## EVOLUTIONARY BIOLOGY

# The evolution of cooperative breeding by direct and indirect fitness effects

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The evolution of cooperative breeding has been traditionally attributed to the effect of kin selection. While there is increasing empirical evidence that direct fitness benefits are relevant, the relative importance of alternative selection mechanisms is largely obscure. Here, we model the coevolution of the cornerstones of cooperative breeding, delayed dispersal, and alloparental care, across different ecological scenarios while allowing individuals to adjust philopatry and helping levels. Our results suggest that (i) direct fitness benefits from grouping are the main driver for the evolution of philopatry; (ii) kin selection is mainly responsible for the emergence of alloparental care, but group augmentation can be a sufficient promoter in harsh environments; (iii) the coevolution of philopatry and alloparental care is subject to positive feedback; and (iv) age-dependent dispersal is triggered by both group benefits and relatedness. Model predictions are supported by empirical data and provide good opportunities for comparative analyses and experimental tests of causality.

## INTRODUCTION

Cooperative breeding involves apparent altruism, as subordinate helpers forgo their own reproduction by delaying dispersal and investing in the care of offspring that are not their own. This intriguing social and life-history trait is distributed widely throughout animals (*1*–*3*). Kin selection can explain alloparental care because of fitness benefits accrued to related individuals (*4, 5*), and genetic relatedness among group members is indeed a good predictor of evolutionary transitions to cooperative breeding (*6*–*8*). However, in many cases, the group members are not related to each other (*9*–*12*). Notably, group living as a result of limited dispersal may bear inevitable direct fitness benefits that can also select for philopatry and helping (*13*–*16*). It remains unclear, however, whether fitness benefits from grouping suffice to select for cooperative breeding. Furthermore, it is unknown how crucial selective forces such as kin selection and group benefits may interact (*17, 18*). Eventually, the relationship between delayed dispersal and alloparental care should be scrutinized in a coevolutionary framework that includes both types of fitness benefits.

Dispersal obviously influences the population's kinship structure (*19*–*21*). Limited dispersal is central to the evolution of cooperative societies, as it builds up genetic relatedness among group members and thereby facilitates the efficacy of kin selection (*22, 23*). Nevertheless, while grouping with kin may generate indirect fitness benefits, it also increases competition between relatives (*24*–*27*). Hence, the effect of dispersal on competition and cooperation within groups needs to be clarified if aiming to understand the evolution of cooperative breeding.

Selection acts on important life-history decisions subject to the respective ecological, social, and life-history contexts (*28, 29*). The dynamics of dispersal and helping decisions influence how localized competition plays out (*26*). For instance, individuals expressing alloparental care early in life and dispersing to breed later may enhance indirect fitness benefits when young, while, at the same time,

reducing reproductive competition with kin through leaving the group before starting to reproduce. Thus, dispersal decisions that vary across life stages or ecological contexts might resolve the cooperation-competition trade-off resulting from philopatry and promote the evolution of cooperation (*29, 30*).

Here, we model the coevolution of philopatry and cooperation driven by both kin selection and group benefits. Ultimately, we aim at identifying the conditions that favor the evolution of delayed dispersal and alloparental care. We construct a series of models in which individuals either adopt fixed behavioral strategies of dispersal and help throughout life or show age-dependent plasticity. To disentangle the role of kin selection and the effects of grouping, we compare the outcome of these models with a benchmark model in which the influence of genetic relatedness is controlled for. Our results suggest that direct survival benefits of group living are the main driver for philopatry and can be sufficient for the evolution of alloparental care under certain ecological conditions. Conversely, indirect fitness benefits can be the main driver for helping behavior after group formation allows for kin structured populations. The relevance of direct versus indirect fitness benefits for the evolution of helping, however, changes depending on the harshness of the environment. Furthermore, behavioral plasticity allows for a developmental response reducing reproductive competition while, at the same time, enhancing help provided to relatives.

## RESULTS

### Rationale

The structure and parameters of our model are informed by the basic components characterizing cooperative breeding systems at large. Systematic variation of ecological conditions is meant to provide a diverse scope enabling subsequent empirical tests of the model predictions. We consider a class-structured population with overlapping generations living in a habitat with a limited number of breeding territories, which are monopolized by groups consisting of one breeder and an undefined number of subordinates. Individuals belong to one of three classes: (i) breeders that monopolize reproduction, (ii) subordinates in their natal or in a different group, and (iii) dispersers that are not part of a group. Group size in our model is an

emergent property of dispersal decisions, mortality, and help-dependent breeders' fertility. We track the age of individuals in the population and use age as a proxy for their resource holding potential (RHP) (*31*) when competing for breeding positions. Dispersers and local subordinates compete for the breeding position when joining a group and win with a probability proportional to their age, which is a realistic assumption in many species (*32–34*). The turnover for the breeding position in a territory occurs when the breeder dies.

If subordinates help to care for the dominant breeders' offspring, then this raises the fertility of the breeder at a cost to the survival of helpers, as shown in cooperatively breeding mammals (*35*), birds (*36*), fishes (*37*), insects (*38*), and spiders (*39*). We assume complete reproductive skew, i.e., helpers will not raise their own offspring but only those of the dominant breeders. Increased productivity of breeders raises the group size, which enhances survival prospects for all group members. We let survival scale positively with group size, according to parameter $x_n$. Thus, if $x_n = 0$, then individuals in larger groups do not enjoy higher survival than individuals in smaller groups. As we increase $x_n$, the relationship between group size and survival is steeper. Similarly, survival depends on the cost of alloparental care; parameter $x_h$ (Table 1) reflects how much the subordinate's survival decreases with increasing investment in care (see Materials and Methods for details).

