Fitness drivers of division of labor in vertebrates

Irene García-Ruiz[1]* and Dustin Rubenstein[1]

[1]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, United States of America.

*Corresponding author. Email: igaru.13@gmail.com

Abstract

Although division of labor as a means to increase productivity is a common feature in animal social groups, most previous studies have focused almost exclusively on eusocial insects with extreme task partitioning. Empirical evidence of division of labor in vertebrates is scarce, largely because we lack a theoretical framework to explore the conditions under which division of labor is likely to evolve. By explicitly considering alternative helping tasks with varying fitness costs, we model how individual decisions on task specialization may influence the emergence of division of labor under both direct and indirect fitness benefits. Surprisingly, we find that direct survival benefits of living in larger groups are the primary force driving the evolution of cooperation to enhance group productivity, and that indirect fitness benefits derived from related group members are only a non-essential facilitator of more stable forms of division of labor. In addition, we find that division of labor is favored by increasingly harsh environments. Ultimately, our model not only makes key predictions that are consistent with existing empirical data, but also proposes novel avenues for new empirical work in vertebrate and invertebrate systems alike.

Introduction

Division of labor as a means to boost productivity holds significance not only in human societies, but also those of other animals [1–5]. Nearly 250 years ago, the economist Adam Smith[2] proposed that division of labor via task specialization within human societies not only improves individual efficiency and group productivity, but also reduces the costs associated with switching tasks. Similarly, in nonhuman animal societies, division of labor to increase group reproductive output (analogous to economic gain) is characterized by group members specializing in particular tasks, either temporarily or permanently [6–8]. To date, all theoretical and the vast majority of empirical work on the selective pressures favoring division of labor via task specialization in animal societies has focused on eusocial insect societies characterized by sterile workers that are unable to ever reproduce [8–12]. Since workers in eusocial societies can, in most cases, only obtain fitness benefits indirectly through kin selection by maximizing their colony reproductive output, selection can occur at the colony level, typically resulting in very low conflict of interest between group members. However, complex societies occur outside of eusocial insects, such as in many birds and mammals, including humans. Because sterile workers are absent in vertebrate societies, conflict can be much higher than in eusocial insect societies. The few studies of division of labor outside of eusocial insects have focused exclusively on reproductive division of labor (i.e., reproductive skew), despite that fact that temporal or permanent non-reproductive organisms can engage in an array of different helping tasks [3, 13]. Given the scarcity of studies examining the selective advantages of division of labor beyond eusocial insects (but see [14]), our understanding of the evolutionary pressures of division of labor is largely confined to instances where task specialization is linked to sterility and where conflict of interest is low.

In cooperatively breeding vertebrates, which live in societies with more equitable sharing of reproduction (i.e., low reproductive skew), low or mixed kinship, and often have unrelated helpers, conflict of interest can be high and direct fitness benefits may be more relevant in the evolution of division of labor than indirect benefits [15–17]. In fact, shared fitness incentives to increase group productivity are not limited to eusocial insects with high within-group relatedness and sterile workers. In cases where group size positively correlates with an increase in the survival or reproduction of group members, division of labor via task specialization may also evolve under direct fitness benefits to subordinate members of a group (i.e., group augmentation [18, 19]). Although a great deal of recent empirical work highlights the importance of direct benefits in the evolution of cooperative breeding behavior in vertebrates [20–23], the joint influence of direct and indirect fitness benefits in the evolution of division of labor has, to our knowledge, never been investigated.

Most previous models of division of labor via task specialization considered all helping tasks under the same fitness umbrella, which is a good approximation in eusocial insect societies because colony members share fitness costs and benefits. In vertebrates, however, helpers may obtain fitness benefits directly via reproduction, and thus, selection occurs more strongly at the individual level than it does in most eusocial insects. Group members in vertebrate societies may then contribute to distinct helping tasks differently according to individual life history

strategies [24–26] or differences in the magnitude or type of fitness costs and benefits that they receive from cooperative tasks [27]. One of the key distinctions between fitness costs is whether a task impacts more immediate survival or direct reproduction. For instance, defensive behaviors such as predator mobbing may have a high risk of injury and death [28–30], whereas other activities such as allofeeding or nest/territory maintenance may affect body condition owing to lower feeding rates and time and energy investment, consequently affecting their own reproductive output [31–33]. Therefore, changes in life histories, such as those linked to the likelihood of becoming a breeder, may select for task specialization according to the relative direct fitness cost associated with different helping tasks.

In addition to life history differences, demographic, social, and ecological factors that affect help workload and the prospect of helpers becoming breeders are likely to have a strong impact on task allocation because they alter the likelihood of obtaining direct fitness benefits [34, 35]. For example, age is known to be an important factor influencing helping workload in vertebrates [36, 37], is often correlated with differences in other life-history traits [33, 38–40], and may be a proxy for other processes involved in the evolution of help [41, 42]. Moreover, age-dependent task allocation (i.e., temporal polyethism) is common in eusocial insects that do not show morphological differentiation [43]. Social and ecological factors are also thought to influence the emergence of division of labor in eusocial insects [44–46]. Indeed, high relatedness may reduce conflict of interest between group members and promote the evolution of division of labor [47–51]. Similarly, in harsh environments where group size strongly influences survival [52–55], division of labor may be favored to more efficiently increase group productivity.

To disentangle the role of direct versus indirect fitness benefits in the evolution of division of labor in vertebrate societies, we created a stochastic model in which we varied the influence of different evolutionary forces to understand under which social and ecological circumstances division of labor may arise to maximize the inclusive fitness of individuals in a group. We used distinct tasks with different fitness costs to maximize the group reproductive output when they were performed to a similar extent. Individuals in our model were allowed to evolve different behavioral responses or reaction norms in task specialization, depending on their likelihood of becoming breeders. We compared the results of this model to those of a benchmark model in which the reproductive outcome was independent of the type of task performed by group members. We present the results for different environmental conditions in the presence or absence of relatedness (indirect) or group size (direct) benefits. Ultimately, this work demonstrates that the direct fitness benefits of group living attained in increasingly harsh environments are key to the evolution of division of labor in vertebrates.

Results

Rationale

Our model consists of a population characterized by overlapping generations residing in a habitat featuring a limited number of breeding territories. These territories are monopolized by groups composed of a single breeder and an unspecified number of subordinate helpers, each of which is capable of reproducing during its lifetime. Individuals in the population fall into one of three categories: (1) *breeders* that monopolize reproduction; (2) *subordinates* that may perform different helping tasks, either in their natal group or in an outside group to which they dispersed; and (3) *floaters* that dispersed from their natal group but did not join another group.

We assume complete reproductive skew such that subordinate group members are prevented from reproducing at a given timestep and may only help raise the offspring of the dominant breeders. Dispersers cannot reproduce without acquiring a territory (i.e., floaters). Helpers are not sterile and may inherit the breeding position when the breeder dies. When this occurs, helpers and dispersers from other groups compete for the breeding position and win with a probability proportional to their dominance value (Table 1). We use the term dominance value to designate the competitiveness of an individual compared to other candidates in becoming a breeder, regardless of group membership, considering both age as a proxy for resource holding potential and helping costs to body condition.

Subordinate helpers in our model may choose between two distinct tasks with differing fitness costs: (1) *defensive tasks* (i.e., defense of the dominant breeders' offspring at cost to their own survival); or (2) *work tasks* (i.e., tasks with an associated cost to their body condition and consequently to their competitiveness to become breeders in the future). Subordinate helpers can then evolve different workloads and exhibit task specialization that is either fixed throughout their lifetime or varies with their dominance value. The parameters x_h and y_h (Table 1) reflect how much the subordinates' survival and dominance values decrease with increasing investment in defense or work tasks, respectively. Although we do not assume an inherent difference in body condition between individuals when born, variance in age and helping propensities can create differences in the fitness costs linked to task performance.

We assume net survival benefits from living in large groups (i.e., group augmentation), which occurs in many social species [53, 54, 56, 57]. Subordinate members of a group may therefore gain both direct and indirect fitness benefits from helping to increase the productivity of breeders, if doing so results in an increase in group size. In the model, the benefit of alloparental care to the productivity of the breeder is maximized when group members provide overall similar workloads for both defensive and work tasks, since both are often needed for the survival of the offspring [58, 59]. To compare between the helper's preferred task and the task needed to maximize group productivity, we created a benchmark model in which the breeder's productivity is not constrained by the type of help provided. Higher productivity translates to larger group sizes, which enhances the survival prospects of all group members. Hence, subordinates have an incentive to develop division of labor. Subordinates that stay in their natal

group may also gain improved fitness by indirectly passing on their genes through kin. Both group size and relatedness in our model are emergent properties of a series of demographic processes, including mortality, dispersal decisions, and help-dependent breeder fertility.

To distinguish between the effects of group augmentation and kin selection on inclusive fitness, we created two additional models. In the first model, we removed the benefits of group size (group augmentation) by setting the parameter $x_n = 0$ (Table 1). In the second model, we removed the effect of kin selection by simulating a cross-foster manipulation in which offspring just born are interchanged between different groups (see Methods for additional details).

To assess how habitat quality affects task specialization and the emergence of division of labor, we systematically varied habitat quality across simulations. Harsh environments are those that have high mortality (i.e., $m = 0.3$; Table 1), which also raises the turnover of the breeding positions. Lower values of m reflect an increased likelihood of individuals surviving another life cycle and, therefore, the chances of habitat saturation. The steps in the lifecycle of the model are illustrated in Figure 1.

