to identify the steady state in all cases. We found that whereas initial levels of evolving variables did not affect the optimal solution when only dispersal frequencies  $\gamma$  and  $z$  evolved, initial conditions could indeed affect the

optimal solution when all three variables evolved. Closer examination showed that alternative stable states were possible, one with either all cheaters ( $n^* = 0$ ) or all cooperators ( $n^* = 1$ ), and a second with both strategies persisting ( $0 < n^* < 1$ ). Although we cannot exclude the existence of alternative interior equilibria, our numerical studies always yielded at most a single interior solution.

## Results

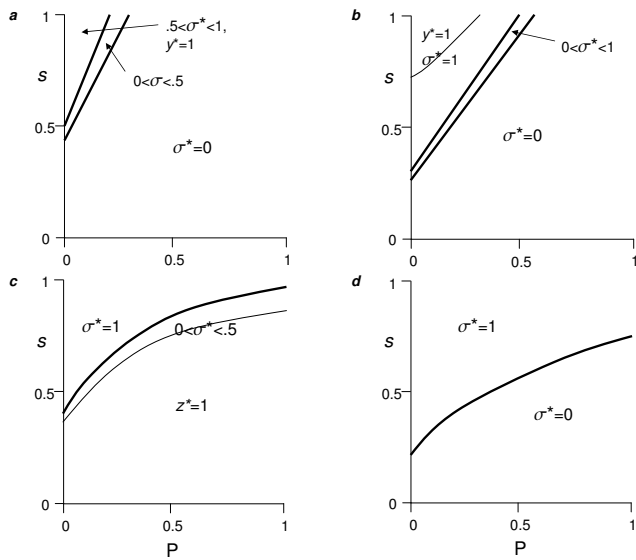
We consider two scenarios. In the first (Model 1) only dispersal in cooperators ( $\gamma$ ) and cheaters ( $z$ ) evolves, but not cooperation ( $n$ ). This situation would be obtained if mechanisms not explicitly included in the model (e.g., policing, [44]) controlled the level of cooperation, or if the frequencies of cooperative behaviors were either not subject to evolution, or labile to it over much longer time scales than dispersal. More generally however, empirical study suggests that cooperative behaviors are subject to selection [78-80] and we consider the case (Model 2) in which dispersal and the frequency of cooperators ( $n$ ) and cheaters ( $1-n$ ) co-evolve.

In addition to optimal levels of dispersal (Model 1), and of cooperation and dispersal (Model 2), we examine the effects of model parameters on dispersal specialization  $\sigma = \gamma^*/(\gamma^* + z^*)$ , and for Model 2 only, overall cooperation  $\Phi = n^*(1-\gamma^*) + (1-n^*)z^*$  (i.e., the sum of cooperators not dispersing and of cheaters dispersing). Note that when  $\sigma = 0$  (or  $\sigma = 1$ ), although all cooperators (cheats for  $\sigma = 1$ ) are sedentary it is not necessarily true that all cheats (cooperators for  $\sigma = 1$ ) disperse.

### Model 1

Optimal solutions always yielded partial or complete specialization, with cooperators tending to disperse more than cheaters (i.e.,  $\sigma > 0.5$ ) for high costs of cooperation ( $s$ ) compared to public good's effect ( $P$ ), and low cooperator frequencies ( $n$ ) (Figure 1). The reverse trends promote relative cheater dispersal ( $\sigma < 0.5$ ; Fig. 1). The impact of effective group size ( $k$ ) is more complex. Higher  $k$  tends to polarize dispersal to either cooperators ( $\gamma^* > 0, z^* = 0$ ) or cheaters ( $\gamma^* = 0, z^* > 0$ ), and increases the parameter space in which cooperators dominate dispersal (areas with  $\sigma^* = 1$ ; Fig. 1).

Low effective group size (low  $k$ ) should positively associate with kin competition, and in agreement with previous work [81,82], we find that low  $k$  is associated with higher overall dispersal,  $d^*$  (Figure 2a). Not surprisingly,  $d^*$  increases with lower cooperator frequencies ( $n$ ) and public good effects ( $P$ ) (Fig. 2a). However, the effects of  $k$  and  $n$  on the separate cooperator ( $\gamma^*$ ) and cheater ( $z^*$ ) dispersal frequencies are more complex (Figs. 2b, c). In particular, low  $k$  was always found to drive cheaters to disperse (Fig. 2c), whereas the effect on cooperators depended



**Figure 1**  
**Globally optimal associations in dispersal and exploitation strategy for Model 1.** Axes:  $P$  measures the impact of the public good on individual fitness, and  $s$  is the individual cost to cooperators in contributing to the public good.  $\sigma^* = \gamma^*/(z^* + \gamma^*)$  indexes the tendency of cooperators to disperse ( $\sigma^* > 0.5$ ) or cheats to disperse ( $\sigma^* < 0.5$ ). Thick curves demarcate areas of parameter space yielding different levels of  $\sigma$ , whereas thin lines show areas in which either  $\gamma^* = 1$  or  $z^* = 1$ . Caption a:  $k = 1.2, n = 0.1$ ; caption b:  $k = 10, n = 0.1$ ; caption c:  $k = 1.2, n = 0.9$ ; caption d:  $k = 10, n = 0.9$ . Note that for legibility, very thin areas parallel to thick lines are omitted, in which  $0.5 < \sigma^* < 1$  for caption c, and  $0 < \sigma^* < 1$  for caption d. Unless otherwise noted, dispersal rates are greater than zero and less than unity. Other parameters:  $c = e = 0.2, Q = 0.2$ . See main text for numerical methods.

strongly on cooperator frequency ( $n$ ) and public good productivity ( $P$ ) (Fig. 2b).

Cheater and cooperator dispersal can be understood as follows. When the group is dominated by cheaters (low  $n$ ) and production of the public good ( $P$ ) is small, increasing cooperator sedentariness ( $1-\gamma^*$ ) has little beneficial effect on fitness ( $w$ ), due to insufficient marginal gains via both individual exploitation ( $E$ ; eqn. 3) and the group effects ( $G$ ; eqn. 4). As a consequence, cooperators are selected to disperse more, relative to cheaters. Cheaters may disperse at high levels nonetheless (e.g., case of  $n = 0.1, k = 1.2$  in Fig. 2c), because in so doing, they lessen the effects of the tragedy of the commons on individual fitness of their kin. In contrast, when the group is dominated by cooperators (high  $n$ ) and public good production is high ( $P$ ), marginal fitness increases with cooperator sedentariness and, due to kin competition ( $k$ ), cheaters are selected to disperse more, relative to cooperators.

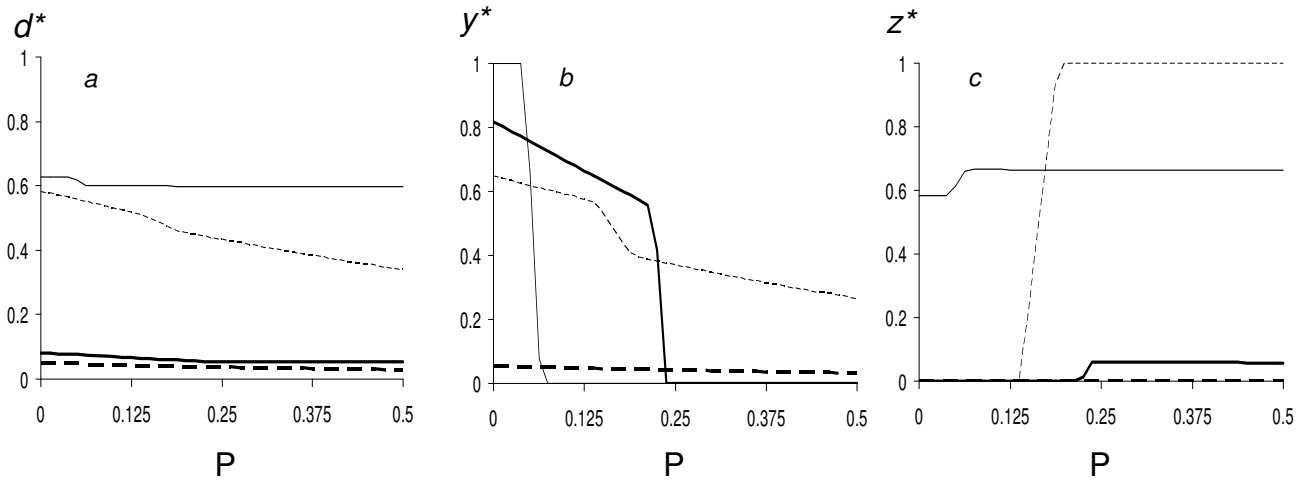
**Model 2**

Permitting social evolution introduces the possibility that the frequency of cooperators or cheaters fixes to zero or one, in which case associations ( $\sigma$ ) between dispersal and social strategies are irrelevant. We find that depending on parameter combinations, either only a single global optimum is obtained, or two alternative local optima are possible. In the latter case, which state is obtained depends on initial levels of  $\gamma, z$  and  $n$  in the numerical simulations. Figure 3 shows the fraction of simulations with random initial levels of  $n, \gamma$  and  $z$ , achieving either an internal equilibrium ( $0 < n^* < 1$ ), or one with all cooperators ( $n^* = 1$ ), or one with all cheaters ( $n^* = 0$ ) for different costs of cooperator dispersal ( $c$ ; Fig. 3a) and effective group sizes ( $k$ , Fig. 3b). For simplicity in the analyses below, we employ a single arbitrary starting condition ( $n = \gamma = z = 0.5$ ).