To assess how different habitats affect life-history decisions, we systematically varied the quality of the habitat across simulations. Low baseline mortality (i.e., $m_0 = 1$) denotes high-quality environments (Table 1). Increasing values of $m_0$ reflect a reduced likelihood of individuals surviving another life cycle and, therefore, raises the turnover of breeding positions. This opens more breeding spots for dispersers and floaters. At the same time, we account for dispersal costs by increasing mortality for individuals outside a group. Values of $m_d > 1$ (Table 1) indicate higher mortality for dispersing individuals than expected only because of their solitary status. Hence, $m_d > 1$ reflects a survival benefit of group membership independent of group size. Last, we also varied the likelihood of dispersers to find a new group to start breeding (parameter $f$; Table 1). This captures a variety of factors like the difficulty to reach or find a new group and the "permeability" of groups to accept new members. Higher values of $f$ translate into a higher likelihood for floaters to find a breeding position. This implies a lower probability of helpers inheriting the breeding position in their territory. Simultaneous variation of these three parameters, $m_0$, $m_d$, and $f$, simulates a range of habitats that differ in their quality and the likelihood of dispersers to survive and to breed, allowing different strategies to evolve depending on the ecological parameters. The life cycle of the model is shown in Fig. 1.

### Direct versus indirect fitness benefits

To investigate the relative importance of direct fitness benefits of group living and indirect fitness benefits from relatedness for the evolution of cooperative breeding, we let relatedness emerge from the species' population dynamics. This allows drawing meaningful predictions for the role of kin selection without a priori assuming a particular evolutionary pathway. To distinguish direct fitness benefits derived from group size from those of kin selection, we created two parallel models for comparison, in one of which relatedness was prevented from building up through the dispersal decisions of individuals (benchmark model; see Materials and Methods for details). In the other model, the effect of indirect fitness benefits was

separated from direct fitness benefits by removing the survival advantage arising from group size (i.e., $x_n = 0$).

Our results show that cooperative breeding can evolve solely because of direct or indirect benefits. However, the conditions under which cooperation is selected are strict when considering each of these mechanisms in isolation. Cooperative breeding can evolve solely by kin selection in cases in which alloparental care has a low cost for the survival of helpers (low $x_h$) while, at the same time, greatly increasing the productivity of the breeders (high $k_h$; fig. S1). In this scenario, the degree of philopatry remains low. More costly forms of help are likely to evolve in harsh environments that greatly decrease the survival of individuals ($m_0 = 0.3$; fig. S1).
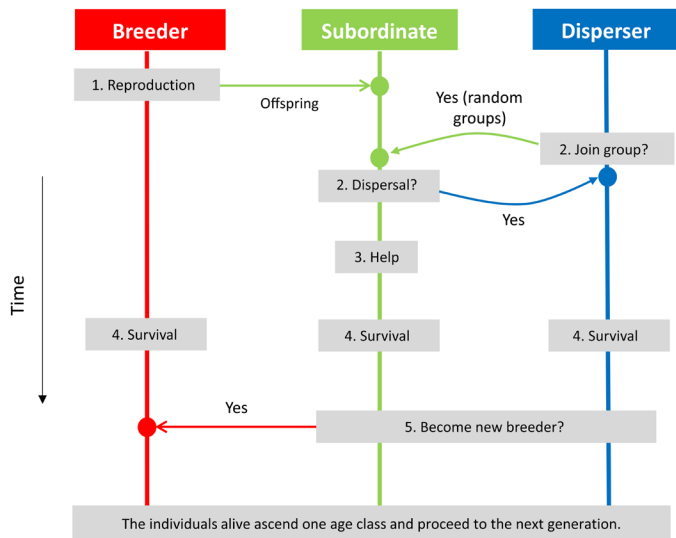
**Table 1. Overview of notation.**

| Symbol | Meaning |
|---|---|
| $f$ | Mean number of groups a floater samples for becoming a breeder |
| $N$ | Group size |
| $N_f$ | Total number of floaters |
| $N_b$ | Number of breeding territories |
| $t$ | Age as a proxy of RHP |
| $\beta$ | Genetic propensity to disperse, without reaction norm to age |
| $\beta_0$ | Intercept in the dispersal reaction norm |
| $\beta_t$ | Effect size of age on dispersal when reaction norms evolve |
| $D$ | Dispersal propensity |
| $\alpha$ | Genetic predisposition to help without reaction norm to age |
| $\alpha_0$ | Level of help independent of age when reaction norms evolve |
| $\alpha_t$ | Linear effect size of age on help when reaction norms evolve |
| $H$ | Level of help provided to the breeder |
| $m_0$ | Baseline mortality |
| $m_d$ | Multiplier of the baseline mortality for dispersers |
| $x_0$ | Intercept in the survival function |
| $x_h$ | Effect size of the cost of help in terms of survival |
| $x_n$ | Effect size of the benefit of group size in terms of survival |
| $S$ | Survival rate |
| $k_0$ | Fecundity of the breeder when no help is provided |
| $k_h$ | Effect size of the cumulative help of subordinates on the fecundity of the breeder |
| $K$ | Fecundity of the breeder |
| $\mu$ | Mutation rate |
| $\sigma_\mu$ | Mutation step size |

**Fig. 1. Process overview and scheduling in the model.** Arrows indicate a transition to a different class (exception: the arrow from step 1 refers to the offspring created, not the breeder). The $y$ axis represents the timeline of the life cycle. (1) A breeder reproduces. Its productivity depends on the cumulative level of brood care provided in the group in the previous life cycle. (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 therein. (3) Subordinates in the group perform help. (4) Individuals survive contingent on group living benefits and dispersal costs. (5) If a breeder dies, then helpers in the group and a sample of floaters compete for the breeding position and win with a probability proportional to their age (as a proxy of RHP). Individuals still alive ascend one age class, and the cycle starts all over (i.e., next generation).