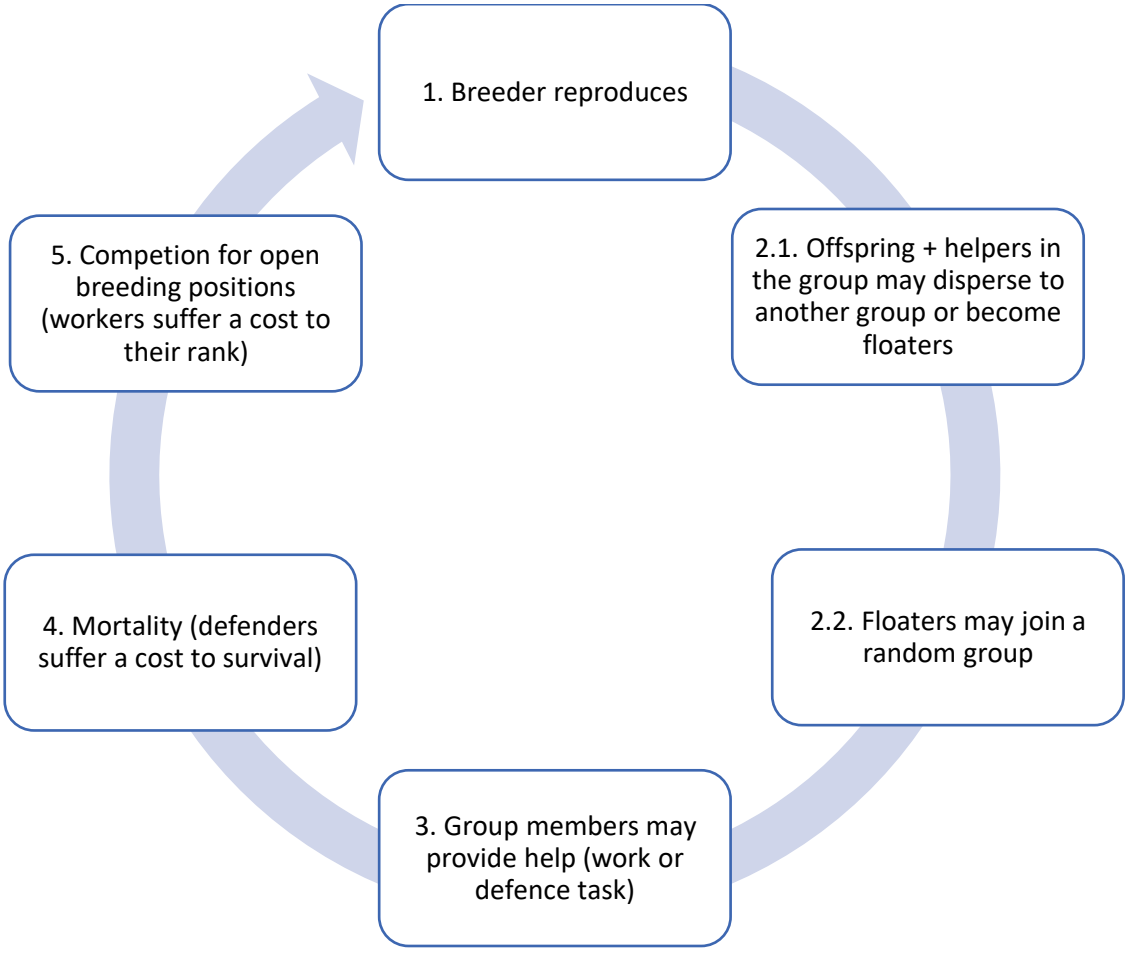

Figure 1. Diagram of the scheduling executed per generation. (1) A breeder reproduces. Its productivity depends on the cumulative level of brood care provided by the group during the previous life cycle. Maximum productivity is achieved when different helping tasks are performed to a similar extent. (2) Subordinates may disperse to become floaters, or they may stay in the group and help. Dispersers/floaters may join a random group to become subordinates. (3) Subordinates in the group either work to provision to the breeder's offspring or display defensive forms of help. (4) Individuals survive contingent on group-living benefits and dispersal costs, as well as the cost of defensive activities. (5) If a breeder dies, helpers in the group and a sample of floaters compete for the breeding position. Individuals still alive ascend one age class, and the cycle starts all over (i.e., next generation).

Direct vs indirect fitness benefits

We first examined how both direct fitness benefits from group living and indirect fitness benefits from aiding kin influence the evolution of division of labor through task specialization across environments of varying quality. Our results show that division of labor initially emerges because of direct fitness benefits (Figure 2; GA), but a combination of direct and indirect fitness benefits leads to higher rates and more stable forms of division of labor (Figure 2; KS + GA). It is important to note that, as depicted in Figure 2, intermediate values of task specialization indicate in all cases age/dominance-mediated task specialization ($\gamma_t \neq 0$; Table 1) and never a lack of specialization ($\gamma_t = 0$; Table 1); further details are shown in the next section "*The role of dominance in task specialization*".

In contrast to expectations from models of eusocial insects, our vertebrate model does not readily evolve division of labor when only kin selection is considered (see Supplemental Material for more details). Specifically, forms of help that impact survival never evolve under any environmental condition when only kin selection occurs (Figure 2; KS). This occurs because with kin competition for the breeding position and no survival benefits of group membership, the reduced incentives to remain in the natal group drive most subordinates to disperse and breed elsewhere (average dispersal rate between 88% in harsh environments and 93% in benign environments; Table S1). The few subordinates that remain in the natal territory help to obtain indirect benefits (average within-group relatedness between 0.36 in benign environments and 0.72 in harsh environments; Table S1). Even though individuals in our model cannot adjust their help according to their relatedness to the breeder, the high levels of relatedness that evolved under this paradigm indicate that allowing for targeted help would not qualitatively change the results. Survival costs of defensive tasks are then avoided, as mortality without group benefits is relatively high, while costs to dominance value are small for close relatives because of indirect fitness benefits and low conflict of interest (Figure 2; KS). Adjusting input parameters to obtain higher survival rates and favoring philopatry did not qualitatively change the results, except for extreme values of baseline survival (see Supplementary Material), which indicates that kin selection alone is unlikely to select for the evolution of defensive tasks and division of labor in vertebrates.

Conversely, under only direct fitness benefits (group augmentation), tasks associated with costs to the dominance value are costlier because the only path to obtain fitness benefits is via direct reproduction. Therefore, defensive tasks that do not affect the dominance value are favored (Figure 2; GA). Under this scenario, division of labor can evolve to maximize the reproductive output of the breeders (Figure 2; GA, $m = 0.3$, $x_h \leq 5$), but also because it is the optimal strategy (Figure 2; GA, $m = 0.3$, $x_h = 7$). In benign environments, however, no help evolves due to the lower incentives to increase survival and the steep competition for reproduction due to the resulting habitat saturation.

When subordinates can obtain both direct and indirect fitness, division of labor is more strongly selected in increasingly harsher environments to increase breeder productivity (Figure 2; KS + GA). Overall, in moderate and harsh environments, work tasks with costs to the dominance

value are more strongly selected than in benign environments due to high mortality increasing both the breeder's turnover, reducing breeding competition (lower effective costs of work tasks), and the costs to survival (high costs of defensive tasks). However, in more benign (and often highly productive) environments with habitat saturation, help can only evolve initially under kin selection and defensive tasks are favored because competition for the breeding position is lower in family groups. In this scenario, kin selection is achieved not only by subordinates in their natal group increasing the productivity of a related breeder (Figure 2; KS), but also by the increased survival of their siblings when augmenting the group size (Figure 2; KS + GA), regardless of whether they are related to the current breeder.

Overall, division of labor seems to be more likely to evolve in increasingly harsh environments where raising breeder productivity effectively enhances the survival of both helpers and relatives. In contrast, help evolves in benign environments, largely due to kin selection benefits and subordinates performing their preferred task of defending the breeder's offspring.

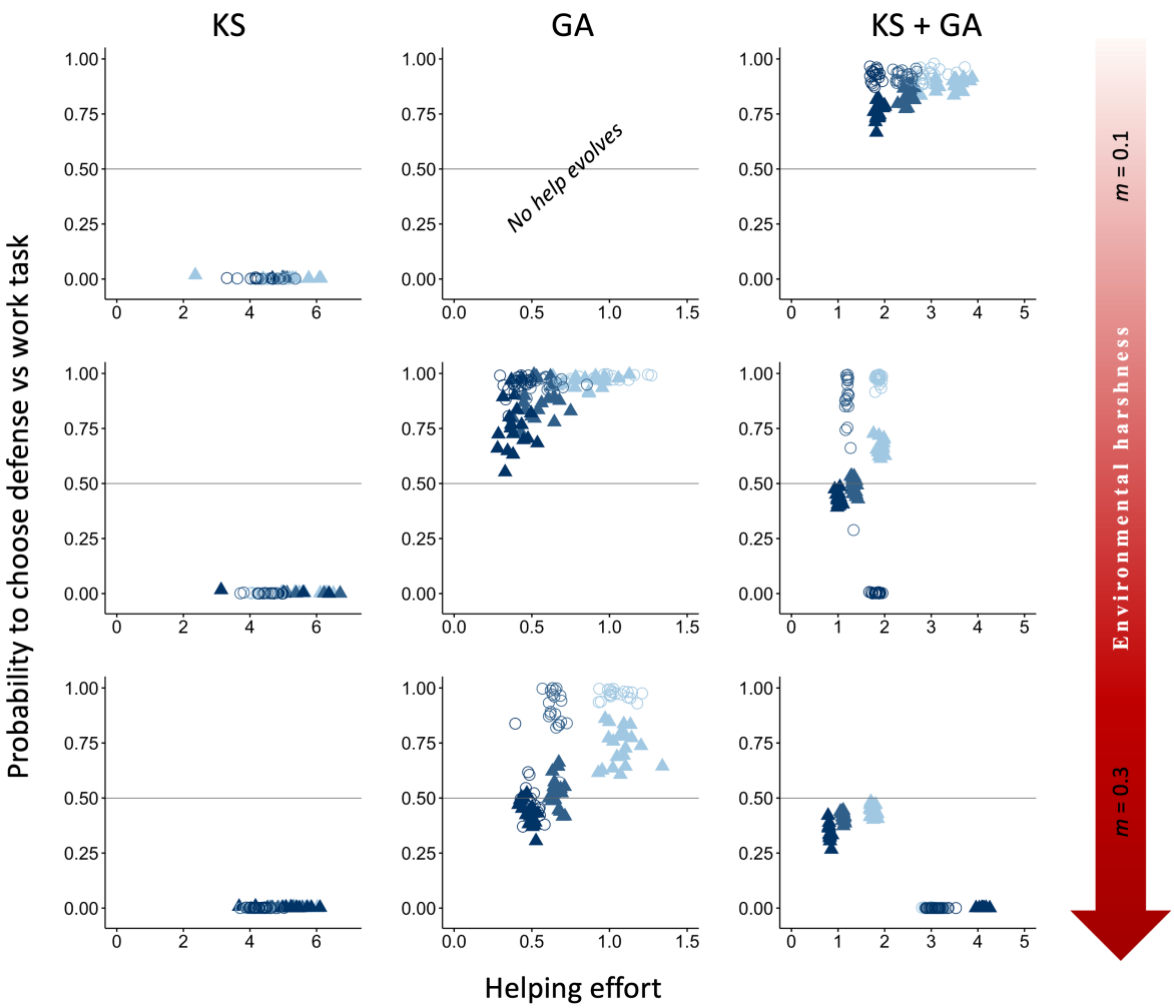

Figure 2. Effect of environmental quality on alloparental care and division of labor. The evolutionary equilibria for levels of helping and task specialization are shown at three different levels of environmental quality, ranging from benign (m=0.1) to harsh (m=0.3), and for three different levels of cost of help on survival (light blue, x_h=3; blue, x_h=5; and dark blue, x_h=7), across 20 replicas. The y-axis expresses the likelihood of individuals choosing a defensive task with a cost to survival versus a work task with a cost to their dominance rank. The optimum breeder productivity per unit of help provided was either when both tasks were performed to a similar extent, potentially selecting for division of labor (▲) or when no restrictions were introduced to the task performed by the group members (○). In each environment, additional details are given on the selective forces that play a role in the evolution of help and task specialization: help can only evolve by kin selection (KS), group augmentation (GA), or both (KS + GA). All parameter values described in Table 1.