We observed four basic outcomes (Fig. 4): (1) fixation of cooperators ( $n^* = 1$ ), (2) fixation of cheaters ( $n^* = 0$ ), or coexistence of cooperators and cheaters with (3) the former only being sedentary ( $\sigma^* = 0$ ), or (4) the latter only being sedentary ( $\sigma^* = 1$ ). When  $\sigma^* = 0$  or  $\sigma^* = 1$  (i.e., all cooperators or cheaters sedentary, respectively), we further found outcomes in which all cheaters dispersed ( $z^* = 1$ ) or all cooperators dispersed ( $\gamma^* = 1$ ), respectively. Parameter effects are generally similar to Model 1, but with some notable contrasts.

Whereas in Model 1, the relative cost of cooperator ( $c$ ) and cheater ( $e$ ) dispersal did not yield a simple threshold condition for optimal outcomes (not shown), it did so for Model 2. We found that when cooperators and cheaters coexisted and  $e > c$ , cooperators dispersed and cheaters did not (i.e.,  $\sigma^* = 1$ ) (Figs. 4a, b). The reverse held when  $c > e$  (Figs. 4c, d). Low effective group size ( $k$ ) increases cooperator persistence (i.e., smaller areas in which  $n^* = 0$  in Fig. 4), with the effects on cheater persistence contingent on other parameters (i.e., differences in areas with  $n^* = 0$  in Fig. 4). More interestingly, whereas when  $e > c$ , lower  $k$  shifts the parameter space permitting cooperators and cheaters to coexist and has little effect on the area in which all cooperators disperse ( $\gamma^* = 1$ ), when  $c > e$ , it expands the area of coexistence and that in which all cheaters disperse ( $z^* = 1$ ) (Fig. 4). Finally, relatedness ( $r^*$ ) generally increases with high  $P:s$  ratios, low  $k$ , and high costs to cooperator dispersal,  $c$ , with respect to cheater dispersal,  $e$  (Fig. 5). Interestingly, specialization in dispersal by cheaters and in sedentariness by cooperators tends to associate with high, but not the highest levels of relatedness (cf Figs. 4c, 5c).

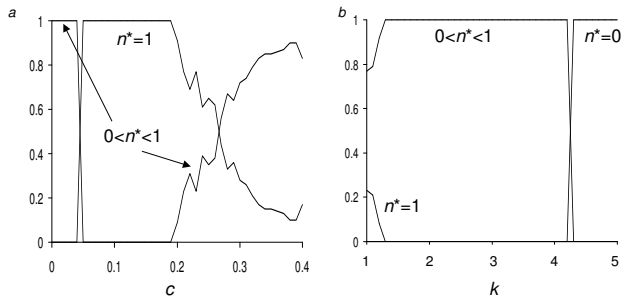
If we define the functional role of a cooperator as contributing to the public good, and that well functioning groups minimize the impact of cheats on the public good, then,



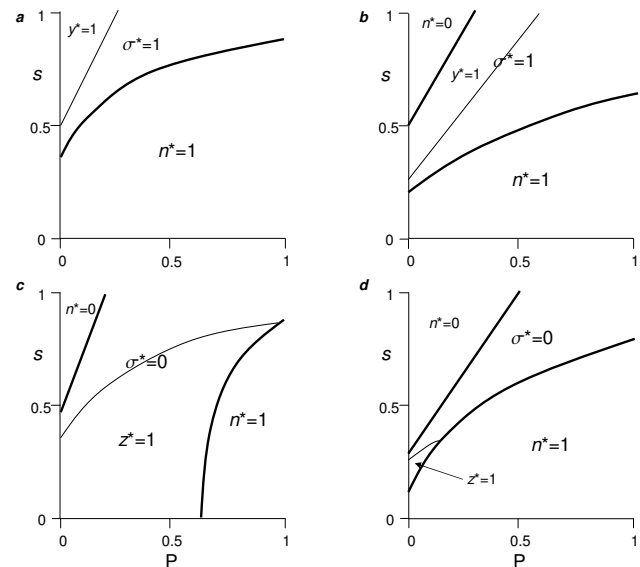
**Figure 2**  
**Effects of parameters on optimal dispersal levels for Model 1.** Effects of public good production ( $P$ ), frequency of cooperators ( $n$ ) and effective group size ( $k$ ). Caption a: overall dispersal  $d^*$ ; Caption b: investment in cooperator dispersal  $y^*$ ; Caption c investment in cheater dispersal  $z^*$ . Thin line:  $k = 1.2, n = 0.1$ ; dashed line:  $k = 10, n = 0.1$ ; thick line:  $k = 1.2, n = 0.9$ ; thick dashed line:  $k = 10, n = 0.9$ . Other parameters:  $c = e = 0.2, Q = 0.2, s = 0.6$ .

trivially, specialization resulting in mobile cooperators and sedentary cheaters corresponds to a non-social, individualistic scenario, and cannot be considered a group related phenomenon. There are however two ways in which the impact of cheaters on the commons can be reduced: either  $1-n^*$  decreases and/or  $z^*$  increases. Figure 6 presents the effects of model processes on overall cooperation, defined as  $\Phi = n^* (1-y^*) + (1-n^*) z^*$ . We see that although high levels of  $\Phi$  are generally promoted for high  $P:s$  ratios, perfect overall cooperation ( $\Phi = 1$ ) is most read-

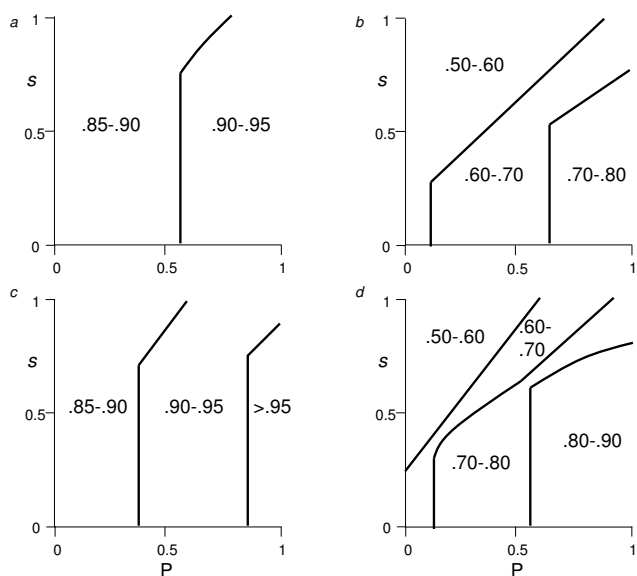
ily obtained at low  $k$  and intermediate  $P:s$  ratios (e.g. Fig. 6c).



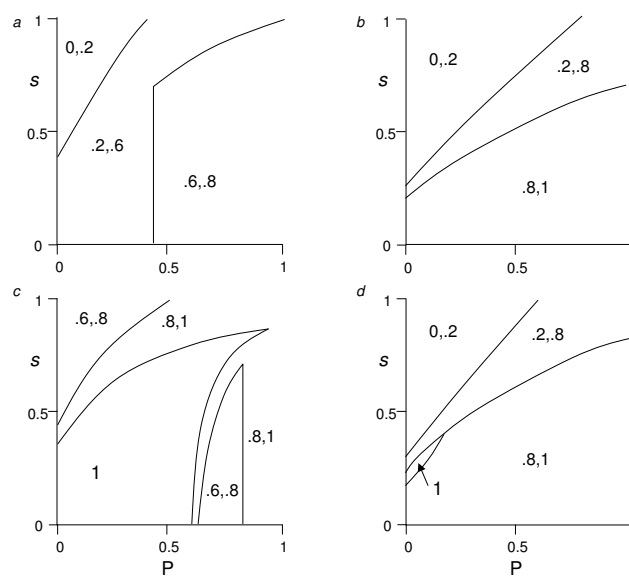
**Figure 3**  
**The fraction of simulations in Model 2 leading to different local optima.** Results based on 100 simulations in which initial levels of  $n, y$ , and  $z$  are each set to a random number between zero and one, inclusive. These simulations produced one of three equilibria:  $n^* = 0, 0 < n^* < 1$  or  $n^* = 1$ . Caption a effect of the cost of cooperator dispersal ( $c$ ) with  $P = Q = 0.3, s = 0.5, k = 2, e = 0.2$ ; caption b effect of effective group size ( $k$ ) with  $P = Q = 0.2, s = 0.6, e = 0.2, c = 0.3$ .