Direct group benefits can also be exclusively responsible for the evolution of cooperative breeding, as suggested by the group augmentation hypothesis. The group augmentation mechanism denotes a scenario where helpers gain fitness benefits by enhancing group size if the recruits that are produced as a result of helping behavior, in turn, increase the survival and/or reproduction of helpers (*13*, *14*). Our results show that when group size benefits on survival take effect, the conditions under which philopatry can evolve are less restrictive with respect to the cost/benefit ratio in Hamilton's rule (when $x_n > 0$; Fig. 2) than when only relatedness effects are considered. Direct group benefits, therefore, seem to be more likely to drive group formation. In addition, alloparental care can also evolve by group augmentation benefits alone (when $x_n \geq 3$ and relatedness is blocked; Fig. 2, B and C). This applies in harsh environments where group living confers a substantial survival benefit, which is often the case in natural systems (*16*, *40–42*). In contrast, in benign environments where habitat saturation is reached and mainly direct fitness benefits select for group formation, help can only evolve in combination of direct and indirect fitness benefits (Fig. 2A). This holds when benefits of helping can be inherited once a former helper attains the breeding position [e.g., by nest building, territory maintenance, and long-term benefits of group augmentation (*13*, *14*)], implying that during their first breeding attempt, the new breeder's fertility is influenced by the help it had previously provided. If no benefits of helping are passed on to the breeder status, then the probability that alloparental care evolves solely by group augmentation, i.e., in the absence of relatedness effects, is substantially reduced (fig. S2). Under these conditions, helping is unlikely to evolve by group augmentation
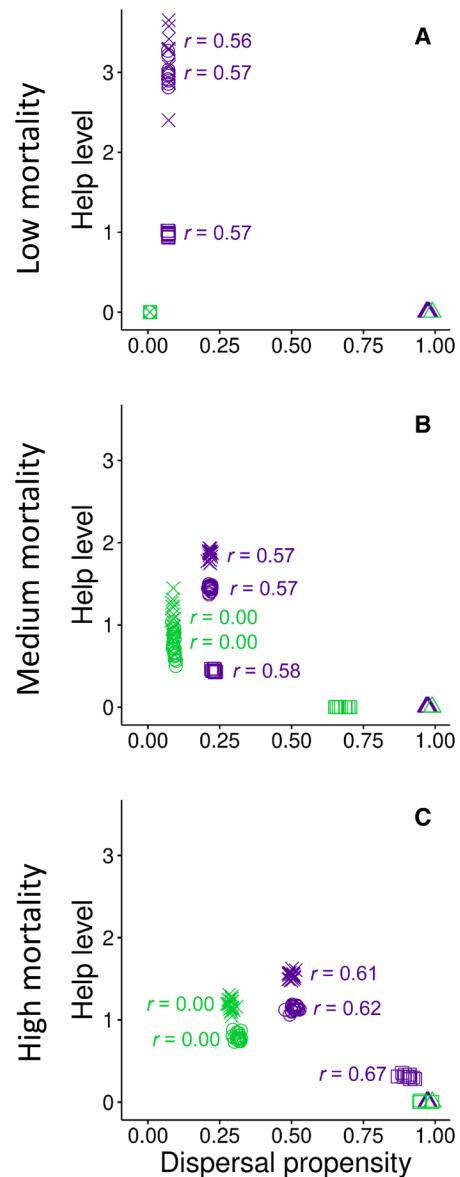


**Fig. 2. Effect of survival benefits of group size on dispersal propensity and alloparental care in the presence and absence of relatedness effects, under three different habitat qualities.** The evolutionary equilibria for levels of helping and dispersal are shown when group membership benefits through reduced mortality risk are absent ($\triangle$, $x_n = 0$), low ($\square$, $x_n = 1$), high ($\circ$, $x_n = 3$), or very high ($\times$, $x_n = 4$). Relatedness was either an emergent property of the model dynamics (purple), or it was blocked by random shuffling (green; see Materials and Methods). Numbers in the figure indicate the levels of relatedness at equilibrium when helping evolved. Different habitat qualities are reflected by three divergent levels of baseline mortality. The results show that survival benefits of group size are the main driver for the evolution of philopatry ($x_n > 0$), while helping evolves mainly because of kin selection or group augmentation, depending on environmental conditions. (**A**) In benign environments ($m_0 = 0.1$), helping can only evolve under kin selection, but some reduction of mortality risk by group membership is still required. (**B** and **C**) In harsher environments ($m_0 = 0.2$ or $0.3$), helping can evolve because of both kin selection ($x_n = 1$ to 4) and group augmentation ($x_n = 3$ to 4), while mortality risk primarily affects differences in dispersal propensity. Results are shown across 20 replicas to assess repeatability. Symbols denoting the absence of relatedness when $x_n = 0$ were slightly jittered horizontally to improve visual discrimination. Other input parameters are $m_d = 1$, $f = 2$, $x_h = 4$, $x_0 = 1.5$, $k_0 = 1$, and $k_h = 1$.

benefits alone due to the resulting production of direct competitors for the breeding position (fig. S3).

While direct group benefits seem to be the primary evolutionary driver of group formation, indirect fitness benefits are likely to select for alloparental care once groups have formed (Fig. 2). Nevertheless, the build-up of relatedness also selects for dispersal due to the effects of kin competition limiting the benefits of philopatry (Fig. 2; for more details, see the "Age-dependent reaction norms" section below).

These results are in line with previous theoretical work suggesting a joint effect of group augmentation and kin selection (13). However, our model reveals that under the coevolution of philopatry and help, in harsh environments, direct benefits on survival are the main driver of philopatry, which enables the evolution of helping. These results suggest a previously unidentified pathway to the evolution of cooperative breeding, where philopatry is originally selected by direct fitness benefits. The ensuing relatedness within the groups in combination with the direct benefits by group augmentation selects for the emergence of alloparental care. This evolutionary pathway is consistent with both the well-known correlation between cooperative breeding and relatedness (43, 44) and the demonstrated group size–dependent survival effects in cooperative breeders (16, 41, 42). Our findings are also in accordance with empirical results revealing that advantages of philopatry often do not offset the costs of delayed reproduction when group size benefits are absent or weak (45).