The role of dominance in task specialization

In the previous section, we explored the role of direct and indirect fitness benefits in the evolution of division of labor via task specialization. However, determining whether parameter γ_t (i.e., the slope of the reaction norm for the dominance value in task specialization) significantly differs from zero is crucial. Intermediate values of phenotypic task specialization may indicate division of labor among different age- or dominant-related groups (if $\gamma_t \neq 0$), or lack of specialization in either task (if $\gamma_t = 0$). Hence, for age-polyethism or temporal division of labor to arise in our model, individuals must switch between tasks based on their age-related dominance (probability of choosing a "defensive task" versus a "work task" $T \neq 0$ or 1, and $\gamma_t \neq 0$; Table 1). Across all scenarios, individuals are selected to perform tasks based on their likelihood of inheriting the territory (Figure 3A). Specifically, when subordinates prefer defensive tasks (Figure 3A, $m < 0.2$, circles), they engage in work tasks at a young age and increasingly undertake defensive tasks as their dominance rises (Figure 3, $m < 0.2$). Similarly, if their preference leans toward work tasks (Figure 3A, $m \geq 0.2$, circles), younger subordinate helpers and those of lower dominance focus more on defense initially, but switch to work tasks as they approach the breeding stage (Figure 3, $m \geq 0.2$). In essence, subordinate helpers allocate more time to tasks with lower fitness costs as they near a competitive dominance value, all without any active enforcement by other group members, resulting in age- or rank-polyethism. These results are consistent with the rise in division of labor, defined as within-individual consistency and between-individual differences in task choice [60].

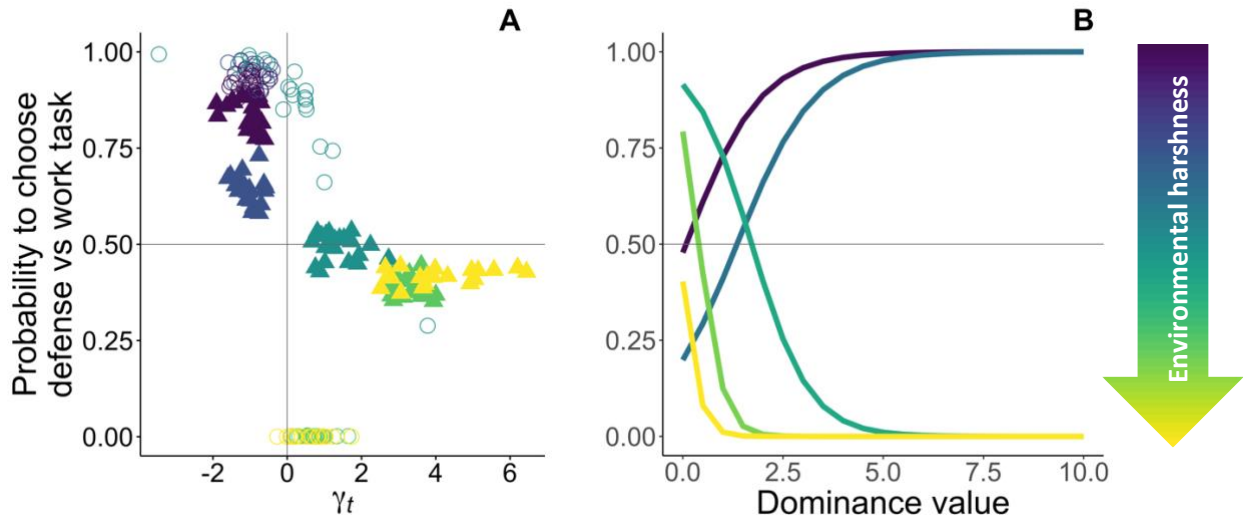

Figure 3. Evolved reaction norms to age on the display of task specialization. The evolutionary equilibria for the reaction norms of task specialization are shown at five different levels of environmental quality, ranging from benign (m=0.1, purple) to harsh (m=0.3, yellow), and x_h=5. **A**: $\gamma_t > 0$ signifies that individuals increase the likelihood of performing work tasks (task = 0; cost to dominance value), whereas $\gamma_t < 0$ signifies that individuals increase the likelihood of performing defensive tasks (task = 1; cost to survival). The optimum breeder productivity per unit of help provided was either when both tasks were performed to a similar extent, potentially selecting for division of labor (▲), or when no restrictions were introduced to the task performed by the group members (○). Results show that at division of labor equilibria, individuals increase the likelihood of performing their preferred task

(circles), when increasing their dominance value. **B**: Evolved reaction norms to dominance value with average γ_0 and γ_t across 20 replicas for varying quality environments. All parameter values described in Table 1.

Discussion

Our findings suggest that direct benefits of group living play a driving role in the evolution of division of labor via task specialization in species with totipotent workers, including all vertebrates. In contrast, in eusocial insects often characterized by high relatedness and reproductive inhibition, sterile workers acquire fitness benefits only indirectly, and so, their fitness is contingent upon the overall success of the colony rather than the individual [61, 62]. Group members in eusocial species are therefore predicted to maximize colony fitness due to the associated lower within-group conflict, and to favor the evolution of division of labor to increase group productivity efficiency [48, 49, 51]. However, in taxa with lower within-group relatedness, such as nearly all vertebrates, division of labor is facilitated when cooperation is crucial for survival and when the benefits of cooperation are evenly distributed among group members [3]. In particular, survival fitness benefits derived from living in larger groups seem to be key for the evolution of cooperative behavior in vertebrates [22, 63], and may also translate into low within-group conflict. This suggest that selection for division of labor in vertebrates is stronger in smaller groups, where increased productivity significantly enhances survival, as opposed to research on social insects that posits division of labor is more likely to evolve in larger groups [64–66]. That is not to say, however, that kin selection is unimportant in vertebrates. Our model demonstrates that vertebrates evolve a more stable division of labor when direct and indirect fitness benefits act in concert. Moreover, our model predicts that the type of task that individuals prefer depends on the type of fitness benefit that subordinates can attain. While direct fitness benefits in the form of group augmentation select more strongly for defensive tasks, kin selection alone seems to select only for work tasks. In groups of unrelated individuals where members can only gain direct fitness benefits, tasks that incur costs to their dominance value and to the likelihood of attaining a breeding position are comparatively large. Conversely, groups with no group benefits tend to be small and suffer high mortality, for which defensive tasks only aggravate the situation.

Previous models of task allocation in eusocial insects have focused on how seemingly identical individuals of the same age and broad morphology may specialize in different types of tasks [8, 60]. In contrast, our model shows that extrinsic ecological factors are also important for the evolution of task specialization in addition to intrinsic factors such as age or dominance rank. In short, our model predicts that task specialization, which varies with age or rank, will depend on environmental quality. In more favorable environments, helpers are predicted to increase defensive tasks with age or rank, whereas in harsh environments, work tasks are predicted to increase with age or rank. Furthermore, harsher environments exert stronger selective pressure for task specialization due to increased survival challenges. Enhanced cooperation and improved group productivity through helping mitigate the negative effects of the environment.

This finding is consistent with previous research on the role of ecological constraints in driving the evolution of cooperation [67–69].

Although rare, evidence of division of labor in cooperative breeding vertebrates comes from a few studies in mammals [70], birds [71, 72], and fishes [73, 74]. Our model predictions are broadly consistent with empirical data from many of these studies. For example, support for the role of age and environmental harshness on the evolution of division of labor via task specialization in vertebrates comes from arguably the most similar vertebrate system to eusocial insects, the naked mole-rat (*Heterocephalus glaber*). Naked mole-rats live in self-dug burrows that protect their inhabitants from predation and climatic extremes [70]. Therefore, even though they inhabit habitats with scarce and unpredictable rainfall, environmental harshness is likely to be limited in their stable subterranean burrows, with mortality mainly spiking during dispersal attempts. Model predictions for species that evolved in benign environments are then met, with individuals shifting from work tasks such as foraging for food, digging, and maintaining the burrow system, to defensive tasks such as guarding and patrolling as individuals grow older and larger [70, 75, 76]. Although naked molre-rats exhibit high levels of within-colony relatedness [77], group size also exerts a positive influence on survival, potentially generating group augmentation benefits [78, 79]. Under these conditions, our model predicts the highest levels of task partitioning and division of labor. In contrast, *Neolamprologus pulcher*, a cooperatively breeding cichlid fish that lives in harsh environments with high risk of predation [59], shows the opposite tendency. In line with our model predictions, larger and older helpers of this species invest relatively more in territory maintenance, whereas younger/smaller helpers defend the breeding shelter of the dominant pair to a greater extent against experimentally exposed egg predators [74]. Territory maintenance has been shown to greatly affect routine metabolic rates and, hence, growth rates [80], which directly translates into a decrease in the likelihood of becoming dominant and attaining breeding status, as predicted by our model. In addition, both group augmentation and kin selection have been found to play a role in the evolution of help in this species [20, 52]. More research is needed to verify whether this trend is widespread in cooperatively breeding vertebrates with division of labor. The preferred form of help provided by individuals throughout their life course might deviate from our expectations if helpers exhibit differing abilities to perform distinct tasks at different ages or life stages. We assumed that individuals of all ages possessed equal capability to perform different tasks. However, as individuals age and their size and body mass increase, they may become more adept at certain tasks such as deterring predators [33, 81–85]. Body condition that is unrelated to age may also influence helper contributions, as individuals in poorer condition may be more constrained on their energy allocation in activities other than self-maintenance [86–88]. Furthermore, our model does not capture instances in which help in general or specific tasks are enforced by the dominant pair or other more dominant group members [89–91].

Despite evidence of task specialization and division of labor across several vertebrate taxa, other empirical studies have failed to find similar results. For instance, researchers failed to find evidence of task specialization in Damaraland mole-rats (*Fukomys damarensis*), despite their social structure resembling that of naked mole-rats [92, 93]. However, it is worth noting

that researchers have only investigated correlates between different work tasks, potentially overlooking negative correlations with other helping activities that pose a more direct cost to survival. In fact, many studies that reported an absence of division of labor did not consider defensive tasks in their analyses [92–95]. Nonetheless, studies exist in which researchers did not find a negative correlation between defense and offspring provisioning or territory maintenance [39, 96, 97]. However, individuals may exhibit a positive or non-relationship between tasks if they also vary in total helpfulness across their lifetime, but may still switch the proportion of time/effort allocated to different types of tasks. In our model, we controlled for this potential tendency by restricting individuals from changing their overall helpfulness with age/dominance rank. We encourage future researchers to consider the proportion of time/energy investment in addition to examining correlations between tasks.