**Figure 4**  
**Locally optimal associations between dispersal and exploitation strategy.** The frequency of dispersal in cooperators ( $y$ ) and cheaters ( $z$ ) evolves, and the frequency of cooperators ( $n$ ) and cheaters ( $1-n$ ) evolves. Initial frequencies in numerical studies:  $y = z = n = 0.5$ . As for Figure 1 except caption a:  $k = 1.2, c = 0.1$ ; caption b:  $k = 10, c = 0.1$ ; caption c:  $k = 1.2, c = 0.3$ ; caption d:  $k = 10, c = 0.3$ .



**Figure 5**  
**Relatedness,  $r^*$ , associated with simulations in Figure 4.**



**Figure 6**  
**Overall cooperation,  $\Phi = n^*(1 - \gamma^*) + (1 - n^*)z^*$ , associated with simulations in Figure 4.**

**Discussion**

Our results are in broad agreement with the tenets of kin selection theory for explaining dispersal [45,81,82] and the maintenance of cooperative behaviors [83-85]. Specifically, we found that dispersal specialization leading to high levels of overall cooperation ( $\Phi$ ) is promoted by sufficient benefit to cost ratios ( $P : s$ ) of cooperation and by kin selection (low  $k$ ). The one apparent discrepancy to previous theory is, whereas higher benefit ( $P$ ) to cost ( $s$ ) ratios promote cooperation, higher kin selection (low  $k$ ) was sometimes observed to reduce the relative frequency of cooperators ( $n^*$ ) (cf. Figs. 4c, d). This can be explained if we consider cheaters dispersing from the group as a type of cooperative behavior. Dispersing cheaters are effectively 'cooperative' because of the incurred individual cost of dispersal ( $e$ ), and the benefits to the group in having less negative impact on the commons ( $Q$ ) (cf. Figs 4c, d with Figs. 6c, d). Moreover, we found that partial or total specialization of otherwise somatic cheats as dispersing germ line occurred without the need for costly modifiers [86] or the repression of cheaters [[87,88], but see [22]], suggesting that the mechanism identified here is applicable to a wider range of organisms where these mechanisms do not sufficiently reduce somatic cheating, or cannot evolve. Conversely, control mechanisms such as rewarding and punishment, which might be operating in many systems (see examples in Additional file 1), do not preclude the functionality of the mechanism demonstrated in this study (cf. Model 1).

The examples presented in Table S1 (see Additional file 1) and our theoretical findings suggest a common conceptual and mechanistic foundation for the evolution of cooperation and individual functional specialization within groups (e.g., multicellularity). Most of the empirical examples share the feature that cooperators are less dispersive than more competitive individuals. For instance, low dispersal coincides with physical binding in bacteria that generate biofilms as a public good by polymer production [79,89] (but see ref. [90] for an alternative interpretation), with alloparental care of offspring in cooperative breeding [91], or with complete genetic altruism in certain eusocial insects [92]. It is worth noting that a consistent differentiation of roles regarding sedentariness and dispersal in relation to cooperation and cheating may be much more common in nature than currently believed (e.g. [93]). Because there is no prior formal theory predicting such a relationship, empirical research on this issue is rare and suitable data are therefore scant. We stress that our theory does not elucidate the precise evolutionary pathway leading to complete multicellularity [16,77], but rather assesses the forces promoting or forestalling different levels of specialization of cooperators and cheaters as functional germ line and soma. As such, the observations of biased dispersal in Table S1 (see Additional file 1) have alternative explanations, including forced eviction [94] and individual-based habitat selection [95]. Experimental (e.g., [79,80,96-98]), phylogenetic (e.g., [6]), and theoretical (e.g., [13,22] and see discussion below) approaches are fruitful avenues to explore alternative explanations and pathways.



Transitions in individuality and social complexity are generally thought to require some form of reduction in genetic variance during the reproductive process [20,77]. Genetic heterogeneity can emerge from many sources [99], and the recursive equation 6 in our framework greatly simplifies these, only explicitly including the effects of dispersal. Our results confirm the importance of relatedness in achieving multicellularity, but also show that the highest levels of relatedness did not necessarily yield full specialization of cooperators or cheaters as dispersers, and that complete specialization could occur at relatedness levels as low as 0.7 (Fig. 4d). As such, our findings could extend to some systems in which groups are formed by the initial aggregation of non-kin [10,74,87,99]. Further study is needed to explore this prediction in detail, since our model did not explicitly account for different lineages, and as such we do not know how spatial heterogeneities in relatedness might influence our results [100].

Our findings have precedent, both in the study of symbiotic associations, and investigations of cooperation within species. With regard to host-parasite and symbiotic interactions, previous research has considered how parasite virulence (which is analogous to cheaters exploiting cooperative groups) may evolve spatially (e.g., [101]; for reviews see [102,103]). In the case of horizontal transmission in parasites, which is analogous to the level of dispersal in our model (see also [73]), theory generally predicts that increased horizontal transmission ( $z$  in our model) associates with higher parasite virulence ( $Q(1-n)$  in our model) [103]. Despite allowing for relatedness between potential cooperators and cheaters we have a comparable finding, whereby an increasing tragedy of the commons pushes cheating individuals to disperse; this is both because of increased individual fitness opportunities through dispersal ( $z$ ) and increased inclusive fitness through lowered group effects for those related individuals that do not disperse ( $Q(1-n)(1-z)$ ).

In a model investigating cooperation in spatially viscous environments, van Baalen and Rand [45] suggested that non-altruists should disperse more readily than altruists and hypothesized that this could be viewed as a transition towards multicellularity. Koella [104] studied the independent dispersal of altruists and of cheaters in a spatially explicit setting and found that a polymorphism could arise in which altruists dispersed and interacted locally, whereas cheaters evolved longer dispersal distances and exploited altruistic clusters. Hamilton and Taborsky [95] showed that when the propensities to cooperate by generalized reciprocity and to disperse evolve independently, under a wide range of conditions either cooperation or defection is associated with dispersal, depending on the probability of finding new groups and on the costs of

being alone. Over most of the range of mobility costs examined, cooperation was negatively correlated with mobility, while defection was not. Ultimately, this leads to assortment between altruists and defectors in the population (see also [105]), which secondarily can generate group selection effects [106,107]. Hamilton and Taborsky [95] did not check for linkage effects, however. In another study of the joint evolution of altruism and mobility, Le Galliard and coworkers [108] found that more altruism enhancing local aggregation can select for increased mobility. The synergistic selective interaction between altruism and mobility may cause dispersal to be considerably higher than that predicted in a purely selfish population, if altruism costs accelerate slowly and mobility costs are moderate. However, their model did not reveal a polymorphism to occur between selfish-mobile and altruistic-sessile phenotypes as found so often in nature, from microbes and unicellular algae to mammals (e.g. [18,32,109]; Additional file 1). Queller [10] argued that the resolution of within-organism conflicts could occur if an altruism allele is expressed conditional on the environment, the altruistic act being an individual removing itself from the germ line in order to perform an enhanced somatic activity. Rainey [110] verbally proposed an idea similar in some respects to these studies, in which group selection acts to promote the functional separation of germ and soma in bacterial biofilms through the dispersal of cheats (see also [79]). Finally, Michod [14] showed how the specialization of lower level units into germ and soma could be associated with the transfer of fitness from lower units to the new higher individual. A critical feature of his model is the tradeoff between the viability and fecundity of lower level units, which, for convex relationships, creates disruptive selection for cooperative germ and soma. Our study, whilst generating congruent results, is to our knowledge the first to demonstrate that the evolution of lower level units based on their effects on the commons can yield dispersal specialization, one of the precursors for selection at the group level and the evolution of full multicellularity.

## Conclusion

Our results suggest that the establishment of trait linkage between dispersal and the propensity of within-group cheating may be a general phenomenon promoting complex social organization and multicellularity. Importantly, we cautiously suggest this should be operative regardless of whether groups ever achieve higher levels of individuality, because selection on individual components will always tend to increase exploitation, and stronger group structure will tend to increase overall cooperation through kin selected benefits [42,84]. Partial or full reduction in the negative effects of cheaters on the commons through their specialization as dispersers offers partial solutions to two problems: the evolution of cooperation in social

groups and the origin of the specialization of germ and soma in multicellular organisms. Our model is, nevertheless, a highly simplified caricature of real systems and future theoretical and empirical study is needed to explore its robustness.

### Authors' contributions

MEH conceived the study, developed and analyzed the model and wrote the manuscript. DJR participated in the design of the study, developed the model and participated in writing the manuscript. MT participated in the design of the study, constructed Table S1, and participated in writing the manuscript. All authors read and approved the final manuscript.

### Additional material

#### Additional file 1

(Table S1). Examples of group formation for which there is some information on dispersal, relatedness and punishment/policing.