Our results demonstrate that different habitat qualities may induce cooperative breeding by divergent selection mechanisms (Fig. 2). Group benefits are more important in harsh environments in which safety in numbers can substantially increase survival prospects, where joint effort may also facilitate the expulsion of predators and defense of resources against competitors. In benign environments, by contrast, helping evolves in connection with indirect fitness benefits obtained by the enhanced production of relatives, even if group survival benefits are the selective driver of philopatry (Fig. 2A). Benign environments bring about habitat saturation, as low mortality results in low breeder replacement rates. Therefore, the main evolutionary driver of philopatry is to queue to inherit the breeding territory. In species that do not follow a gerontocratic succession but instead a scramble contest for the breeding position, this result also holds true (fig. S4). When survival is high because of philopatry, group size increases, and alloparental care raises the number of competitors for the breeding position for which they are queuing. Consequently, in benign environments, helping is more likely to evolve where indirect fitness benefits accrue, even if a certain level of dispersal serves to reduce competition for the breeding position among relatives. Previous models similarly predicted that philopatric tendencies leading to group formation vary in accordance with habitat quality (46). In stable and predictable environments, high population density and resulting habitat saturation can lead to a severe shortage of territory openings, while in variable and unpredictable environments, the cost of successfully reproducing can be magnified to prohibitive levels, which may select for individuals to remaining as nonbreeders within their natal groups (46). Another model studying ecological pressures in benign and harsh environments predicted that resource defense benefits select for cooperative breeding in saturated habitats, while collective action benefits matter in harsh environments in which group size aids to cope with environmental challenges (47, 48). The results presented here, hence, support a growing consensus that cooperative breeding evolves by alternative mechanisms depending on environmental harshness.

## The coevolution of helping and philopatry

Group living is a precondition for the emergence of alloparental care. Once group living evolves because of direct survival benefits as shown in the previous section, kin structure builds up, which affects the level of cooperation and competition between group members. Hence, it is worth clarifying how helping and philopatry coevolve against the backdrop of relatedness structure. To this end, we first scrutinized the evolution of dispersal rate until reaching its equilibrium, which was satisfied after 25,000 generations for all 20 runs. Concerning the coevolution of helping and dispersal, we found that philopatry is required for the evolution of alloparental care, whereas helping, in turn, selects for higher levels of philopatry in a positive feedback loop (see the "Age-dependent reaction norms" section below). This corroborates previous modeling results (19, 20, 49). Our simulation demonstrates that this positive feedback is also maintained by direct group benefits even in the absence of kin selection (fig. S5). The results were similar both when the evolution of age-dependent reaction norms was considered or not.

## Age-dependent reaction norms

The likelihood of subordinates obtaining a breeding position within a group typically varies with their rank or RHP, which may affect their dispersal and helping strategies (10, 50, 51). To investigate this relationship, we analyzed a state-dependent model in which individuals show age-dependent plasticity based on reaction norms for their dispersal propensity and alloparental investment. Age is typically linked to competitive ability; hence, individuals may adjust their dispersal and helping strategies with time according to changes in their likelihood to obtain breeder status. Evolved reaction norms of dispersal and helping decisions according to different levels of habitat saturation and relatedness are summarized in Figs. 3 and 4.

High dispersal costs and high environmental quality (reflected by high $m_d$ and low values of $m_0$ and $f$) result in reduced chances of dispersers to breed outside of their natal group early in life; hence, individuals are selected to queue for the breeding position either in their natal or in a foreign group (Figs. 3, top left, and 4, C and D). With the resulting rise in habitat saturation, philopatric tendencies increase with age, i.e., when subordinate group members are more competitive to become breeders (Fig. 4, A and B). High dispersal rates at early life stages instead of staying in the natal territory allow individuals to avoid competing with relatives for the breeding position (Figs. 3 and 4). This result is further supported by the comparison between the two scenarios with and without the build-up of relatedness within groups, since after the removal of relatedness, all individuals choose to stay in their home territory to queue for the breeding position (Fig. 3, top, and fig. S8). Under these environmental conditions, groups are formed by a mixture of related and unrelated subordinates (Fig. 4, E and F).

Our results indicate that individuals staying in their natal territory should decrease help over time as the degree of relatedness between them and the young declines with their own age due to time-dependent breeder replacement and dispersal dynamics (Fig. 3, top left) (9). Reduced helping levels with low relatedness have been observed in several cooperative breeders (52). Nevertheless, the opposite tendency may also emerge when other selective forces are at play, such as a pay-to-stay negotiation process (18, 53, 54). Our model further shows that when the build-up of genetic relatedness is prevented, individuals increase help as their likelihood of becoming a breeder increases, thereby obtaining delayed reciprocity benefits if
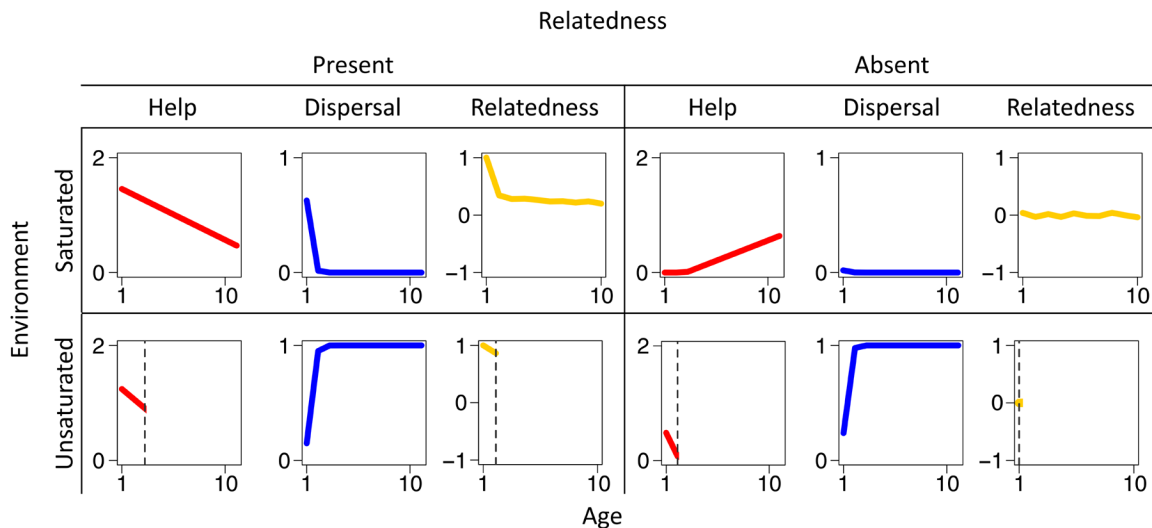
Relatedness