In summary, our study represents the first theoretical model aimed at elucidating the potential mechanisms underlying division of labor between temporal non-reproductives via task specialization in taxa beyond eusocial organisms. Harsh environments, where individuals can obtain direct fitness benefits from group living, favor division of labor thereby enhancing group productivity and, consequently, group size. Variation in the relative fitness costs of different helping tasks with age favors temporal polyethism, with individuals changing their behavior patterns to improve their chances of becoming breeders. Hence, future empirical research on division of labor should prioritize cooperatively breeding species inhabiting relatively harsh environments where subordinates benefit greatly from group membership, such as protection or improved food acquisition. Additionally, we emphasize the importance of including sentinel and defense behaviors in future studies to encompass a broader spectrum of fitness costs of cooperation, and to investigate potential changes in task investment throughout the helpers' lifetimes.

Materials and Methods

We developed an individual-based model in which individuals may display and vary their efforts in different helping tasks. The ancestral state features an absence of alloparental care and no task specialization. We assume that residing in larger groups yields overall survival advantages, potentially resulting in direct fitness benefits associated with the increase in group size, as proposed by the group augmentation hypothesis. We also include the coevolution of the helping strategies with their dispersal propensity, as dispersal affects group size and kin structure, and thus may impact the strength of indirect fitness benefits.

Life cycle

We model a population consisting of a fixed number of breeding territories, each comprising a dominant breeder that reproduces asexually and monopolizes reproduction, as well as an undefined number of subordinates that queue for the breeding position. The number of

subordinates is determined by the productivity of the breeders and the dispersal decisions of the group members. Subordinates may help increase the fecundity of the breeder, so that the breeder's fecundity depends on the cumulative level of help provided by the subordinates within the group, with an optimum increase when different helping tasks are performed to a similar degree.

Offspring inherit the genes for dispersal and helping tendencies from the breeders, potentially exhibiting slight variation in the presence of mutations (Figure 1, Step 1). Mutations occur at each genetic locus at a frequency of μ, causing minor adjustments to the allele's value inherited from the parent. This alteration involves the addition of a value drawn from a normal distribution characterized by a mean of 0 and a standard deviation of σ_μ (Table 1).

After breeders reproduce, their offspring and the subordinates in the group may disperse independently from each other. Dispersal propensity is controlled by a gene with values ranging from 0 to 1, where 0 represents complete philopatry and 1 represents consistent dispersal (Table 1). Dispersers may migrate to another group to become subordinates or remain as floaters waiting for breeding opportunities (Figure 1, Step 2). Successful dispersers enter the breeding queue within the group based on their dominance value rather than starting at the bottom of the hierarchy. Individuals that remain in a group express some level of help in the form of alloparental care, which can potentially evolve to zero (Figure 1, Step 3). To be conservative, we use the term help as synonymous with altruistic behavior, which increases the fitness of the beneficiary (i.e., breeder) with an immediate decrease in the actor's fitness. Hence, cooperative behaviors such as defense from adult predators that incur immediate benefits to the actor as well as by-product mutualistic benefits to other group members, are not considered in this study. Dispersal propensity, alloparental care provisions, and the type of helping task they perform all depend on their genetic predisposition. They may perform tasks that reduce their body condition and, therefore, their chances of becoming breeders, such as feeding offspring or territory maintenance (hereafter called "work tasks"), or they may perform tasks that reduce their immediate survival such as predator defense (hereafter called "defensive tasks") [32]. For simplification, we assume complete dichotomous, short-term non-cumulative fitness consequences between the different types of tasks (i.e., survival and dominance costs are only sustained during the breeding cycle in which they perform the task, and individuals only perform one of the tasks in the given cycle). We note that the names given for each type of task are meant to facilitate interpretation, and that in some species, some tasks classified as work tasks may have a higher immediate cost in survival than in the likelihood to breed, and vice versa. Note that authors should classify helping tasks in their model species repertoire based on the primary fitness cost associated with each type of helping activity (e.g., if a work activity mostly impacts survival in a given species, this task is described in this paper as defensive).

Individual survival depends on environmental quality, group membership, group size, and the amount of help provided during defensive tasks to the breeder's offspring (Figure 1, Step 4). Environmental quality is expressed as a varying maximum survival rate, independent of social factors. Additional environmental effects, such as variation in mortality linked to dispersal, or

on the likelihood of dispersers finding a new group to start breeding, have been explored elsewhere [63].

If the breeder in a group dies, all subordinates in the group and a sample of floaters compete for the breeding position (Figure 1, Step 5). The number of floaters bidding for an empty breeding spot is then proportional to the relative abundance of floaters with regard to the total number of breeding territories, to account for spatial viscosity and the likelihood of being accepted in a new group (Table 1). In this model, age influences the likelihood of attaining the breeding position. Older individuals, owing to their higher resource holding potential, have a greater probability of becoming breeders, as observed in various species [59, 98–106]. Age in our model corresponds to the number of breeding cycles that an individual survives. Additionally, work tasks reduce an individual's dominance value as a result of the impact on their body condition.

The likelihood of filling an empty breeding position is then implemented as a lottery weighted by the dominance value of the candidates. Therefore, subordinates may stay in the natal group and queue to inherit the dominant position [100, 107–110], but they may also disperse and breed or queue in another group [34, 108, 111].

We ran simulations for 200’000 generations or until equilibrium was reached for all genetic traits, across 20 replicas to assess consistency.

Age-dependent task specialization

The likelihood of choosing defensive versus work tasks T takes a logistic function with boundaries between 0 and 1 as given in Eq. 1, in which individuals may adjust their helping task as they age,

$$T = \frac{1}{1+exp(-\gamma_t t-\gamma_0)} \qquad (1),$$

where γ_t modifies the strength and direction of the effect of age (t) on task choice, and γ_0 acts as the intercept. Therefore, when T approaches zero, individuals specialize in work tasks throughout their lives, and when T approaches one, they specialize in defensive tasks. If $\gamma_t \neq 0$, given that $T \neq 0$ and $T \neq 1$, individuals show age-dependent task specialization.

In addition, the phenotypic value of help (H) is regulated by another gene and equals the allelic value of gene α, which remains fixed throughout the helper’s life. Even though individuals are likely to change the total amount of help given throughout their lives, we make this simplification to allow easier interpretation of how individuals may switch between task types as they age. For more details on how individuals may adapt their level of help with age and social and environmental conditions, see [63]. The fitness costs of helping are described in the following section.

Fitness costs of different helping tasks

Helping tasks are classified in our model according to their short-term fitness consequences. We assume that work tasks incur a more immediate cost to the body condition of helpers because of expenses in terms of time and energy. Work tasks reduce the dominance value R to inherit the breeding position in our model following Eq. 2, where γ_h is a parameter that influences the strength of the cost of help (H_{work}) in the dominance value. We assume that dominance is influenced by age (t) as a proxy for resource holding potential, with older individuals having a greater dominance value,

$$R = t - y_h H_{work} \qquad (2).$$

Note that the cost to an individual's dominance value is influenced by their current age and the current specific task that they are performing, the cost of which is not cumulative over time. Therefore, an individual's effective rank within the dominance hierarchy is, irrespective of whether they belong to a group or not, determined by their dominance value relative to other competitors for the breeding position, with higher dominance values corresponding to higher ranks in the hierarchy.

In contrast, we assume that defensive tasks have a more immediate fitness cost on survival (e.g., predator or space competitor defense) due to the high risk of injury. Therefore, helpers that defend have a survival rate (S_H) proportional to the amount of help provided ($H_{defense}$) given by the logistic Eq. 3.1, where x_h is a parameter that influences the strength of the cost of help in survival,

$$S_H = \frac{1-m}{1+exp\,(-x_0+x_h H_{defence}-x_n N)} \qquad (3.1).$$

In addition to defensive tasks, social and ecological factors also influence the survival of group members. The term m denotes the baseline mortality that determines how harsh the environment is. Higher values of m indicate higher overall environmental mortality for all individuals in the population, irrespective of social factors. For simplicity, we assume that the harshness of the environment only impacts survival, although other effects such as on reproductive output or the strength in which help improves fecundity are likely to have an effect in nature [112]. Group size (N) provides survival benefits for both subordinates and breeders (Eq. 3.1 and 3.2 respectively), where x_n is a parameter that quantifies the effect size of the benefit of group size in survival, and x_0 an intercept. Floaters sustain the highest mortality (S_F, Eq. 3.3) since they do not benefit from group protection,

$$S_B = \frac{1-m}{1+exp\,(-x_0-x_n N)} \quad (3.2) \text{ and}$$

$$S_F = \frac{1-m}{1+exp\,(-x_0)} \qquad (3.3).$$

Need for division of labor

To assess the rules governing task specialization and division of labor, we first outline a basic model in which individuals evolve their preferred helping task and then compare it to a scenario in which the breeder's reproductive outcome is maximized by performing both tasks to an approximately equivalent extent. Thus, the maximum amount of cumulative help of each type (ΣH_{max}) that can affect fecundity is given by Eq. 4:

$$\sum H_{max} = \frac{\sum H_{defence} + \sum H_{work}}{2} + k_m \qquad (4),$$

where k_m is a parameter that relaxes the need for division of labor. The breeders then reproduced asexually. The quantity of offspring produced is contingent upon the breeders' baseline fecundity (k_0) and the collective amount of help contributed by the helpers in the group. The increase in fecundity shows diminishing returns as given in the Eq. 5, where k_h is a scaling parameter that modifies the benefit of the cumulative help provided by the subordinates to increase the fecundity of the breeder,

$$K = k_0 + \frac{k_h(\sum H_{defence} + \sum H_{work})}{1+\sum H_{defence} + \sum H_{work}} \qquad (5).$$

If $\sum H_{defense} > \sum H_{max}$ or $\sum H_{work} > \sum H_{max}$, then we use the value H_{max} instead. The breeder's fecundity is determined by a randomly selected value drawn from a Poisson distribution with mean of K.

Fitness benefits of helping

We include both direct and indirect fitness benefits of helping to assess the relative importance of each in the evolution of task specialization. Indirect fitness benefits from relatedness among group members (i.e., kin selection) emerge from demographic factors such as dispersal tendencies, mortality rates, and group dynamics, though they were not coded explicitly. To calculate the coefficient of relatedness between the breeder and subordinates in a group, we calculated the coefficient of a linear regression between the allelic values of the breeders and helpers of a neutral gene that changes exclusively by genetic drift [113, 114]. Direct benefits may also be obtained by enhancing group size by helping to increase the breeder's fecundity, as larger groups benefit from higher survival rates in our model (i.e., group augmentation).