Click here for file

[<http://www.biomedcentral.com/content/supplementary/1471-2148-8-238-S1.doc>]

### Acknowledgements

We thank Daniel Blumstein, Ross Crozier, Steve Frank, Toby Kiers, Barbara Taborsky, Peter Taylor and Don Waller for helpful discussions, and Steve Frank, Andy Gardner, Paul Rainey, Stuart West and two anonymous reviewers for comments on earlier drafts. MEH acknowledges the Santa Fe Institute (2005), the National Center of Ecological Analysis and Research (2006–2007), and the Centre National de la Recherche Scientifique for financial support. MT and DJR acknowledge the Swiss National Science Foundation for support (SNF-grant 3100A0-105626).

### References

- Buss LW: *The Evolution of Individuality* Princeton: Princeton University Press; 1987.
- Michod RE: **Cooperation and conflict in the evolution of individuality. II. Conflict mediation.** *Proc R Soc Lond B* 1996, **263**:813-822.
- Michod RE, Roze D: **Cooperation and conflict in the evolution of individuality. III. Transitions in the unit of fitness.** In *Mathematical and Computational Biology: Computational Morphogenesis, Hierarchical Complexity, and Digital Evolution* Edited by: Nehaniv CL. Providence: American Mathematical Society; 1999:47-92.
- Michod RE, Nedelcu AM, Roze D: **Cooperation and conflict in the evolution of individuality IV. Conflict mediation and evolvability in *Volvox carteri*.** *Biosystems* 2003, **69**:95-114.
- Maynard Smith J, Szathmari E: *The Major Transitions in Evolution* New York: WH Freeman; 1995.
- Bell G, Mooers AO: **Size and complexity among multicellular organisms.** *Biol J Linn Soc* 1997, **60**:345-363.
- Bonner JT: **The Origins of Multicellularity.** *Integr Biol* 1998, **1**:27-36.
- Grosberg RK, Strathmann RR: **The evolution of multicellularity: A minor major transition.** *Ann Rev Ecol Syst* 2007, **38**:621-654.
- Kirk DL: **A twelve-step program for evolving multicellularity and a division of labor.** *Bioessays* 2005, **27**:299-310.
- Queller DC: **Relatedness and the fraternal major transitions.** *Phil Trans Roy Soc Lond B* 2000, **355**:1647-1655.
- Wilson DS: **Theory of group selection.** *Proc Natl Acad Sci USA* 1975, **72**:143-146.
- Bell G: **The origin and early evolution of germ cells as illustrated in the Volvocales.** In *The Origin and Evolution of Sex* Edited by: Halvorson H, Monroy A. New York: Liss; 1985:221-56.
- Pfeiffer T, Bonhoeffer S: **An evolutionary scenario for the transition to undifferentiated multicellularity.** *Proc Natl Acad Sci USA* 2003, **100**:1095-1098.
- Michod RE: **The group covariance effect and fitness trade-offs during evolutionary transitions.** *Proc Natl Acad Sci USA* 2006, **103**:9113-9117.
- Michod R: *Darwinian Dynamics* Princeton; Princeton University Press; 1999.
- Michod RE: **Cooperation and conflict during the origin of multicellularity.** In *Genetic and Cultural Evolution of Cooperation* Edited by: Hammerstein P. Cambridge: MIT Press; 2003:261-307.
- Hurst LD: **Parasite diversity and the evolution of diploidy, multicellularity and anisogamy.** *J theor Biol* 1990, **144**:429-443.
- Koufopanou V, Bell G: **Soma and germ: an experimental approach using *Volvox*.** *Proc R Soc London Ser B* 1993, **254**:107-13.
- Otto SP, Hastings IM: **Mutation and selection within the individual.** *Genetica* 1998, **102/103**:507-24.
- Frank SA: **Host control of symbiont transmission: the separation of symbionts into germ and soma.** *Am Nat* 1996, **148**:1113-1124.
- Firtel RA: **Integration of signaling information in controlling cell-fate decisions in *Dictyostelium*.** *Genes and Development* 1995, **9**:1427-1444.
- Hudson RE, Aukema JE, Rispe C, Roze D: **Altruism, cheating, and anticheater adaptations in cellular slime molds.** *Am Nat* 2002, **160**:31-43.
- Foster KR, Shaulsky G, Strassmann JE, Queller DC, Thompson CRL: **Pleiotropy as a mechanism to stabilize cooperation.** *Nature* 2004, **431**:693-696.
- Rinkevich B: **Natural chimerism in colonial urochordates.** *Journal of Experimental Marine Biology and Ecology* 2005, **322**:93-109.
- Taborsky M: **Breeder-helper conflict in a cichlid fish with broodcare helpers – an experimental analysis.** *Behaviour* 1985, **95**:45-75.
- Balshine-Earn S, Neat FC, Reid H, Taborsky M: **Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish.** *Behavioral Ecology* 1998, **5**:432-438.
- Bergmüller R, Taborsky M: **Experimental manipulation of helping in a cooperative breeder: helpers 'pay to stay' by pre-emptive appeasement.** *Animal Behaviour* 2005, **69**:19-28.
- Bergmüller R, Heg D, Taborsky M: **Helpers in a cooperatively breeding cichlid stay and pay or disperse and breed, depending on ecological constraints.** *Proc R Soc Lond B* 2005, **272**:325-331.
- Young AJ, Carlson AA, Clutton-Brock T: **Trade-offs between extraterritorial prospecting and helping in a cooperative mammal.** *Animal Behaviour* 2005, **70**:829-837.
- Skubic E, Taborsky M, McNamara JM, Houston AI: **When to parasitize? A dynamic optimization model of reproductive strategies in a cooperative breeder.** *J theor Biol* 2004, **227**:487-501.
- Stephens PA, Russell AF, Young AJ, Sutherland WJ, Clutton-Brock TH: **Dispersal, eviction, and conflict in meerkats (*Suricata suricatta*): an evolutionarily stable strategy model.** *Am Nat* 2005, **165**:120-35.
- O'Riain MJ, Jarvis JUM, Faulkes CG: **A dispersive morph in the naked mole-rat.** *Nature* 1996, **380**:619-621.
- O'Riain MJ, Jarvis JUM, Alexander R, Buffenstein R, Peeters C: **Morphological castes in a vertebrate.** *PNAS* 2000, **97**:13194-13197.
- Scantlebury M, Speakman JR, Oosthuizen MK, Roper TJ, Bennett NC: **Energetics reveals physiologically distinct castes in a eusocial mammal.** *Nature* 2006, **440**:795-797.
- Bennett NC, Faulkes CG, Molteno AJ: **Reproductive suppression in subordinate, non-breeding female Damaraland mole-rats: Two components to a lifetime of socially induced infertility.** *Proc R Soc Lond B* 1996, **263**:1599-1603.
- Clarke FM, Faulkes CC: **Intracolony aggression in the eusocial naked mole-rat, *Heterocephalus glaber*.** *Animal Behaviour* 2001, **61**:311-324.
- Velicer GJ, Yu YTN: **Evolution of novel cooperative swarming in the bacterium *Myxococcus xanthus*.** *Nature* 2003, **425**:75-78.
- Hardin G: **Tragedy of commons.** *Science* 1968, **162**:1243-1248.