**Fig. 3. Evolution of age-dependent reaction norms of dispersal propensity and help levels, at different habitat saturation levels.** Age (abscissa) is plotted against helping levels (red), dispersal propensity (blue), and relatedness (yellow) at the equilibrium (mean values from 20 replicas each). Dashed lines in the "help" graphs denote the age from which help is no longer expressed because of the lack of helpers from that age-group onward. Relatedness per age group is only shown when a sufficient sample was available to calculate relatedness reliably, i.e., until the dotted lines. In saturated habitats (which often coincides with benign environments), subordinates show philopatric tendencies, and they may either reduce help with age when kin selection is enabled or increase help with age when indirect fitness benefits are absent, thereby obtaining long-term group augmentation benefits. In unsaturated habitats (often concurring with harsh environments), subordinates stay philopatric at young age benefitting from a safe haven until they are competitive enough to disperse and breed independently. When relatedness is present, young subordinates obtain indirect fitness benefits by providing help to close kin. Input parameters for saturated habitats are $f = 1$, $m_0 = 0.2$, $m_d = 1$, $x_n = 3$, $x_h = 4$, $x_0 = 1.5$, $k_0 = 1$, and $k_h = 1$. Input parameters for unsaturated habitats are the same except for $f = 2$ and $m_0 = 0.3$. Input parameters for presence/absence of relatedness are the same for the corresponding condition. Top left panel summarizes results from Fig. 5, top right panel from fig. S5, bottom left panel from fig. S6, and bottom right from fig. S7.

they inherit the territory, a phenomenon referred to as long-term group augmentation benefits (Fig. 3, top right, and fig. S5B) (13, 14, 17).

When habitat saturation is low (reflecting high values of $m_0$ and $f$ and low $m_d$), individuals disperse from the natal group at some point to become breeders elsewhere. Initially, they stay in their natal territory for protection, which serves as a "safe haven," and to help raising related young (Figs. 3, bottom left, and 4, A and B). At an older age, dispersal propensity increases (Figs. 3, bottom left, and 4, A and B). Under these environmental conditions, groups are mainly formed by helpers related to the breeding pair (Fig. 4, E and F). These results are in line with data from a range of species (2), where delayed dispersal of young yields survival benefits and philopatry prevails until local vacancies become available. In these cases, subordinates may obtain additional indirect fitness benefits by enhancing the production and survival of kin.

Our results show that the evolution of reaction norms for the levels of help and dispersal propensity allow for a well-adjusted response to individual, social, and ecological circumstances determining the likelihood of inheriting the territory and the level of relatedness among group members. Optimal dispersal strategies may vary during an individual's lifetime and across different ecological and social scenarios. When behavioral plasticity is not evolving and environmental properties select for individuals to remain in a group and queue for the breeding position, evolved helping levels are likely suboptimal for a particular age of a subordinate, since behavioral strategies cannot adjust to the dynamics of relatedness among group members (Fig. 5B). Likewise, nonplastic subordinates will show an intermediate tendency for dispersal, reflecting a compromise between the optimal strategies for young and old individuals. In highly saturated habitats, inflexible subordinates exhibit a degree of philopatry

that reflects a compromise between queueing for the breeding position and the reduction of kin competition (Fig. 5C). In contrast, in unsaturated environments, nonplastic individuals respond with a low dispersal propensity corresponding to a compromise between remaining in the territory for safe resource use and helping kin and dispersing for independent breeding (fig. S6C).

Our model effectively merges the ecological constraints and benefits of philopatry hypotheses that are often viewed as alternative explanations for the evolution of philopatry. Habitat saturation is a result of environmental variables that affect mortality and dispersal rates rather than an externally determined constraint that favors philopatry (55, 56). Low baseline mortality and constraints to disperse or to find a breeding position lead to both philopatry and saturated habitats as a result, which may generate a positive feedback loop. Therefore, both hypotheses are part of a continuum in which individuals are selected to weigh the odds between achieving independent breeding by dispersing against successfully queuing to inherit the breeding position at home. Additional indirect fitness benefits can then be obtained when individuals delay dispersal from their natal territory and are still related to their current owners.