To distinguish the effect of kin selection from group augmentation, we created two parallel models for comparison to the default model (group augmentation and kin selection acting independently), in which one of the fitness benefits was removed. In the "only group augmentation" implementation, individuals just born (i.e., age = 1) that decide to stay in the natal territory as subordinates (Figure 1, Step 2) are shuffled into another group, thereby removing the influence of relatedness from the model. In the "only kin selection"

implementation, we removed the survival benefits linked to living in a group ($x_n = 0$). It is possible that direct and indirect fitness benefits could have an additive effect on the evolution of alloparental care, since group size enhancement has a positive effect on the survival of kin group members, not only on the individual.

Table 1. Overview of notation. Values conveyed for the genes are initial input values, values given for the scaling parameters are fixed throughout the simulations. If more than one value is given, results are shown to display the effect of this parameter's variation. *: Additional values of these parameters are discussed in the Supplemental Material.

Symbol	Meaning	Value
Genes		
α	Genetic propensity to help	0
β	Genetic predisposition to disperse	1
γ_0	Intercept in the task specialization reaction norm	0
γ_t	Effect size of age on task specialization	0
Scaling parameters		
y_h	Effect size of cost of help on dominance when performing "work tasks"	0.1
x_h	Effect size of cost of help in survival when performing "defensive tasks"	3 / 5 / 7
x_n	Effect size of the benefit of group size in survival	0 / 3
x_0	Intercept in the survival function	1.5*
m	Baseline mortality	0.1 - 0.3
f	Mean number of groups a floater samples for becoming a breeder	2*
k_m	Deviation from a perfect split in the need of both defense and work tasks	0.1
k_h	Effect size of the cumulative help of subordinates on the fecundity of the breeder	1
k_0	Fecundity of the breeder in the absence of help	1
t_{min}	Minimum age to come breeder in the scramble context implementation	2
q	Baseline individual quality in the scramble context implementation	4
μ	Mutation rate	0.05
σ_μ	Mutation step size	0.04
N_b	Number of breeding territories	5000
Phenotypic traits		
H	Level of help of either kind provided to the breeder $H = \alpha$. We express cumulative level of help given in a group as $\sum H_i$	
D	Dispersal propensity $D = \beta$, applying boundaries between 0 and 1	
R	Dominance value	
T	Probability of choosing "defensive task" vs "work task"	
S	Survival rate	
K	Fecundity of the breeder	
Variables		
t	Age	
N	Emergent group size	
N_f	Total number of floaters	
$N_{f,b}$	Number of floaters bidding for a breeding position, given by $N_{f,b} = f * N_f / N_b$	

Acknowledgements: We thank Patrick Kennedy for comments on earlier versions of the manuscript and Tobias Zobrist for help with the coding implementation.

Funding: Funding was provided by the SNSF grant P500PB_214371 to Irene García-Ruiz.

Data and materials availability: Custom code used to generate the simulations is available at https://github.com/IreneGR92/Task_specialization

Author Contributions: conceptualization IGR & DR, methodology IGR, investigation IGR, visualization IGR, supervision DR, writing—original draft IGR, writing—review & editing DR.

Competing Interest Statement: The authors declare no competing interests.

References

1. Dunbar RIM, Lehmann J, Korstjens AJ, Gowlett JAJ (2014) The road to modern humans: time budgets, fission-fusion sociality, kinship and the division of labour in hominin evolution. In: Lucy to language: The benchmark papers. Oxford University Press Oxford, pp 333–355

2. Smith A (1776) An Inquiry into the Nature and Causes of the Wealth of Nations. Wiley Online Library, London

3. Cooper GA, West SA (2018) Division of labour and the evolution of extreme specialization. Nat Ecol Evol 2:1161–1167. https://doi.org/10.1038/s41559-018-0564-9

4. Zhang Z, Claessen D, Rozen DE (2016) Understanding Microbial Divisions of Labor. Front Microbiol 7:2070. https://doi.org/10.3389/fmicb.2016.02070

5. Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press

6. Jeanne RL (2016) Division of labor is not a process or a misleading concept. Behav Ecol Sociobiol 70:1109–1112. https://doi.org/10.1007/s00265-016-2146-7

7. Michener CD (1974) The social behavior of the bees: a comparative study. Harvard University Press

8. Beshers SN, Fewell JH (2001) Models of division of labor in social insects. Annu Rev Entomol 46:413–440. https://doi.org/10.1146/annurev.ento.46.1.413

9. Wilson EO (1971) The insect societies. Cambridge, Massachusetts, USA, Harvard University Press

10. Wheeler WM (1928) Emergent evolution and the development of societies. WW Norton, Incorporated

11. Ispolatov I, Ackermann M, Doebeli M (2012) Division of labour and the evolution of multicellularity. Proceedings of the Royal Society B: Biological Sciences 279:1768–1776. https://doi.org/10.1098/rspb.2011.1999

12. Willensdorfer M (2009) On the evolution of differentiated multicellularity. Evolution (N Y) 63:306–323. https://doi.org/10.1111/j.1558-5646.2008.00541.x

13. Yanni D, Jacobeen S, Márquez-Zacarías P, et al (2020) Topological constraints in early multicellularity favor reproductive division of labor. Elife 9:e54348. https://doi.org/10.7554/eLife.54348

14. Ridley AR, Raihani NJ (2008) Task partitioning increases reproductive output in a cooperative bird. Behavioral Ecology 19:1136–1142. https://doi.org/10.1093/beheco/arn097

15. Dunn PO, Cockburn A, Mulder RA (1995) Fairy-wren helpers often care for young to which they are unrelated. Proc R Soc Lond B Biol Sci 259:339–343. https://doi.org/10.1098/rspb.1995.0050

16. Doutrelant C, Dalecky A, Covas R (2011) Age and relatedness have an interactive effect on the feeding behaviour of helpers in cooperatively breeding sociable weavers. Behaviour 148:1393–1411. https://doi.org/10.1163/000579511X608701

17. Riehl C (2013) Evolutionary routes to non-kin cooperative breeding in birds. Proceedings of the Royal Society B: Biological Sciences 280:20132245. https://doi.org/10.1098/rspb.2013.2245

18. Kokko H, Johnstone RA, Clutton-Brock TH (2001) The evolution of cooperative breeding through group augmentation. Proceedings of the Royal Society B: Biological Sciences 268:187–196. https://doi.org/10.1098/rspb.2000.1349

19. Kingma SA, Santema P, Taborsky M, Komdeur J (2014) Group augmentation and the evolution of cooperation. Trends Ecol Evol 29:476–484. https://doi.org/10.1016/j.tree.2014.05.013

20. Zöttl M, Heg D, Chervet N, Taborsky M (2013) Kinship reduces alloparental care in cooperative cichlids where helpers pay-to-stay. Nat Commun 4:1341. https://doi.org/10.1038/ncomms2344

21. Sparkman AM, Adams JR, Steury TD, et al (2011) Direct fitness benefits of delayed dispersal in the cooperatively breeding red wolf (*Canis rufus*). Behavioral Ecology 22:199–205. https://doi.org/10.1093/beheco/arq194

22. Shah SS, Rubenstein DR (2023) Group augmentation underlies the evolution of complex sociality in the face of environmental instability. Proceedings of the National Academy of Sciences 120:e2212211120. https://doi.org/10.1073/pnas.2212211120

23. Richardson DS, Burke T, Komdeur J (2002) Direct benefits and the evolution of female-biased cooperative breeding in Seychelles warblers. Evolution (N Y) 56:2313–2321. https://doi.org/10.1111/j.0014-3820.2002.tb00154.x

24. Cockburn A (1998) Evolution of Helping Behavior in Cooperatively Breeding Birds. Annu Rev Ecol Syst 29:141–177. https://doi.org/10.1146/annurev.ecolsys.29.1.141

25. Kitchen D, Beehner J (2007) Factors affecting individual participation in group-level aggression among non-human primates. Behaviour 144:1551–1581. https://doi.org/10.1163/156853907782512074

26. Anderson C (2001) Teams in animal societies. Behavioral Ecology 12:534–540. https://doi.org/10.1093/beheco/12.5.534

27. Charles L. Nunn, Rebecca J. Lewis (2001) Cooperation and collective action in animal behaviour. In: Ronald Noë, Jan A.R.A.M. Van Hooff, Peter Hammerstein (eds) Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge University Press, Cambridge (United Kingdom), pp 42–66

28. Poiani A, Yorke M (1989) Predator Harassment: More Evidence on the Deadly Risk. Ethology 83:167–169. https://doi.org/10.1111/j.1439-0310.1989.tb00526.x

29. Tórrez L, Robles N, González A, Crofoot MC (2012) Risky business? Lethal attack by a jaguar sheds light on the costs of predator mobbing for capuchins (*Cebus capucinus*). Int J Primatol 33:440–446. https://doi.org/10.1007/s10764-012-9588-1

30. Sordahl TA (1990) The risks of avian mobbing and distraction behavior: an anecdotal review. Wilson Bull 102:349–352

31. Grantner A, Taborsky M (1998) The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: Cichlidae). J Comp Physiol B 168:427–433. https://doi.org/10.1007/s003600050162

32. Heinsohn R, Legge S (1999) The cost of helping. Trends Ecol Evol 14:53–57. https://doi.org/10.1016/S0169-5347(98)01545-6

33. Heinsohn R, Cockburn A (1994) Helping is costly to young birds in cooperatively breeding white-winged choughs. Proceedings of the Royal Society B: Biological Sciences 256:293–298. https://doi.org/10.1098/rspb.1994.0083

34. Zöttl M, Chapuis L, Freiburghaus M, Taborsky M (2013) Strategic reduction of help before dispersal in a cooperative breeder. Biol Lett 9:20120878. https://doi.org/10.1098/rsbl.2012.0878

35. Young AJ, Carlson AA, Clutton-Brock T (2005) Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. Anim Behav 70:829–837. https://doi.org/10.1016/j.anbehav.2005.01.019

36. Komdeur J (1996) Influence of age on reproductive performance in the Seychelles warbler. Behavioral Ecology 7:417–425. https://doi.org/10.1093/beheco/7.4.417

37. Boland CRJ, Heinsohn R, Cockburn A (1997) Deception by helpers in cooperatively breeding white-winged choughs and its experimental manipulation. Behav Ecol Sociobiol 41:251–256. https://doi.org/10.1007/s002650050386

38. Taborsky M (1984) Broodcare helpers in the cichlid fish *Lamprologus brichardi*: Their costs and benefits. Anim Behav 32:1236–1252. https://doi.org/10.1016/S0003-3472(84)80241-9

39. Clutton-Brock TH, Russell AF, Sharpe LL (2003) Meerkat helpers do not specialize in particular activities. Anim Behav 66:531–540. https://doi.org/10.1006/anbe.2003.2209