39. Rankin DJ, Bargum K, Kokko H: **The tragedy of the commons in evolutionary biology.** *Trends Ecol Evol* 2007, **22**:643-651.
40. Hamilton WD: **Kinship, recognition, disease, and intelligence: constraints of social evolution.** In *Animal Societies: Theories and Facts* Edited by: Ito J, Brown JL, Kikkawa K. Tokyo: Jpn Sci Soc; 1987:81-102.
41. Queller DC: **A general model for kin selection.** *Evolution* 1992, **46**:376-80.
42. Frank SA: *Foundations of social evolution* Princeton: Princeton University Press; 1998.
43. Trivers RL: **The evolution of reciprocal altruism.** *Q Rev Biol* 1971, **46**:35-57.
44. Frank SA: **Repression of competition and the evolution of cooperation.** *Evolution* 2003, **57**:693-705.
45. van Baalen M, Rand DA: **The unit of selection in viscous populations and the evolution of altruism.** *J theor Biol* 1998, **143**:631-648.
46. West SA, Pen I, Griffin AS: **Cooperation and competition between relatives.** *Science* 2002, **296**:72-75.
47. Santos FC, Rodrigues JF, Pacheco JM: **Graph topology plays a determinant role in the evolution of cooperation.** *Proc Royal Soc London B* 2006, **273**:51-55.
48. Grafen A: **Do animals really recognize kin?** *Anim Behav* 1990, **39**:42-54.
49. Hochberg ME, Sinervo B, Brown SP: **Socially mediated speciation.** *Evolution* 2003, **57**:154-158.
50. Axelrod R, Hammond RA, Grafen A: **Altruism via kin-selection strategies that rely on arbitrary tags with which they co-evolve.** *Evolution* 2004, **58**:1833-48.
51. Crespi BJ: **The evolution of social behavior in microorganism.** *Trends Ecol Evol* 2001, **16**:178-83.
52. Sachs J, Mueller IG, Wilcox TP, Bull JJ: **The evolution of cooperation.** *Q Rev Biol* 2004, **79**:135-60.
53. Lehmann L, Keller L: **The evolution of cooperation and altruism – a general framework and a classification of models.** *J Evol Biol* 2006, **19**:1365-1376.
54. West SA, Griffin AS, Gardner A: **Evolutionary explanations for cooperation.** *Current Biology* 2007, **17**:R661-R672.
55. Santelices B: **How many kinds of individuals are there?** *Trends Ecol Evol* 1999, **14**:152-155.
56. Müller WEG: **The origin of metazoan complexity: Porifera as integrated animals.** *Integrative and Comparative Biology* 2003, **43**:3-10.
57. Foster KR, Fortunato A, Strassmann JE, Queller DC: **The costs and benefits of being a chimera.** *Proc R Soc London Ser B* 2002, **269**:2357-62.
58. Wilson DS, Sober E: **Reviving the superorganism.** *J theor Biol* 1989, **136**:337-356.
59. Gardner A, West SA, Barton NH: **The relation between multilocus population genetics and social evolution theory.** *Am Nat* 2007, **169**:207-226.
60. Keller L, Ed: *Levels of Selection in Evolution* Princeton; Princeton University Press; 1999.
61. Helms Cahan S: **Cooperation and conflict in social groups: insights from geographic variation.** *Anim Behav* 2001, **61**:819-825.
62. Taylor PD, Frank SA: **How to make a kin selection model.** *J theor Biol* 1996, **180**:27-37.
63. Helms Cahan S, Blumstein DT, Sundstrom L, Liebig J, Griffin A: **Social trajectories and the evolution of social behavior.** *Oikos* 2002, **96**:206-216.
64. Bonner JT: **Evolutionary strategies and developmental constraints in the cellular slime molds.** *American Naturalist* 1982, **119**:530-552.
65. Nonacs P: **A life-history approach to group living and social contracts between individuals.** *Ann Zool Fenn* 2001, **38**:239-254.
66. Taborsky M: **The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes.** *J Heredity* 2001, **92**:100-110.
67. Roff DA: *The Evolution of Life Histories* New York: Chapman & Hall; 1992.
68. Zera AJ, Denno RF: **Physiology and ecology of dispersal polymorphism in insects.** *Ann Rev Entom* 1997, **42**:207-230.
69. Zera AJ, Harshman LG: **The physiology of life history trade-offs in animals.** *Ann Rev Ecol Syst* 2001, **32**:95-126.
70. Zera AJ, Zhao ZW: **Intermediary metabolism and life-history trade-offs: Differential metabolism of amino acids underlies the dispersal-reproduction trade-off in a wing-polymorphic cricket.** *Am Nat* 2006, **167**:889-900.
71. Langellotto GA, Denno RF, Ott JR: **A trade-off between flight capability and reproduction in males of a wing-dimorphic insect.** *Ecology* 2000, **81**:865-875.
72. Hughes CL, Hill JK, Dytham C: **Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries.** *Proc R Soc Lond B* 2003, **270**:S147-S150.
73. Frank SA: **Kin selection and virulence in the evolution of protozoa and parasites.** *Proc R Soc Lond B* 1994, **258**:153-161.
74. Avilés L, Fletcher JA, Cutter AD: **The kin composition of social groups: Trading group size for degree of altruism.** *Am Nat* 2004, **164**:132-144.
75. Clutton-Brock TH: **Behavioral ecology – Breeding together: Kin selection and mutualism in cooperative vertebrates.** *Science* 2002, **296**:69-72.
76. Gardner A, West SA: **Demography, altruism, and the benefits of budding.** *J Evol Biol* 2006, **19**:1707-1716.
77. Maynard Smith J: **Evolutionary progress and the levels of selection.** In *Evolutionary Progress* Edited by: Nitecki MH. Chicago: University of Chicago Press; 1989:219-230.
78. Dugatkin LA: *Cooperation Among Animals an Evolutionary Perspective* Oxford: Oxford University Press; 1997.
79. Rainey PB, Rainey K: **Evolution of cooperation and conflict in experimental bacterial populations.** *Nature* 2003, **425**:72-74.
80. Brockhurst MA, Hochberg ME, Bell T, Buckling A: **Character displacement promotes cooperation in bacterial biofilms.** *Current Biology* 2006, **16**:2030-2034.
81. Hamilton WD, May RM: **Dispersal in stable habitats.** *Nature* 1977, **269**:578-581.
82. Frank SA: **Dispersal polymorphisms in subdivided populations.** *J theor Biol* 1986, **122**:303-309.
83. Hamilton WD: **The genetical evolution of social behavior, I & II.** *J theor Biol* 1964, **1**:1-52.
84. Lehmann L, Keller L, West S, Roze D: **Group selection and kin selection: Two concepts but one process.** *Proc Natl Acad Sci USA* 2007, **104**:6736-6739.
85. Taylor PD: **Altruism in viscous populations – an inclusive fitness model.** *Evol Ecol* 1992, **6**:352-356.
86. Frank SA: **Host-symbiont conflict over the mixing of symbiotic lineages.** *Proc R Soc Lond B* 1996, **263**:339-344.
87. Dierkes P, Taborsky M, Kohler U: **Reproductive parasitism of broodcare helpers in a cooperatively breeding fish.** *Behav Ecol* 1999, **10**:510-515.
88. Boyd R, Richerson PJ: **Punishment allows the evolution of cooperation (or anything else) in sizable groups.** *Ethol Sociobiol* 1992, **13**:171-195.
89. Hall-Stoodley L, Costerton JW, Stoodley P: **Bacterial biofilms: From the natural environment to infectious diseases.** *Nature Reviews Microbiology* 2004, **2**:95-108.
90. Xavier JB, Foster KR: **Cooperation and conflict in microbial biofilms.** *Proc Natl Acad Sci USA* 2007, **104**:876-881.
91. Komdeur J: **Variation in individual investment strategies among social animals.** *Ethology* 2006, **112**:729-747.
92. Hamilton WD: **Altruism and related phenomena mainly in the social insects.** *Ann Rev Ecol Syst* 1972, **3**:193-232.
93. Fjerdingstad EJ, Schtickzelle N, Manhes P, Gutierrez A, Clobert J: **Evolution of dispersal and life history strategies – *Tetrahymena ciliates*.** *BMC Evolutionary Biology* 2007, **7**:133.
94. Hamilton IM, Taborsky M: **Unrelated helpers will not fully compensate for costs imposed on breeders when they pay to stay.** *Proc R Soc Lond B* 2005, **272**:445-454.
95. Hamilton IM, Taborsky M: **Contingent movement and cooperation evolve under generalized reciprocity.** *Proc R Soc Lond B* 2005, **272**:2259-2267.
96. Velicer GJ, Kroos L, Lenski RE: **Loss of social behaviors by *Myxococcus xanthus* during evolution in an unstructured habitat.** *PNAS* 1998, **95**:12376-12380.
97. Strassmann JE, Zhu Y, Queller DC: **Altruism and social cheating in the social amoeba *Dictyostelium discoideum*.** *Nature* 2000, **408**:965-967.
98. Gilbert O, Foster KR, Mehdiabadi NJ, Strassmann JE, Queller DC: **High relatedness maintains multicellular cooperation in a**