## DISCUSSION
Our results suggest that for the evolution of cooperative breeding, direct benefits of group living are often the main driver of group formation, which is a requirement for the consequent emergence of helping. At the same time, delayed dispersal builds up genetic relatedness within groups, which facilitates the evolution of alloparental care by kin selection in addition to direct fitness benefits derived from enhanced group size. Although kin selection and group augmentation
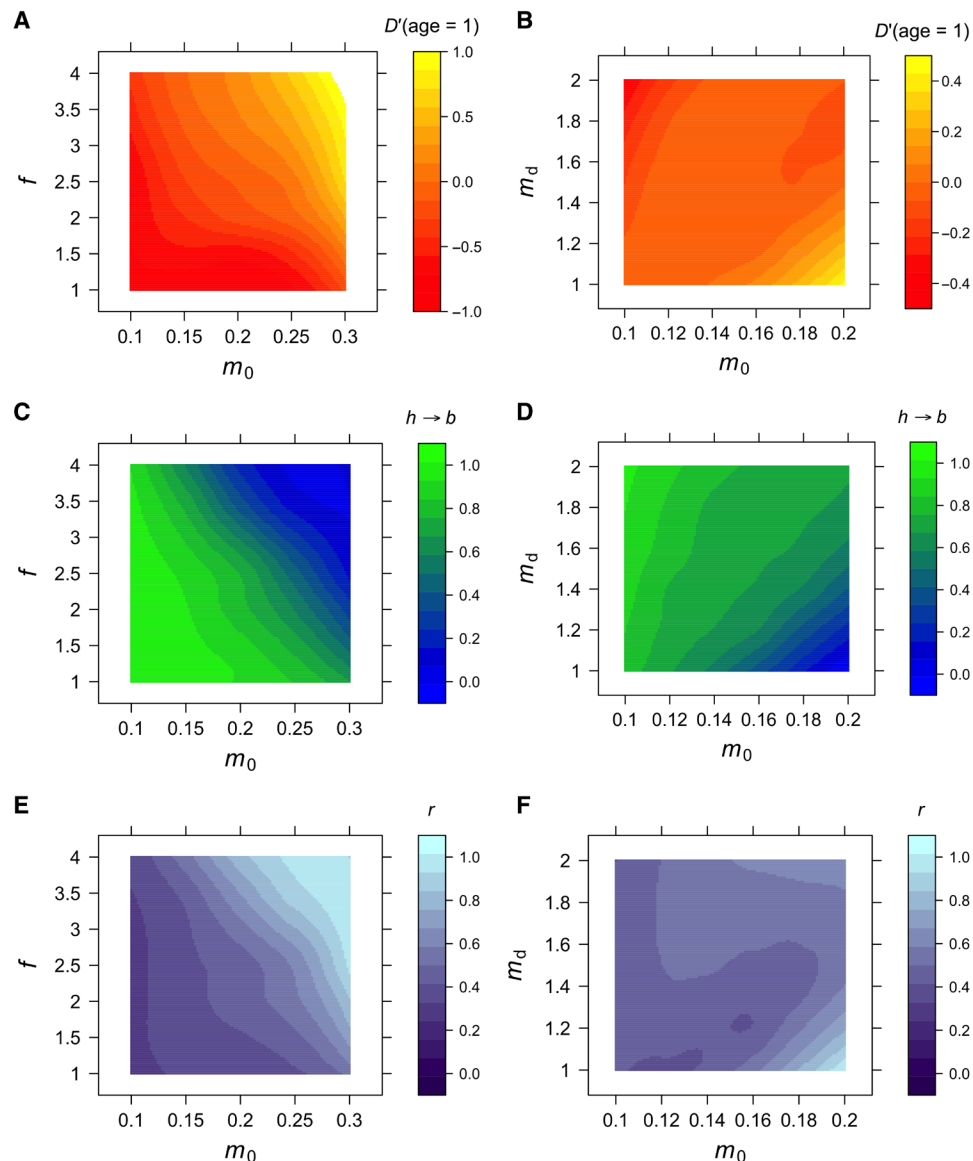
**Fig. 4. Evolution of age-dependent reaction norms for dispersal across different ecological scenarios, and the proportion of helpers becoming breeders when relatedness is present.** Different levels of habitat saturation were modeled by varying the overall mortality ($m_0$), the likelihood that floaters find a group to breed ($f$; panels **A**, **C**, and **D**), and the mortality linked to dispersal ($m_d$; panels **B**, **D**, and **F**). (A and B) The derivative of the reaction norm ($D'$; evaluated at age 1), at the evolutionary equilibrium, determining dispersal propensity, was plotted for scenarios when relatedness is present. Positive values of $D'$ denote a positive slope and an increase in dispersal with age, while negative values of $D'$ indicate a decrease in dispersal propensity with age. Both overall mortality ($m_0$) and group permeability ($f$) select for positive $D'$, which is an increase in the level of dispersal with age (A). In contrast, mortality associated with dispersal ($m_d$) has the opposite effect (B). (**C** and **D**) The proportion of helpers that become breeders (inheritance of breeding position as opposed to takeover by floaters) at the equilibrium. (**E** and **F**) Relatedness levels between breeders and subordinates in the group at the population level.

can both select for the evolution of alloparental care in isolation, the conditions are restrictive, and a combination of both mechanisms selecting for cooperative breeding is the most plausible scenario under natural conditions. In contrast to the common view, our model suggests that indirect fitness benefits alone are unlikely to select for the evolution of cooperative breeding without direct survival benefits of group living, seemingly because the prevalence of kin competition prevents the evolution of the relatedness structure that generates sufficient indirect fitness benefits. Apparently, the selection pressures on philopatry are, in general, not enough to allow high levels

of relatedness in Hamilton's rule to favor helping (*25, 26*). Previous theoretical work has shown that the prevalence of kin competition can prevent the coevolution of philopatry and help (*19, 49*). In these models, the hurdle created by kin competition can be overcome by more extreme costs to dispersal or by kin discrimination (*49*). Here, we show that direct fitness benefits based on grouping can overcome the negative effect of kin competition, which leads to the evolution of philopatry and promotes a positive feedback between philopatry and help, the two pillars of cooperative breeding. At the same time, kin selection facilitates the evolution of alloparental care by relaxing
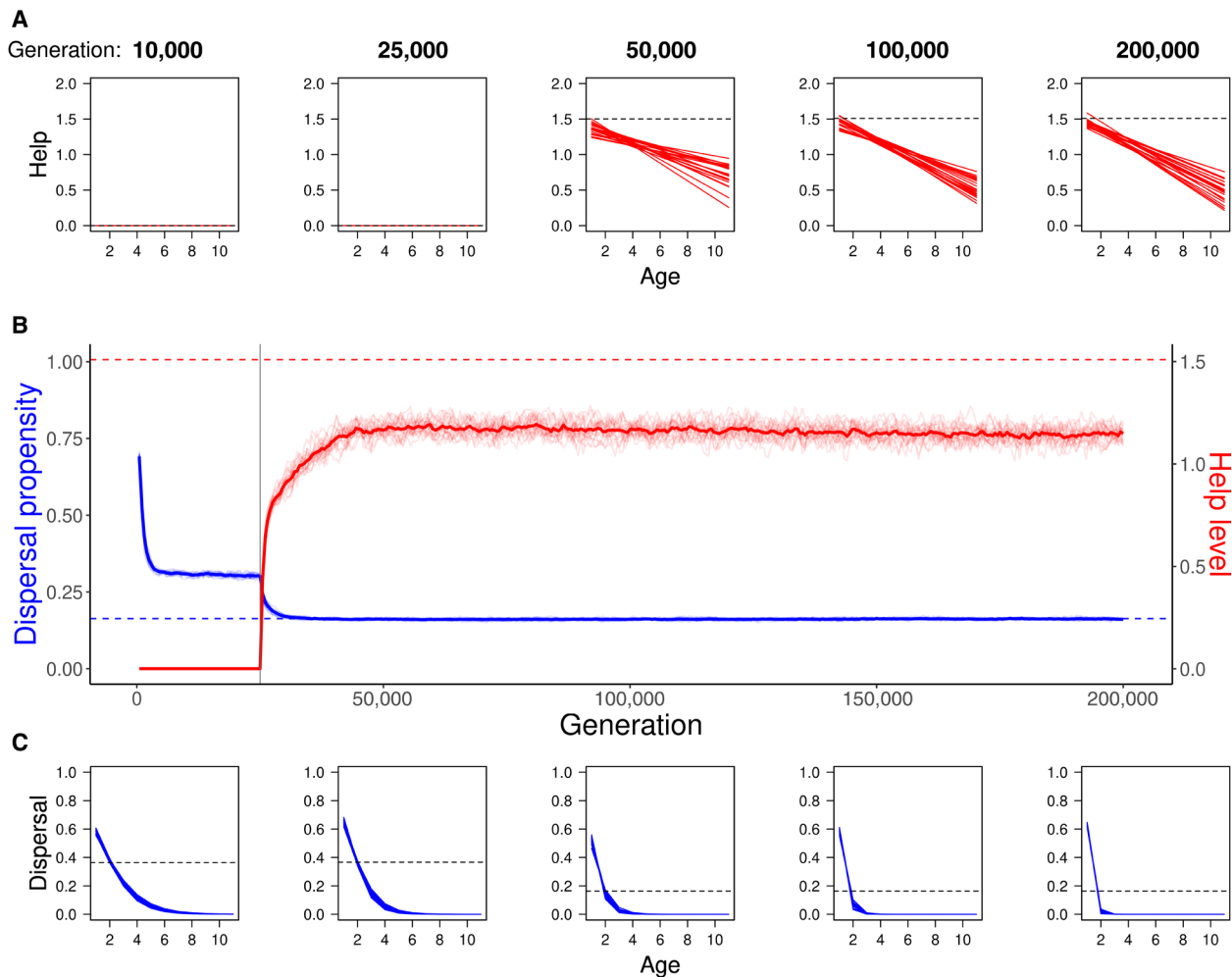
**Fig. 5. Evolution of age-dependent reaction norms of philopatry and help levels in a highly saturated habitat when relatedness takes effect and subordinates queue to inherit the breeding position.** (**B**) Evolutionary dynamics of helping levels (red lines, right $y$ axis) and dispersal (blue lines, left $y$ axis). Bold lines represent the total mean values across replicas, while shades show the mean values for each of the 20 replicas of the stochastic model. Help was allowed to evolve from generation 25,000 onward (gray vertical line). (**A** and **C**) Reaction norms of help (A) and dispersal (C) at five different points in time. Dashed lines in all three figures represent the equilibrium values for levels of help and dispersal in the absence of the evolution of reaction norms. The input parameter values are $f = 1$, $m_0 = 0.2$, $m_d = 1$, $x_n = 3$, $x_h = 4$, $x_0 = 1.5$, $k_0 = 1$, and $k_h = 1$.