40. Boesch C (2002) Cooperative hunting roles among taï chimpanzees. Human Nature 13:27–46. https://doi.org/10.1007/s12110-002-1013-6

41. Fischer B, van Doorn GS, Dieckmann U, Taborsky B (2014) The evolution of age-dependent plasticity. American Naturalist 183:108–125. https://doi.org/10.1086/674008

42. Johnstone RA, Cant MA (2010) The evolution of menopause in cetaceans and humans: the role of demography. Proceedings of the Royal Society B: Biological Sciences 277:3765–3771. https://doi.org/10.1098/rspb.2010.0988

43. Hölldobler B, Wilson EO (1990) The ants. Harvard University Press

44. Sendova-Franks A, Franks NR (1993) Task allocation in ant colonies within variable environments (a study of temporal polyethism: experimental). Bull Math Biol 55:75–96. https://doi.org/10.1007/BF02460295

45. Traniello JFA, Rosengaus RB (1997) Ecology, evolution and division of labour in social insects. Anim Behav 53:209–213. https://doi.org/10.1006/anbe.1996.0289

46. Ferguson-Gow H, Sumner S, Bourke AFG, Jones KE (2014) Colony size predicts division of labour in attine ants. Proceedings of the Royal Society B: Biological Sciences 281:20141411. https://doi.org/10.1098/rspb.2014.1411

47. Keller L, Chapuisat M (2010) Eusociality and Cooperation. In: Encyclopedia of Life Sciences. Wiley

48. West SA, Fisher RM, Gardner A, Kiers ET (2015) Major evolutionary transitions in individuality. Proceedings of the National Academy of Sciences 112:10112–10119. https://doi.org/10.1073/pnas.1421402112

49. Fisher RM, Cornwallis CK, West SA (2013) Group formation, relatedness, and the evolution of multicellularity. Current Biology 23:1120–1125

50. Queller DC, Strassmann JE (1998) Kin selection and social insects. Bioscience 48:165–175

51. Gardner A, Grafen A (2009) Capturing the superorganism: a formal theory of group adaptation. J Evol Biol 22:659–671. https://doi.org/10.1111/j.1420-9101.2008.01681.x

52. García-Ruiz I, Taborsky M (2022) Group augmentation on trial: helpers in small groups enhance antipredator defence of eggs. Biol Lett 18:20220170. https://doi.org/10.1098/rsbl.2022.0170

53. Rood JP (1990) Group size, survival, reproduction, and routes to breeding in dwarf mongooses. Anim Behav 39:566–572. https://doi.org/10.1016/S0003-3472(05)80423-3

54. Heg D, Brouwer L, Bachar Z, Taborsky M (2005) Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. Behaviour 142:1615–1641. https://doi.org/10.1163/156853905774831891

55. Clutton-Brock TH, Gaynor D, McIlrath GM, et al (1999) Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. Journal of Animal Ecology 68:672–683. https://doi.org/10.1046/j.1365-2656.1999.00317.x

56. Guindre-Parker S, Rubenstein DR (2020) Survival Benefits of Group Living in a Fluctuating Environment. Am Nat 195:1027–1036. https://doi.org/10.1086/708496

57. Bilde T, Coates KS, Birkhofer K, et al (2007) Survival benefits select for group living in a social spider despite reproductive costs. J Evol Biol 20:2412–2426. https://doi.org/10.1111/j.1420-9101.2007.01407.x

58. Rubenstein DR, Koenig WD, Dickinson JL (2016) Superb starlings: cooperation and conflict in an unpredictable environment. In: Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior. Cambridge University Press Cambridge, pp 181–196

59. Taborsky M (2016) Cichlid fishes: A model for the integrative study of social behavior. In: Koenig WD, Dickinson JL (eds) Cooperative Breeding in Vertebrates. Cambridge University Press, Cambridge, pp 272–293

60. Ulrich Y, Saragosti J, Tokita CK, et al (2018) Fitness benefits and emergent division of labour at the onset of group living. Nature 560:635–638. https://doi.org/10.1038/s41586-018-0422-6

61. Hughes WOH, Oldroyd BP, Beekman M, Ratnieks FLW (2008) Ancestral monogamy shows kin selection is key to the evolution of eusociality. Science (1979) 320:1213–1216. https://doi.org/10.1126/science.1156108

62. Foster K, Wenseleers T, Ratnieks F (2006) Kin selection is the key to altruism. Trends Ecol Evol 21:57–60. https://doi.org/10.1016/j.tree.2005.11.020

63. García-Ruiz I, Quiñones A, Taborsky M (2022) The evolution of cooperative breeding by direct and indirect fitness effects. Sci Adv 8:eabl7853. https://doi.org/10.1126/sciadv.abl7853

64. Nakahashi W, Feldman MW (2014) Evolution of division of labor: Emergence of different activities among group members. J Theor Biol 348:65–79. https://doi.org/10.1016/j.jtbi.2014.01.027

65. Dornhaus A, Powell S, Bengston S (2012) Group Size and Its Effects on Collective Organization. Annu Rev Entomol 57:123–141. https://doi.org/10.1146/annurev-ento-120710-100604

66. Ulrich Y, Saragosti J, Tokita CK, et al (2018) Fitness benefits and emergent division of labour at the onset of group living. Nature 560:635–638. https://doi.org/10.1038/s41586-018-0422-6

67. Hatchwell BJ, Komdeur J (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. Anim Behav 59:1079–1086. https://doi.org/10.1006/anbe.2000.1394

68. Emlen ST (1982) The evolution of helping. I. An ecological constraints model. Am Nat 119:29–39. https://doi.org/10.1086/283888

69. Kokko H, Ekman J (2002) Delayed dispersal as a route to breeding: Territorial inheritance, safe havens, and ecological constraints. American Naturalist 160:468–484. https://doi.org/10.1086/342074

70. Lacey EA, Sherman PW (1996) Cooperative breeding in naked mole-rats: implications for vertebrate and invertebrate sociality. In: Cooperative Breeding in Mammals. Cambridge University Press, pp 267–301

71. Arnold KE, Owens IPF, Goldizen AW (2005) Division of labour within cooperatively breeding groups. Behaviour 142:1577–1590. https://doi.org/10.1163/156853905774831927

72. Ridley AR, Raihani NJ (2008) Task partitioning increases reproductive output in a cooperative bird. Behavioral Ecology 19:1136–1142. https://doi.org/10.1093/beheco/arn097

73. Josi D, Freudiger A, Taborsky M, Frommen JG (2021) Experimental predator intrusions in a cooperative breeder reveal threat-dependent task partitioning. Behavioral Ecology 31:1369–1378. https://doi.org/10.1093/beheco/araa094

74. Bruintjes R, Taborsky M (2011) Size-dependent task specialization in a cooperative cichlid in response to experimental variation of demand. Anim Behav 81:387–394. https://doi.org/10.1016/j.anbehav.2010.10.004

75. Lacey EA, Sherman PW (1991) Social organization of naked mole-rat colonies: evidence for divisions of labor. In: The Biology of the Naked Mole-Rat. Princeton University Press, pp 275–336

76. Faulkes CG, Abbott DH, Jarvis JUM (1991) Social suppression of reproduction in male naked mole-rats, *Heterocephalus glaber*. Reproduction 91:593–604. https://doi.org/10.1530/jrf.0.0910593

77. Reeve HK, Westneat DF, Noon WA, et al (1990) DNA “fingerprinting” reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. Proceedings of the National Academy of Sciences 87:2496–2500. https://doi.org/10.1073/pnas.87.7.2496

78. Le Comber SC, Spinks AC, Bennett NC, et al (2002) Fractal dimension of African mole-rat burrows. Can J Zool 80:436–441. https://doi.org/10.1139/z02-026

79. O’Riain MJ, Braude S (2001) Inbreeding versus outbreeding in captive and wild populations of naked mole-rats. In: Dispersal. Oxford University PressOxford, pp 143–154

80. Taborsky M, Grantner A (1998) Behavioural time–energy budgets of cooperatively breeding *Neolamprologus pulcher* (Pisces: Cichlidae). Anim Behav 56:1375–1382. https://doi.org/10.1006/anbe.1998.0918

81. Brown JL (1985) The evolution of helping behavior—an ontogenetic and comparative perspective. In: The comparative development of adaptive skills. Routledge, pp 137–171

82. Clutton-Brock TH, Russell AF, Sharpe LL, et al (2002) Evolution and development of sex differences in cooperative behavior in meerkats. Science (1979) 297:253–256. https://doi.org/10.1126/science.1071412

83. Erb WM, Porter LM (2020) Variable infant care contributions in cooperatively breeding groups of wild saddleback tamarins. Am J Primatol 82:e23190. https://doi.org/10.1002/ajp.23190

84. Zahed SR, Kurian A V., Snowdon CT (2010) Social dynamics and individual plasticity of infant care behavior in cooperatively breeding cotton-top tamarins. Am J Primatol 72:296–306. https://doi.org/10.1002/ajp.20782

85. Woxvold IA, Mulder RA, Magrath MJL (2006) Contributions to care vary with age, sex, breeding status and group size in the cooperatively breeding apostlebird. Anim Behav 72:63–73. https://doi.org/10.1016/j.anbehav.2005.08.016

86. Clutton-Brock TH, Brotherton PNM, O'Riain MJ, et al (2000) Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. Proceedings of the Royal Society B: Biological Sciences 267:301–305. https://doi.org/10.1098/rspb.2000.1000

87. Clutton-Brock TH, Brotherton PNM, O'Riain MJ, et al (2001) Contributions to cooperative rearing in meerkats. Anim Behav 61:705–710. https://doi.org/10.1006/anbe.2000.1631

88. Nichols HJ, Amos W, Bell MBV, et al (2012) Food availability shapes patterns of helping effort in a cooperative mongoose. Anim Behav 83:1377–1385. https://doi.org/10.1016/j.anbehav.2012.03.005

89. García-Ruiz I, Taborsky M (2024) Nepotism mediates enforced cooperation in asymmetric negotiations. iScience 27:110334. https://doi.org/10.1016/j.isci.2024.110334

90. Kokko H, Johnstone RA, Wright J (2002) The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? Behavioral Ecology 13:291–300. https://doi.org/10.1093/beheco/13.3.291

91. Hellmann JK, Hamilton IM (2018) Dominant and subordinate outside options alter help and eviction in a pay-to-stay negotiation model. Behavioral Ecology 29:553–562. https://doi.org/10.1093/beheco/ary006

92. Zöttl M, Vullioud P, Mendonça R, et al (2016) Differences in cooperative behavior among Damaraland mole rats are consequences of an age-related polyethism. Proceedings of the National Academy of Sciences 113:10382–10387. https://doi.org/10.1073/pnas.1607885113