- social amoeba by controlling cheater mutants. *Proceedings of the National Academy of Sciences* 2007, **104**:8913-8917.
99. Pineda-Krch M, Lehtilä K: **Costs and benefits of genetic heterogeneity within organisms.** *J Evol Biol* 2004, **17**:1167-77.
  100. Roze D, Rousset F: **The robustness of Hamilton's rule with inbreeding and dominance: kin selection and fixation probabilities under partial sibmating.** *The American Naturalist* 2004, **164**:214-231.
  101. Kamo M, Boots M: **The evolution of parasite dispersal, transmission, and virulence in spatial host populations.** *Evol Ecol Res* 2006, **8**:1333-1347.
  102. Ewald PVW: *Evolution of Infectious Disease* Oxford: Oxford University Press; 1994.
  103. Frank SA: **Models of parasite virulence.** *Q Rev Biol* 1996, **71**:37-78.
  104. Koella JC: **The spatial spread of altruism versus the evolutionary response of egoists.** *Proc R Soc Lond B* 2000, **267**:1979-1985.
  105. Pepper JW, Smuts BB: **A mechanism for the evolution of altruism among nonkin: Positive assortment through environmental feedback.** *Am Nat* 2002, **160**:205-213.
  106. Wilson DS, Dugatkin LA: **Group selection and assortative interactions.** *Am Nat* 1997, **149**:336-351.
  107. Aktipis CA: **Know when to walk away: contingent movement and the evolution of cooperation.** *J theor Biol* 2004, **231**:249-260.
  108. Le Galliard J-F, Ferrière R, Dieckmann U: **Adaptive evolution of social traits: Origin, trajectories, and correlations of altruism and mobility.** *Am Nat* 2005, **165**:206-224.
  109. Kirk DL: **Seeking the ultimate and proximate causes of *Volvox* multicellularity and cellular differentiation.** *Integrative and Comparative Biology* 2003, **43**:247-253.
  110. Rainey PB: **Unity from conflict.** *Nature* 2007, **446**:616.
  111. Turner PE, Chao L: **Sex and the evolution of intrahost competition in RNA virus  $\Phi 6$ .** *Genetics* 1998, **150**:523-532.
  112. Turner PE, Chao L: **Escape from prisoner's dilemma in RNA phage  $\Phi 6$ .** *American Naturalist* 2003, **161**:497-505.
  113. Chao L, Levin BR: **Structured habitats and the evolution of anticompensator toxins in bacteria.** *Proc Natl Acad Sci USA* 1981, **78**:6324-6328.
  114. Riley MA, Wertz JE: **Bacteriocins: evolution, ecology and application.** *Annual Review of Microbiology* 2002, **56**:117-137.
  115. Feldgarden M, Riley MA: **The phenotypic and fitness effects of colicin resistance in *Escherichia coli* K-12.** *Evolution* 1999, **53**:1019-1027.
  116. Klausen M, Gjermansen M, Kreft JU, Tolker-Nielsen T: **Dynamics of development and dispersal in sessile microbial communities: examples from *Pseudomonas aeruginosa* and *Pseudomonas putida* model biofilms.** *Fems Microbiology Letters* 2006, **261**:1-11.
  117. Bantinali E, Kassen R, Knight CG, Robinson Z, Spiers AJ, Rainey PB: **Adaptive divergence in experimental populations of *Pseudomonas fluorescens*. III. mutational origins of wrinkly spreader diversity.** *Genetics* 2007, **176**:441-453.
  118. Spormann AM: **Gliding motility in bacteria: insights from studies of *Myxococcus xanthus*.** *Microbiol Mol Biol Rev* 1999, **63**:621-641.
  119. Fiegna F, Velicer GJ: **Exploitative and hierarchical antagonism in a cooperative bacterium.** *Plos Biology* 2005, **3**:1980-1987.
  120. Fiegna F, Yu YTN, Kadam SV, Velicer GJ: **Evolution of an obligate social cheater to a superior cooperater.** *Nature* 2006, **441**:310-314.
  121. Vos M, Velicer GJ: **Genetic population structure of the soil bacterium *Myxococcus xanthus* at the centimeter scale.** *Applied and Environmental Microbiology* 2006, **72**:3615-3625.
  122. Sesti F, Shih TM, Nikolaeva N, Goldstein SA: **Immunity to KI killer toxin: internal TOKI blockade.** *Cell* 2001, **105**:637-644.
  123. Greig D, Travisano M: **The Prisoner's Dilemma and polymorphism in yeast *SUC* genes.** *Proceedings of the Royal Society of London B* 2004, **271**:S25-S26.
  124. Greig D, Travisano M: **The prisoner's dilemma and polymorphism in yeast *SUC* genes.** *Proc R Soc Lond B* 2004, **271**:S25-S26.
  125. MacLean RC, Gudelf I: **Resource competition and social conflict in experimental populations of yeast.** *Nature* 2006, **441**:498-501.
  126. Filosa MF: **Heterocytosis in cellular slime molds.** *American Naturalist* 1962, **96**:73-91.
  127. Buss LW: **Somatic cell parasitism and the evolution of somatic tissue compatibility.** *Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences* 1982, **79**:5337-5341.
  128. Dao DN, Kessin RH, Ennis HL: **Developmental cheating and the evolutionary biology of *Dictyostelium* and *Myxococcus*.** *Microbiology-Uk* 2000, **146**:1505-1512.
  129. Ennis HL, Dao DN, Pukatzki SU, Kessin RH: ***Dictyostelium* amoebae lacking an F-box protein form spores rather than stalk in chimeras with wild type.** *Proceedings of the National Academy of Sciences of the United States of America* 2000, **97**:3292-3297.
  130. Hilson JA, Kolmes SA, Nellis LF: **Fruiting body architecture, spore capsule contents, selfishness, and heterocytosis in the cellular slime mold *Dictyostelium discoideum*.** *EtholEcolEvol* 1994, **6**:529-535.
  131. Fortunato A, Strassmann JE, Santorelli L, Queller DC: **Co-occurrence in nature of different clones of the social amoeba, *Dictyostelium discoideum*.** *Molecular Ecology* 2003, **12**:1031-1038.
  132. Queller DC, Foster KR, Fortunato A, Strassmann JE, Kikuchi T, Kubo T, Higashi S: **Cooperation and conflict in the social amoeba, *Dictyostelium discoideum*.** In *Social insects and sociogenetics* Sapporo: Hokkaido University Press; 2003:173-200.
  133. Castillo DI, Switz GT, Foster KR, Queller DC, Strassmann JE: **A cost to chimerism in *Dictyostelium discoideum* on natural substrates.** *Evolutionary Ecology Research* 2005, **7**:263-271.
  134. Kuzdzal-Fick JJ, Foster KR, Queller DC, Strassmann JE: **Exploiting new terrain: an advantage to sociality in the slime mold *Dictyostelium discoideum*.** *Behavioral Ecology* 2007, **18**:433-437.
  135. Santorelli LA, Thompson CRL, Villegas e, Svetz J, Dinh C, Parikh A, Suggang R, Kuspall A, Strassmann JE, Queller DC, Shaulsky G: **Facultative cheater mutants reveal the genetic complexity of cooperation in social amoebae.** *Nature* 2008. doi:10.1038/nature06558
  136. Darden WH: **Sexual differentiation in *Volvox aureus*.** *Journal of Protozoology* 1966, **13**:239-255.
  137. Kirk DL: **The ontogeny and phylogeny of cellular differentiation in *Volvox*.** *Trends in Genetics* 1988, **4**:32-36.
  138. Kirk DL: **The genetic program for germ-soma differentiation in *Volvox*.** *Annual Review of Genetics* 1997, **31**:359-380.
  139. Kirk DL: **Seeking the ultimate and proximate causes of *Volvox* multicellularity and cellular differentiation.** *Integrative and Comparative Biology* 2003, **43**:247-253.
  140. Koufopanou V: **The evolution of soma in the Volvocales.** *American Naturalist* 1994, **143**:907-931.
  141. Desnitski AG: **A review on the evolution of development in *Volvox*: morphological and physiological aspects.** *European Journal of Protistology* 1995, **31**:241-247.
  142. Nedelcu AM, Michod RE: **The evolutionary origin of an altruistic gene.** *Molecular Biology and Evolution* 2006, **23**:1460-1464.
  143. Solari CA, Kessler JO, Michod RE: **A hydrodynamics approach to the evolution of multicellularity: Flagellar motility and germ-soma differentiation in volvoclean green algae.** *American Naturalist* 2006, **167**:537-554.
  144. Michod RE: **Evolution of individuality during the transition from unicellular to multicellular life.** *Proceedings of the National Academy of Sciences of the United States of America* 2007, **104**:8613-8618.
  145. Leadbeater BSC: **Life-history and ultrastructure of a new marine species of *Proterospongia* (Choanoflagellida).** *Journal of the Marine Biological Association of the United Kingdom* 1983, **63**:135-160.
  146. Blackstone NW: **Redox control and the evolution of multicellularity.** *Bioessays* 2000, **22**:947-953.
  147. Maldonado M: **Choanoflagellates, choanocytes, and animal multicellularity.** *Invertebrate Biology* 2004, **123**:1-22.
  148. Kaestner A: *Lehrbuch der speziellen Zoologie; Wirbellose. Volume 1.* Stuttgart: Fischer Verlag; 1969.
  149. Galtsoff PS: **The amoeboid movement of dissociated sponge cells.** *Biological Bulletin* 1923, **45**:153-161.
  150. Kuhns WJ, Weinbaum G, Turner R, Burger MM: **Sponge aggregation: model for studies on cell-cell interactions.** *Annals of the New York Academy of Sciences* 1974, **234**:58-74.
  151. Simpson TL: **The cell biology of sponges.** New York: Springer; 1984.
  152. Usher KM, Sutton DC, Toze S, Kuo J, Fromont J: **Sexual reproduction in *Chondrilla australiensis* (Porifera: demospongiae).** *Marine and Freshwater Research* 2004, **55**:123-134.