the competition between new recruits and the subordinates queueing for the breeding position in the territory. This points toward the importance of identifying eco-evolutionary feedbacks, particularly when the change in a trait value affects population structure, which, in turn, modifies the selective pressures on that trait (*57*, *58*). To unravel the evolutionary pathway to cooperative breeding based on the joint action of direct fitness benefits and kin selection, future studies might disentangle the order of appearance of traits along evolutionary time using modern phylogenetically controlled comparative methods, which can unveil the pathway and causal direction relating those traits, while taking into account the ecological context (*59*).

Our findings highlight that kin selection is likely not the initial evolutionary force behind cooperative breeding despite high relatedness between subordinates and breeders. For instance, in the cooperatively breeding purple-crowned fairy wrens, subordinates feed siblings more than unrelated nestlings, at first glance, suggesting that kin selection explains cooperation. However, the effect of relatedness

on feeding effort and defense from nest predators varies depending on the probability of inheriting a breeding position, suggesting that long-term group augmentation might, in fact, explain alloparental investment by subordinate group members (*17*, *60*). In the Florida scrub jay, group size increases territory size, which raises the chances of males splitting off part of the territory for independent breeding (*56*). Therefore, helping in this species increases not only the production of kin but also the chances to inherit part of the territory due to the ensuing rise in group size. This points toward the importance of considering multiple hypotheses when investigating the evolution of cooperative breeding (*4*, *17*). The emergence of helping after group formation can result from both group augmentation benefits and kin selection. Direct and mutual fitness benefits from increased group size as a driver of cooperation can explain puzzling phenomena like the "kidnapping" of members from other groups observed in several species (*40*, *61*) or the presence of unrelated helpers within groups (*9*, *12*).

Life-history decisions typically vary during an animal's lifetime (*62*–*64*), yet previous studies have generally modeled static behavioral

rules. In contrast, our approach allows individuals to evolve age-dependent plasticity in their decisions to disperse and help according to the ecological context. This yields more realistic predictions on fundamental life-history decisions based on the level of habitat saturation, a crucial parameter for the evolution of group living and cooperation. Our results show that cooperative breeding is driven by both grouping and kinship effects, but the prevalence of each mechanism is predicted to vary depending on the quality of the habitat. A comparative study on birds found that while cooperatively breeding starling species tend to occur in harsh and unpredictable environments in which helpers greatly increase the reproductive success of the breeders, cooperatively breeding hornbills tend to live in benign and stable environments where overcoming competition is likely to be the ecological driver for the evolution of cooperation (48).

In highly saturated habitats or where group membership is strongly linked to survival, our model predicts early dispersal to reduce kin competition for the breeding position. Empirical data in a range of taxa are in accordance with the prediction that early dispersal is triggered by breeding competition with siblings. For example, in the hover wasp (*Liostenogaster flavolineata*) and the cooperatively breeding stripe-backed wren (*Campylorhynchus nuchalis*), lower-ranked helpers are the most likely individuals to disperse from their natal nests (65, 66). In most social mammals, female dispersal from their natal groups seems to be linked to the avoidance of local competition with kin for resources and breeding opportunities (67). Local competition among kin may also explain why, in some species, subordinates expel siblings from their natal territory (68). Our model further predicts that alloparental care can evolve in low-quality habitats with high mortality rates, where the natal territory serves as a safe haven. Offspring that delay dispersal to benefit from group protection may help to raise kin, thereby gaining indirect fitness benefits while waiting for a safe opportunity to leave for independent reproduction elsewhere. Empirical results from a wide range of animal taxa conform to this prediction, including birds (69), mammals (70), and insects (71). This composite conditionality helps to solve the paradox of environmental quality and sociality, as both benign and harsh environments seem to promote the evolution of sociality, and supports previous predictions on the duality of different selective benefits depending on the harshness of the environment (46–48). A formal test of the predictions from our model would require analyses considering effects of habitat saturation and mortality levels either by experimental manipulation at a species level or phylogenetically controlled interspecific comparisons.