93. Thorley J, Mendonça R, Vullioud P, et al (2018) No task specialization among helpers in Damaraland mole-rats. Anim Behav 143:9–24. https://doi.org/10.1016/j.anbehav.2018.07.004

94. English S, Nakagawa S, Clutton-Brock TH (2010) Consistent individual differences in cooperative behaviour in meerkats (*Suricata suricatta*). J Evol Biol 23:1597–1604

95. Smith MG, LaPergola JB, Riehl C (2024) Workload inequality increases with group size in a cooperatively breeding bird. Anim Behav 207:87–99. https://doi.org/10.1016/j.anbehav.2023.10.015

96. van Asten T, Hall ML, Mulder RA (2016) Who cares? Effect of coping style and social context on brood care and defense in superb fairy-wrens. Behavioral Ecology arw096

97. Teunissen N, Kingma SA, Peters A (2020) Nest defence and offspring provisioning in a cooperative bird: individual subordinates vary in total contribution, but no division of tasks among breeders and subordinates. Behav Ecol Sociobiol 74:94. https://doi.org/10.1007/s00265-020-02877-2

98. Kingma SA, Hall ML, Peters A (2011) Multiple benefits drive helping behavior in a cooperatively breeding bird: An integrated analysis. American Naturalist 177:486–495. https://doi.org/10.1086/658989

99. Shaw P (1986) The relationship between dominance behaviour, bill size and age group in Greater Sheathbills *Chionis alba*. Ibis 128:48–56. https://doi.org/10.1111/j.1474-919X.1986.tb02091.x

100. Bridge C, Field J (2007) Queuing for dominance: Gerontocracy and queue-jumping in the hover wasp *Liostenogaster flavolineata*. Behav Ecol Sociobiol 61:1253–1259. https://doi.org/10.1007/s00265-007-0355-9

101. Doolan SP, Macdonald DW (1996) Dispersal and extra-territorial prospecting by slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari. J Zool 240:59–73. https://doi.org/10.1111/j.1469-7998.1996.tb05486.x

102. Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. J Theor Biol 47:223–243. https://doi.org/10.1016/0022-5193(74)90111-8

103. Brown JL, Brown ER, Sedransk J (1997) Dominance, age, and reproductive success in a complex society: a long-term study of the mexican jay. Auk 114:279–286. https://doi.org/10.2307/4089168

104. Buston PM (2004) Territory inheritance in clownfish. Proc R Soc Lond B Biol Sci 271:S252–S254. https://doi.org/10.1098/rsbl.2003.0156

105. Bang A, Gadagkar R (2012) Reproductive queue without overt conflict in the primitively eusocial wasp *Ropalidia marginata*. Proceedings of the National Academy of Sciences 109:14494–14499. https://doi.org/10.1073/pnas.1212698109

106. Unnikrishnan S, Gadagkar R (2021) Dominance behaviour and division of labour in the tropical primitively eusocial wasp *Ropalidia cyathiformis*. Insectes Soc 68:123–132. https://doi.org/10.1007/s00040-020-00803-3

107. Woolfenden GE, Fitzpatrick JW (1978) The inheritance of territory in group-breeding birds. Bioscience 28:104–108. https://doi.org/10.2307/1307423

108. Russell EM, Rowley I (1993) Philopatry or dispersal: competition for territory vacancies in the splendid fairy-wren, *Malurus splendens*. Anim Behav 45:519–539. https://doi.org/10.1006/anbe.1993.1063

109. Dierkes P, Heg D, Taborsky M, et al (2005) Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. Ecol Lett 8:968–975. https://doi.org/10.1111/j.1461-0248.2005.00801.x

110. Balshine-Earn S, Neat FC, Reid H, Taborsky M (1998) Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. Behavioral Ecology 9:432–438. https://doi.org/10.1093/beheco/9.5.432

111. Walters JR, Doerr PD, Carter JH (1988) The cooperative breeding system of the red-cockaded woodpecker. Ethology 78:275–305. https://doi.org/10.1111/j.1439-0310.1988.tb00239.x

112. Rubenstein DR (2011) Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. Proceedings of the National Academy of Sciences 108:10816–10822

113. Gardner A, West SA, Wild G (2011) The genetical theory of kin selection. J Evol Biol 24:1020–1043. https://doi.org/10.1111/j.1420-9101.2011.02236.x

114. Michod RE, Hamilton WD (1980) Coefficients of relatedness in sociobiology. Nature 288:694–697. https://doi.org/10.1038/288694a0

Supporting information

Kin selection and the evolution of division of labor

To assess the robustness of our findings on the evolution of division of labor driven by kin selection, independent of group survival benefits, we further examined the influence of survival, dispersal, relatedness, and breeding opportunities outside the natal group.

One factor contributing to defense not readily evolving under kin selection alone is that the cost to dominance is relatively small when competing against relatives. Another possible explanation is that without group benefits, mortality rates are too high for survival-costly helping tasks such as defense to evolve. In Figure S1, we examine the effects of increasing the baseline survival from $x_0 = 1.5$ (as in Figure 2) to $x_0 = 4.5$ (which simulates the addition of a group benefit of $x_n = 3$ to the baseline survival) and $x_0 = 10$ (an extreme scenario that greatly reduces the survival cost of defense tasks; see Eq. 3.1).

Our results indicate that even with high baseline survival, kin selection strongly favors work over defense tasks. However, in harsh environments ($m = 0.3$), where the survival costs of defense tasks are minimal ($x_0 = 10$ and $x_h = 3$; Table S2), some degree of task specialization and division of labor emerges (Figure S1). Despite this, most individuals still choose to disperse and breed outside their natal territory when no group survival benefits exist (Table S2). This suggests that, without such benefits, offspring have little incentive to stay and help due to reduced reproductive opportunities and competition with kin. To test this, we eliminated the dispersal advantage by reducing the number of sampled groups from two ($f = 2$) to one ($f = 1$), incentivizing individuals to queue for breeding in their natal territory (Figure S2).

Even when increased philopatry, resulting from reduced outbreeding opportunities for dispersers, potentially enhances the indirect fitness benefits of helping and task partitioning, division of labor only evolves when survival costs are exceedingly low ($x_0 = 10$; Figure S2; Table S3). This suggests that while kin selection can promote the evolution of division of labor, it does so only under highly restrictive conditions with minimal survival costs. Therefore, in natural settings, other selective forces, such as direct fitness benefits, are more likely to drive the evolution of division of labor.

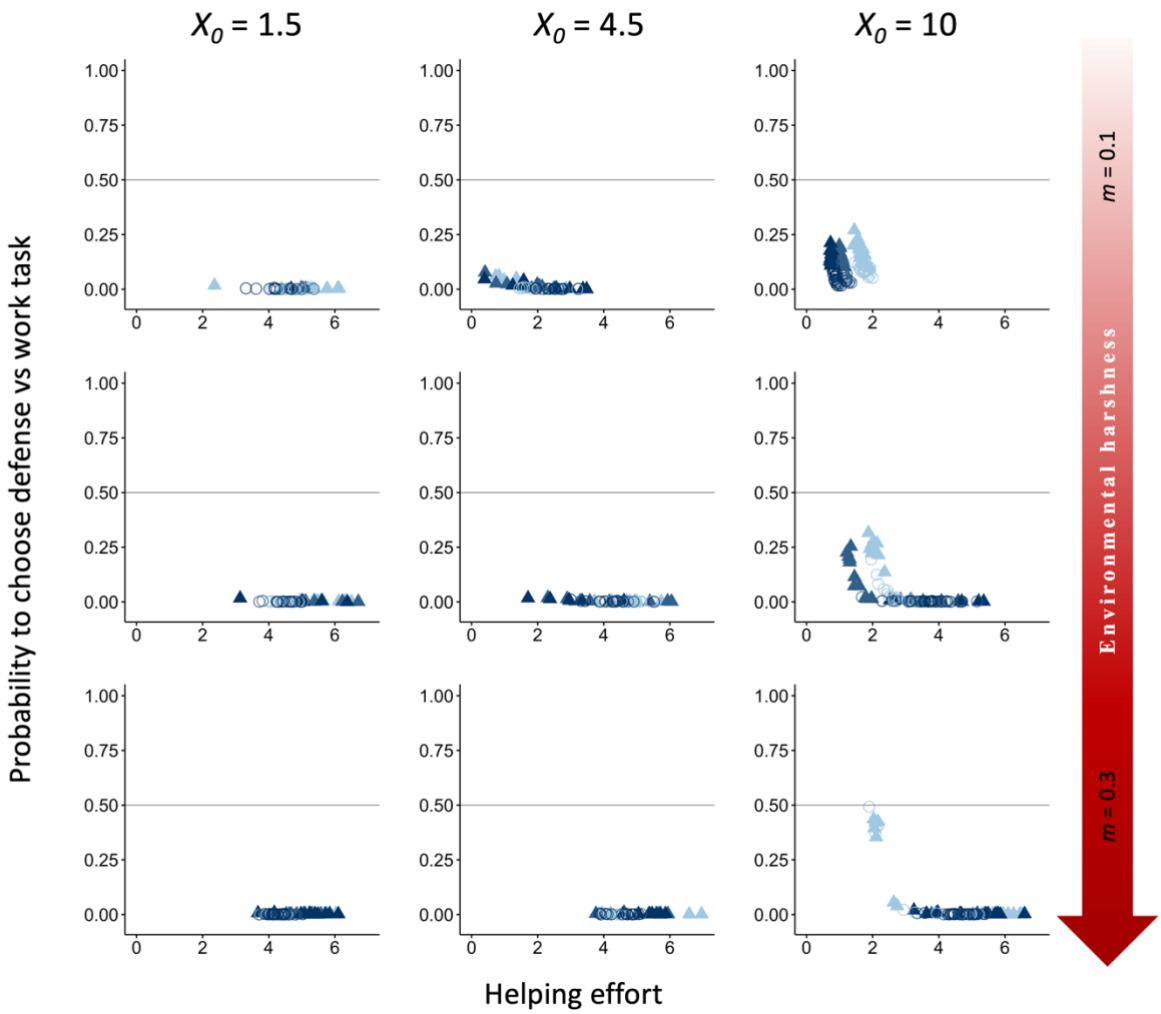

Figure S1. Effect of increasing the baseline survival x_0 to favor the evolution of division of labor under only kin selection. The evolutionary equilibria for levels of helping and task specialization are shown at three different levels of environmental quality, ranging from benign (m = 0.1) to harsh (m = 0.3), and for three different levels of cost of help on survival (light blue, x_h = 3environmental= 5; and, ranging x_h = 7). The y-axis expresses the likelihood of individuals choosing a defensive task with a cost to survival versus a work task with a cost to dominance. The optimum breeder productivity per unit of help provided was either when both tasks were performed to a similar extent, potentially selecting for division of labor (▲), or when no restrictions were introduced to the task performed by the group members (○). Input parameters are the same as in Figure 2 (where x_0 = 1.5) except for x_0 = 4.5 and x_0 = 10 (higher survival for all individuals irrespective of group membership or environment; Table 1). Further details are provided in Table S2.