153. Degnan BM, Leys SP, Larroux C: **Sponge development and antiquity of animal pattern formation.** *Integrative and Comparative Biology* 2005, **45**:335-341.
154. Whalan S, Johnson MS, Harvey E, Battershill C: **Mode of reproduction, recruitment, and genetic subdivision in the brooding sponge *Haliclona* sp.** *Marine Biology* 2005, **146**:425-433.
155. Agata K, Nakajima E, Funayama N, Shibata N, Saito YUY: **Two different evolutionary origins of stem cell systems and their molecular basis.** *Seminars in Cell & Developmental Biology* 2006, **17**:503-509.
156. Müller W: **Experimentelle untersuchungen über stockentwicklung, polypendifferenzierung und sexualchimären bei *Hydractinia echinata*.** *Roux' Archiv für Ent* 1964, **155**:181-268.
157. Buss LW, Shenk MA, Marchalonis JJ, Reinisch C: **Hydroid allorecognition regulates competition at both the level of the colony and the level of the cell lineage.** In *Defense molecules* New York: Liss; 1990:85-105.
158. Shenk MA, Buss LW: **Ontogenetic changes in fusibility in the colonial hydroid *Hydractinia symbiolongicarpus*.** *J Exp Zool* 1991, **257**:80-86.
159. Grosberg RK, Levitan DR, Cameron BB: **Evolutionary genetics of allorecognition in the colonial marine hydroid *Hydractinia symbiolongicarpus*.** *Evolution* 1996, **50**:2221-2240.
160. Cartwright P: **Developmental insights into the origin of complex colonial Hydrozoans.** *Integr Comp Biol* 2003, **43**:82-86.
161. Francis L: **Social organization within clones of sea-anemone *Anthopleura elegantissima*.** *Biological Bulletin* 1976, **150**:361-376.
162. Ayre DJ, Grosberg RK: **Behind anemone lines: factors affecting division of labour in the social cnidarian *Anthopleura elegantissima*.** *Animal Behaviour* 2005, **70**:97-110.
163. Silen L: **Zur Kenntnis des Polymorphismus der Bryozoen. Die avicularien der Cheilostomata *Anasca*.** *Zool Bidr Upps* 1938, **17**:149-366.
164. Silen L, Woollacott RM, Zimmer RL: **Polymorphism.** In *Biology of Bryozoans* New York: Academic Press; 1977:183-231.
165. Ryland JS, Hayward PJ: **British Anascan Bryozoans.** London: Academic Press; 1977.
166. Harvell CD: **The evolution of polymorphism in colonial invertebrates and social insects.** *Quarterly Review of Biology* 1994, **69**:155-185.
167. Sabbadin A, Zaniolo G: **Sexual differentiation and germ cell transfer in the colonial ascidian *Botryllus schlosseri*.** *J Exp Zool* 1979, **207**:289-304.
168. Pancer Z, Gershon H, Rinkevich B: **Coexistence and possible parasitism of somatic and germ-cell lines in chimeras of the colonial urochordate *Botryllus schlosseri*.** *Biological Bulletin* 1995, **189**:106-112.
169. Stoner DS, Rinkevich B, Weissman IL: **Heritable germ and somatic cell lineage competitions in chimeric colonial protochordates.** *Proceedings of the National Academy of Sciences of the United States of America* 1999, **96**:9148-9153.
170. Rinkevich B, Yankelevich I: **Environmental split between germ cell parasitism and somatic cell synergism in chimeras of a colonial urochordate.** *The Journal of Experimental Biology* 2004, **207**:3531-3536.
171. Hartl DL, Hiraizumi Y, Crow JF: **Evidence for sperm dysfunction as mechanism of segregation distortion in *Drosophila melanogaster*.** *Proceedings of the National Academy of Sciences of the United States of America* 1967, **58**:2240-2245.
172. Hiraizumi Y, Thomas AM: **Suppressor systems of segregation distorter (SD) chromosomes in natural populations of *Drosophila melanogaster*.** *Genetics* 1984, **106**:279-292.
173. Merrill C, Bayraktaroglu L, Kusano A, Ganetzky B: **Truncated Ran-GAP encoded by the segregation distorter locus of *Drosophila*.** *Science* 1999, **283**:1742-1745.
174. Atlan A, Mercot H, Landre C, Montchamp-Moreau C: **The sex-ratio trait in *Drosophila simulans*: Geographical distribution of distortion and resistance.** *Evolution* 1997, **51**:1886-1895.
175. Silver LM: **Mouse T-haplotypes.** *Annual Review of Genetics* 1985, **19**:179-208.
176. Gummere GR, McCormick PJ, Bennett D: **The influence of genetic background and the homologous chromosome-17 on T-haplotype transmission ratio distortion in mice.** *Genetics* 1986, **114**:235-245.
177. Ardlie KG: **Putting the brake on drive: meiotic drive of t haplotypes in natural populations of mice.** *Trends in Genetics* 1998, **14**:189-193.
178. Korb J, Schmidinger S: **Help or disperse? Cooperation in termites influenced by food conditions.** *Behavioral Ecology and Sociobiology* 2004, **56**:89-95.
179. Roux EA, Korb J: **Evolution of eusociality and the soldier caste in termites: a validation of the intrinsic benefit hypothesis.** *Journal of Evolutionary Biology* 2004, **17**:869-875.
180. Crespi BJ: **Eusociality in Australian gall thrips.** *Nature* 1992, **359**:724-726.
181. Chapman TW, Crespi B: **High relatedness and inbreeding in two species of haplodiploid eusocial thrips (Insecta: Thysanoptera) revealed by microsatellite analysis.** *Behavioral Ecology and Sociobiology* 1998, **43**:301-306.
182. Chapman TW, Crespi BJ, Kranz BD, Schwarz MP: **High relatedness and inbreeding at the origin of eusociality in gall-inducing thrips.** *Proceedings of the National Academy of Sciences of the United States of America* 2000, **97**:1648-1650.
183. Chapman TW, Kranz BD, Bejah KL, Morris DC, Schwarz MP, Crespi BJ: **The evolution of soldier reproduction in social thrips.** *Behavioral Ecology* 2002, **13**:519-525.
184. Wills TE, Chapman TW, Kranz BD, Schwarz MP: **Reproductive division of labour coevolves with gall size in Australian thrips with soldiers.** *Naturwissenschaften* 2001, **88**:526-529.
185. Foster WA: *Behavioral Ecology and Sociobiology* 1990, **27**:421-430.
186. Stern DL, Foster WA: **The evolution of soldiers in aphids.** *Biological Reviews of the Cambridge Philosophical Society* 1996, **71**:27-79.
187. Abbot P, Withgott JH, Moran NA: **Genetic conflict and conditional altruism in social aphid colonies.** *Proceedings of the National Academy of Sciences of the United States of America* 2001, **98**:12068-12071.
188. Johnson PCD, Whitfield JA, Foster WA, Amos W: **Clonal mixing in the soldier-producing aphid *Pemphigus spyrothecae* (Hemiptera: Aphididae).** *Molecular Ecology* 2002, **11**:1525-1531.
189. Ratnieks FLW, Visscher PK: **Worker policing in the honeybee.** *Nature* 1989, **342**:796-797.
190. Visscher PK: **A quantitative study of worker reproduction in honeybee colonies.** *Behavioral Ecology and Sociobiology* 1989, **25**:247-254.
191. Visscher PK: **Reproductive conflict in honey bees: A stalemate of worker egg-laying and policing.** *Behavioral Ecology and Sociobiology* 1996, **39**:237-244.
192. Barron AB, Oldroyd BP, Ratnieks FLW: **Worker reproduction in honey-bees (*Apis*) and the anarchic syndrome: a review.** *Behavioral Ecology and Sociobiology* 2001, **50**:199-208.
193. Ratnieks FLW, Foster KR, Wenseleers T: **Conflict resolution in insect societies.** *Annual Review of Entomology* 2006, **51**:581-608.
194. Imperatriz-Fonseca VL, Zucchi R: **Virgin queens in stingless bee (*Apidae*, *Meliponinae*) colonies – a review.** *Apidologie* 1995, **26**:231-244.
195. Peters JM, Queller DC, Imperatriz-Fonseca VL, Roubik DW, Strassmann JE: **Mate number, kin selection and social conflicts in stingless bees and honeybees.** *Proceedings of the Royal Society of London Series B-Biological Sciences* 1999, **266**:379-384.
196. Taborsky M: **Broodcare helpers in the cichlid fish *Lamprologus brichardi* – their costs and benefits.** *Anim Behav* 1984, **32**:1236-1252.
197. Dierkes P, Heg D, Taborsky M, Skubic E, Achmann R: **Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid.** *Ecology Letters* 2005, **8**:968-975.
198. Heg D, Bachar Z: **Cooperative breeding in the Lake Tanganyika cichlid *Julidochromis ornatus*.** *Environmental Biology of Fishes* 2006, **76**:265-281.
199. Heg D, Bachar Z, Brouwer L, Taborsky M: **Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid.** *Proc R Soc Lond B* 2004, **271**:2367-2374.
200. Rowley I: **Communal activities among white-winged choughs *Corcorax melanorhamphos*.** *Ibis* 1978, **120**:178-197.
201. Heinsohn R, Cockburn A: **Helping is costly to young birds in cooperatively breeding white-winged choughs.** *Proceedings of the Royal Society of London Series B-Biological Sciences* 1994, **256**:293-298.
202. Heinsohn R, Dunn P, Legge S, Double M: **Coalitions of relatives and reproductive skew in cooperatively breeding white-**