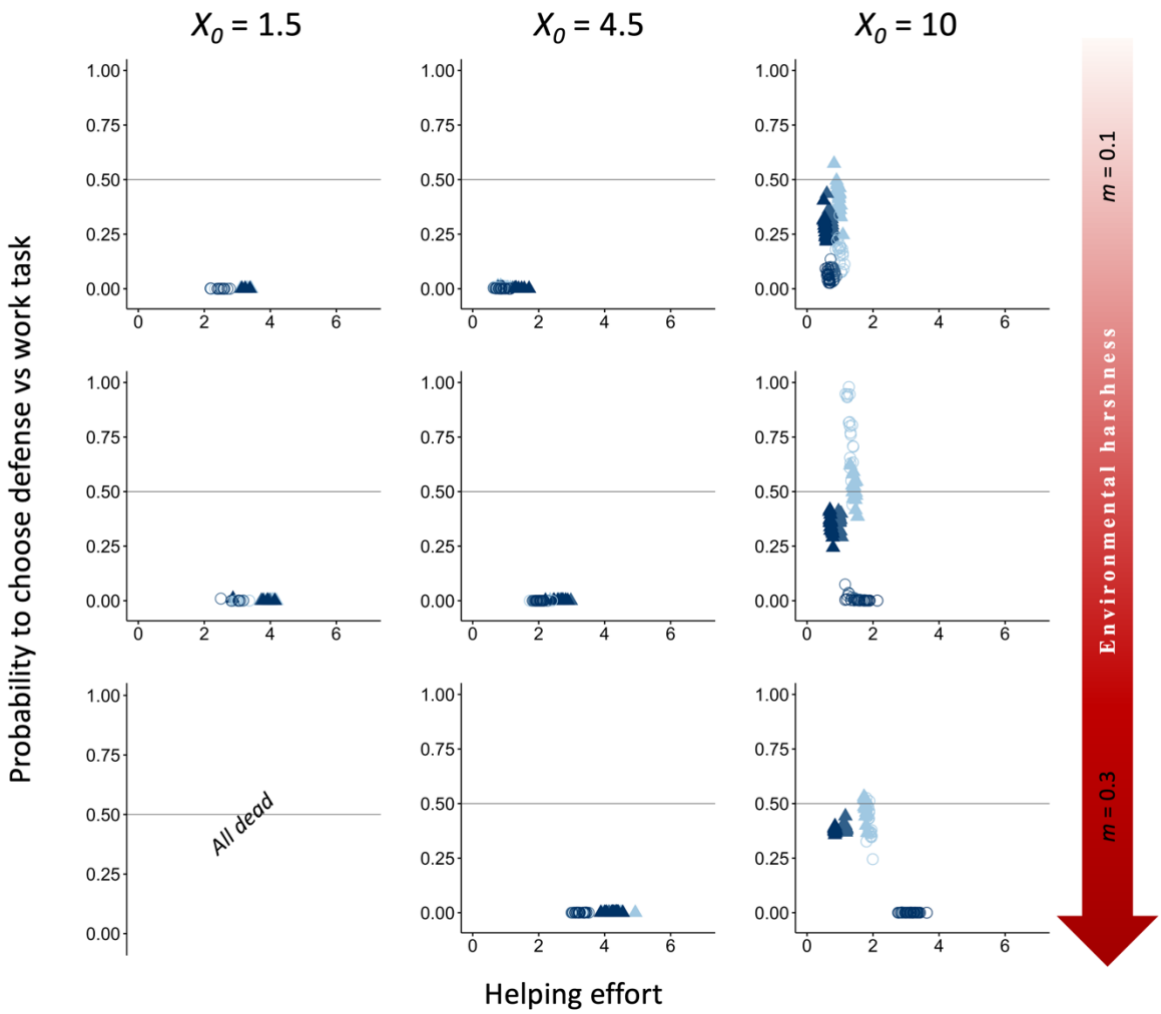

Figure S2. Effect of reducing the incentives to disperse to favor the evolution of division of labor under only kin selection. An increase in incentives to remain philopatric was achieved by reducing f to 1 ($f = 2$ in Figure 2; Table 1). The evolutionary equilibria for levels of helping and task specialization are shown at three different levels of environment quality that range from benign (m=0.1) to harsh (m = 0.3), and for three different levels of cost of help on survival (light blue, $x_h = 3$; blue, $x_h = 5$; and dark blue, $x_h = 7$). The y-axis expresses the likelihood of the individuals to choose a defensive task with cost to survival versus a work task with a cost to dominance. The optimum breeder productivity per unit of help provided was either when both tasks were performed to a similar extent, potentially selecting for division of labor (▲), or when no restrictions were introduced to the task performed by the group members (○). Other input parameters are the same as in Figure 2 (where $x_0 = 1.5$) except for $x_0 = 4.5$ and $x_0 = 10$ (higher survival for all individuals irrespective of group membership or environment; Table 1).

Table S1. Supplementary data for Figure 2. Mean values are shown for dispersal propensity, survival rate, group size (± SD), and within-group relatedness for three environmental qualities ranging from benign (m = 0.1) to harsh (m = 0.3) across 20 replicas. Selective forces at play include kin selection (KS), group augmentation (GA), or both (KS + GA). The optimum breeder productivity per unit of help provided was either when both tasks were performed to a similar extent, potentially selecting for division of labor (DoL), or when no restrictions were introduced to the task performed by the group members (No DoL).

	KS						GA						KS + GA					
	$m = 0.1$		$m = 0.2$		$m = 0.3$		$m = 0.1$		$m = 0.2$		$m = 0.3$		$m = 0.1$		$m = 0.2$		$m = 0.3$	
	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL
Dispersal	0.95	0.92	0.94	0.90	0.91	0.84	0.01	0.01	0.11	0.10	0.37	0.33	0.07	0.07	0.22	0.22	0.43	0.52
Survival	0.74	0.74	0.65	0.65	0.57	0.57	0.90	0.90	0.79	0.79	0.66	0.67	0.89	0.89	0.77	0.77	0.65	0.65
Group size	1.16 ±0.16	1.34 ±0.30	1.14 ±0.12	1.25 ±0.19	1.14 ±0.08	1.29 ±0.11	9.85 ±0.08	9.83 ±0.05	6.94 ±0.43	7.52 ±0.41	3.04 ±0.35	3.40 ±0.36	16.42 ±0.10	16.55 ±0.07	6.42 ±0.14	6.61 ±0.11	2.95 ±0.25	2.83 ±0.05
Relatedness	0.37	0.36	0.54	0.52	0.73	0.71	0	0	0	0	0	0	0.56	0.57	0.57	0.57	0.65	0.60

Table S2. Supplementary data for the effect of increasing the baseline survival x_0 to favor the evolution of division of labor under only kin selection shown in Figure S1. Mean values are shown for dispersal propensity, survival rate, group size (± SD), and within-group relatedness for three environmental qualities ranging from benign ($m = 0.1$) to harsh ($m = 0.3$) across 20 replicas. Results are shown for $x_0 = 1.5$ (default), $x_0 = 3.5$ and $x_0 = 10$. The optimum breeder productivity per unit of help provided was either when both tasks were performed to a similar extent, potentially selecting for division of labor (DoL), or when no restrictions were introduced to the task performed by the group members (No DoL).

	$x_0 = 1.5$						$x_0 = 4.5$						$x_0 = 10$					
	$m = 0.1$		$m = 0.2$		$m = 0.3$		$m = 0.1$		$m = 0.2$		$m = 0.3$		$m = 0.1$		$m = 0.2$		$m = 0.3$	
	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL
Dispersal	0.95	0.92	0.94	0.9	0.91	0.84	0.84	0.85	0.89	0.86	0.89	0.85	0.79	0.83	0.88	0.85	0.9	0.86
Survival	0.74	0.74	0.65	0.65	0.57	0.57	0.89	0.89	0.79	0.79	0.69	0.69	0.90	0.90	0.80	0.80	0.70	0.70
Group size	1.16 ±0.16	1.34 ±0.30	1.14 ±0.12	1.25 ±0.19	1.14 ±0.08	1.29 ±0.11	3.02 ±0.33	3.14 ±0.14	1.61 ±0.26	1.86 ±0.21	1.33 ±0.13	1.5 ±0.09	4.19 ±0.19	3.75 ±0.20	1.68 ±0.22	1.96 ±0.07	1.28 ±0.11	1.48 ±0.07
Relatedness	0.37	0.36	0.54	0.52	0.73	0.71	0.15	0.15	0.28	0.28	0.45	0.44	0.17	0.15	0.27	0.27	0.44	0.43

Table S3. Supplementary data for the effect of reducing the incentives to disperse to favor the evolution of division of labor under only kin selection shown in Figure S2. The increased incentive was achieved by reducing the parameter *f* that signifies the mean number of groups a floater samples for becoming a breeder from 2 (default) to 1. Mean values are shown for dispersal propensity, survival rate, group size (± SD), and within-group relatedness for three environmental qualities ranging from benign (m = 0.1) to harsh (m = 0.3) across 20 replicas. Results are shown for x_0 = 1.5 (default), x_0 = 3.5 and x_0 = 10. The optimum breeder productivity per unit of help provided was either when both tasks were performed to a similar extent, potentially selecting for division of labor (DoL), or when no restrictions were introduced to the task performed by the group members (No DoL).

	x_0 = 1.5						x_0 = 4.5						x_0 = 10					
	m = 0.1		m = 0.2		m = 0.3		m = 0.1		m = 0.2		m = 0.3		m = 0.1		m = 0.2		m = 0.3	
	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL	DoL	No DoL
Dispersal	0.82	0.75	0.79	0.79	NA	NA	0.23	0.24	0.49	0.50	0.72	0.68	0.25	0.25	0.44	0.47	0.49	0.66
Survival	0.74	0.74	0.65	0.65	0	0	0.89	0.89	0.79	0.79	0.69	0.69	0.90	0.90	0.80	0.80	0.70	0.70
Group size	1.90 ±1.07	2.34 ±1.26	1.71 ±0.62	1.75 ±0.75	0	0	13.09 ±0.23	13.35 ±0.40	4.84 ±0.38	4.90 ±0.08	2.04 ±0.06	2.33 ±0.05	14.29 ±0.26	14.59 ±0.16	5.17 ±0.37	5.30 ±0.08	3.10 ±0.26	2.47 ±0.05
Relatedness	0.40	0.39	0.55	0.56	NA	NA	0.32	0.32	0.37	0.36	0.46	0.46	0.29	0.29	0.38	0.36	0.52	0.46