- winged choughs.** *Proceedings of the Royal Society of London Series B-Biological Sciences* 2000, **267**:243-249.
203. Heinsohn RG: **Cooperative enhancement of reproductive success in white-winged choughs.** *Evolutionary Ecology* 1992, **6**:97-114.
204. Boland CRJ, Heinsohn R, Cockburn A: **Deception by helpers in cooperatively breeding white-winged choughs and its experimental manipulation.** *Behavioral Ecology and Sociobiology* 1997, **41**:251-256.
205. Jarvis JUM: **Eusociality in a mammal: cooperative breeding in naked mole-rat colonies.** *Science* 1981, **212**:571-573.
206. Reeve HK: **Queen activation of lazy workers in colonies of the eusocial naked mole-rat.** *Nature* 1992, **358**:147-149.
207. Jarvis JUM, Bennett NC: **Eusociality has evolved independently in 2 genera of bathyergid mole-rats, but occurs in no other subterranean mammal.** *Behavioral Ecology and Sociobiology* 1993, **33**:253-260.
208. Jarvis JUM, O'Riain MJ, Bennett NC, Sherman PW: **Mammalian eusociality: a family affair.** *Trends EcolEvol* 1994, **9**:46-51.
209. Bennett NC, Faulkes CG: **African Mole-rats Ecology and Eusociality.** Cambridge: Cambridge Univ Press; 2000.
210. Burland TM, Bennett NC, Jarvis JUM, Faulkes CG: **Eusociality in African mole-rats: new insights from patterns of genetic relatedness in the Damaraland mole-rat (*Cryptomys damarensis*).** *Proceedings of the Royal Society of London Series B-Biological Sciences* 2002, **269**:1025-1030.

Publish with **BioMed Central** and every scientist can read your work free of charge

*"BioMed Central will be the most significant development for disseminating the results of biomedical research in our lifetime."*

Sir Paul Nurse, Cancer Research UK

Your research papers will be:

- available free of charge to the entire biomedical community
- peer reviewed and published immediately upon acceptance
- cited in PubMed and archived on PubMed Central
- yours — you keep the copyright

Submit your manuscript here:  
[http://www.biomedcentral.com/info/publishing\\_adv.asp](http://www.biomedcentral.com/info/publishing_adv.asp)



**Table 1. Examples of group formation for which there is some information on dispersal, relatedness and punishment/policing.**

Gross taxonomic level	Species	Public good	Cooperators or cooperation performed	Cooperator dispersal	Defectors or way of cheating	Defector dispersal	Relatedness Coop./Def.	Punishment, policing	References
Viruses	Plant <i>RNA-virus</i>	diffusible intracellular products	complete RNA-virus	via insects	sequester intracellular products	requires presence of cooperators	defective interfering particle(?)	?	[111, 112]
Bacteria	<i>Escherichia coli</i>	protection against competitors	production of diffusible bacteriocins	?	no colicin production	?	mutant	colicin production	[113-115]
Bacteria	<i>Pseudomonas sp.</i>	biofilm	polymer production	shearing	no polymer production	planktonic disperser cells	mutant	Apparent niche exclusion	[79, 80, 89, 116, 117]
Myxobacteria	<i>Myxococcus xanthus</i>	fruiting body	formation of fruiting body, C-signal production, cell autolysis	S-motility (social gliding)	no contribution to fruiting body	A-motility (individual)	High within group relatedness; mutations	?	[37, 96, 118-121]
Yeast	<i>Sacharomyces cerevisiae</i>	Sucrose digestion	production of invertase via <i>SUC2</i> gene	Free living	deleted <i>SUC2</i> gene, no invertase prod.	Free living	Polymorphic SUC genes	k1 killer toxin production	[122 – 125]
Slime moulds	<i>Dictyostelium mucoroides</i>	stalk for spore dispersal	production of signals and stalk, adhesion of cooperators stalk formation	no	specialization in spore production	yes	mutant, clone chimeras	somatic compatibility system	[126-127]
	<i>D. discoideum</i>	stalk for spore dispersal		no		<i>chtA/FbxA</i> - mutant: almost pure spore production	yes	mutant clone chimaeras	
Protozoa 1. Flagellata a) Phyto-monadina b) Proto-monadina	<i>Volvox carteri</i> , <i>V. aureus</i>	multicellular body, nutrition, locomotion	somatic cells	no	gonidia: specialize in reproduction	yes	clonal	?	[1, 18, 136-147]
	<i>Proterospongia haeckeli</i>	multicellular body	flagellated cells moving the colony	no (?)	amoeboid cells: asexual reproduction	?	clonal	programmed cell death	

2. Euciliata Peritricha	<i>Zoothamnium arbuscula</i>	multicellular colony	feeding zooids, nutrition	no	macrozooids: no feeding	yes	clonal (?)	?	[148]
Porifera	<i>Spongilla lacustris</i> , <i>Ephydatia sp.</i> , <i>Reniera sp.</i> , <i>Haliclona sp.</i>	multicellular body, care for gametes & embryos	up to 14 different cell types, various functions	if disassocia ted or as gemmul es	gamete production	yes	clonal or chimeric	allorecognition restraining exploitation after fusion	[56, 149-155]
Coelenterata	<i>Hydractinia spp.</i>	nutrition, protection	gastrozooids, dactylozooids, tentaculozooids	no	gonozooids (♂+♀): no feeding and defence	production of dispersing gametes	clonal	partner rejection	[156-160]
	<i>Anthopleura elegantissima</i>	nutrition, protection	scout, warrior and free-edge polyps	no	pure reproductive functions	production of dispersing gametes	clonal	?	[161, 162]
Bryozoa	<i>Dendrobeania murrayana</i>	nutrition, protection	various zooids	no	gonozooids	production of dispersing gametes	clonal		[163-166]
Urochordata	<i>Botryllus schlosseri</i>	gonads & somatic organs	primordial somatic cells	no	primordial germ cells	yes	distinct cell lineages	gametic cell competition	[24, 167-170]
Insecta	<i>Drosophila melanogaster</i> , <i>D. simulans</i>	eggs	wild-type sperm (fair meiosis)	yes	segregation distortion	yes	one gene difference	genetic suppression of meiotic drive	[171-174]
Mammalia	<i>Mus musculus</i>	eggs	wild-type sperm (fair meiosis)	yes	transmission ratio distortion by <i>t</i> haplotypes	yes	gene complex diff. on chromos. 17	mitigating effect of other genes	[175-177]
<b>Analogies in higher Metazoan communities</b>									
Isoptera	<i>Cryptotermes secundus</i>	nutrition, protection	workers, soldiers	no	reproductives	yes	diploid siblings	?	[178, 179]
Thysanoptera	<i>Oncothrips habrus</i> , <i>O. tepperi</i>	gall	micropterous soldiers	no	macropterous reproductives	yes	haplodiploid sisters	?	[180-184]
Aphidae	<i>Pemphigus spyrothecae</i> , <i>P. obesinymphae</i>	gall	soldiers	as asex. virginop arae	no defence, accelerated development	as adult sexuparae	partly mixed clones	?	[185-188]
Hymenoptera	<i>Apis mellifera</i>	nutrition, protection	workers	no	reproductives, egg-laying	queens yes, workers no	haplodiploid sisters	by workers	[189-193]



	<i>Meliponini</i>	production of highly related females	mother queen (singly mated)	no	workers daughter queens (own reprod. lowering colony relatedness)	yes	mother-daughter	by workers	[194, 195]
Pisces	<i>Neolamprologus pulcher</i>	protection	breeders and brood care helpers	low	reproductive parasitism by mature helpers	high	very low	expulsion	[25, 27, 28, 87, 196-199]
Aves	<i>Corcorax melano-rhamphos</i>	group membership, recruitment of allies	breeders and brood care helpers	conditional	deceptive brood care	conditional	usually high	aggression by group members	[200-204]
Mammalia	<i>Heterocephalus glaber</i> , <i>Cryptomys damarensis</i>	group membership, protection	breeders and non-reproductives	no	dispersive morph saves effort and accumulates reserves	yes	high	queen punishment of lazy workers	[32-34, 36, 205-210]

The public good is the action of cooperators, while defectors do not contribute to the public good. The cooperators or the cooperation performed, and the defectors or their way of cheating, are listed together with information about their respective dispersal, the relatedness between cooperators and defectors, and information about potential coercion in the form of punishment or policing. Note that due to difficulties in obtaining equivalent functional assessments of public goods and dispersal across examples, we considered the former to be a behavior resulting in a potential benefit for one or more group members, and the latter to be movement away from the group. Stricter criteria would be necessary for a more conclusive comparison with model predictions, and thus our objective is to highlight possible similarities and differences, based on first approximations for these complex processes. Question marks denote where respective information is unknown.