We would like to point out potential deviations from our model assumptions that might yield different predictions. These deviations can be broadly classified along four lines. First, patterns of genetic relatedness; we assumed asexual reproduction, which affects relatedness. Consequently, in sexual systems, we expect two opposing factors that might balance each other out: Avoiding competition with kin may be weaker, whereas avoiding inbreeding may be more important. Second, social determination of the behavioral phenotype; in our model, dispersal and help are determined individually, but this is not necessarily the case. For example, rules of dispersal may be different where individuals leaving their home territory form coalitions or join certain groups preferably (72, 73). Third, enforcement and eviction by dominants; we have not included this possibility in our model, which is why it does not account for pay-to-stay negotiation processes (53, 54). Last, environmental variation; we considered an island population model with random dispersal, overlapping generations, and a constant environment in space and time. These assumptions imply that habitat saturation and relatedness levels are maintained roughly constant throughout the life of individuals. In contrast, marked changes in habitat saturation can occur in predictably seasonal environments. An example of this is the bivoltine model of the evolution of eusociality (57), where the formation of breeding territories takes place at a specific time of the year (spring). Social insects that follow this type of life history show variation in the tendency to disperse and help, not along an individual's lifetime but among the different generations that complete the life cycle. Despite the potential effects of these deviations, which might highlight different routes in social evolution, we believe that our model captures a great portion of the variance existing in different cooperatively breeding species under various ecological settings, thereby helping to explain the interplay between dispersal and cooperation that is driven by direct and indirect fitness benefits.

In conclusion, our model suggests that fitness benefits of group living, and not kin selection, are the main driver of the evolution of philopatry, a prerequisite for the emergence of alloparental care. Furthermore, the model indicates that a combination of direct and indirect fitness benefits is the most likely selective pressures behind the evolution of cooperative breeding. We found that a positive feedback relationship between philopatry and alloparental care is maintained by direct group benefits even in the absence of kin selection, while relatedness can be an important promoter of cooperation. In addition, age-dependent plasticity allows individuals to adjust their dispersal and helping strategies to social and environmental conditions to maximize their own reproductive outcome, while, at the same time, increasing cooperation and reducing competition among kin. Predictions from the model are met by empirical results from a wide range of taxa, and they can be scrutinized experimentally or by phylogenetically controlled comparisons across different biological systems.

## MATERIALS AND METHODS

We aim to determine circumstances under which subordinate group members gain direct fitness benefits by staying and helping dominants to raise offspring in their group due to survival benefits related to group size. We further examine the interplay of group benefits with the level of relatedness emerging from dispersal dynamics. To this end, we develop an individual-based model in which helping behavior and dispersal coevolve. We start from an ancestral state featuring the absence of alloparental care and dispersal of all individuals and assume net benefits of survival from living in larger groups.

### Life cycle

We consider an asexual, haploid population consisting of 5000 breeding territories. Each breeding territory consists of a dominant breeder monopolizing reproduction and an indefinite number of subordinates, which may aid the breeder's reproduction. In the simulations, groups are initialized with one breeder and three helpers. In the subsequent generations, the number of helpers is determined by the reproduction of the breeders and the dispersal decisions of the offspring. The breeder's fecundity depends on the cumulative level of help provided by the subordinates within the group. The offspring inherit the dispersal and helping tendency from the breeders (see following sections and Fig. 1, step 1). We keep track of the age of individuals in terms of the number of breeding cycles they keep up.

After breeders reproduce, the recently created offspring and subordinates in the group may disperse, and dispersers may settle in another randomly chosen group or remain floaters (Fig. 1, step 2). For simplification, we consider only individual dispersal, not budding dispersal (72, 73). Subordinates choosing to disperse stay in a vagrancy state for at least one generation, until they may bid for a breeding position or decide to join another group as subordinate.

Individuals that stay within a group henceforth express some level of help (Fig. 1, step 3). Since we are interested in the evolution of alloparental care, breeders are exempted from helping. The level of help performed has a survival cost. Note that the decision to help occurs after the decision to disperse, and individuals can potentially evolve a help level of 0. This reflects the fact that in some species, delayed dispersal occurs without the offspring helping their parents (74, 75), suggesting that direct fitness benefits can be sufficient to select for delayed dispersal (46, 76). It also allows for the evolution of solitary life if offspring never remain as subordinates in the group.

Individual-specific survival depends on (i) the environmental conditions, (ii) group membership, (iii) group size, and (iv) the level of help provided to the breeder (Fig. 1, step 4). Note that the fitness benefits of increasing the breeder's productivity by helping only occur after mortality takes place, ensuring that selection acts on the cost of helping before benefits are perceived.

If the breeder in a group dies, then all helpers inside the group and a sample of floaters compete for the breeding position (Fig. 1, step 5). We let the number of floaters bidding for a breeding position be proportional to the relative abundance of floaters with respect to the number of breeding positions. Specifically, the number of floaters in each bid is given by $f * N_f/N_b$, where $N_f$ and $N_b$ are the numbers of floaters and territories, respectively, and $f$ is a parameter that measures the access floaters have to breeding positions. This implementation reflects the likelihood of floaters to join a new group to breed, for instance, conditioned by spatial viscosity, since it is unlikely that floaters can prospect all open breeding spots or by the acceptance probability of new members. It also accounts for the fact that a high number of floaters in the population results in a higher probability that floaters will visit groups for reproductive purposes. If there are fewer floaters available than the calculated floater biding sample, then all floaters are taken as bidders.

The likelihood of filling an empty breeding position is implemented as a lottery weighted by the age of the candidates, with older individuals having a higher probability, regardless of relatedness levels. This contrasts with previous models assuming that dispersers join the queue for inheritance at the end (13, 77, 78) and conforms with empirical observations (79, 80). Age was chosen as a proxy for RHP since it enables individuals to assess their competitiveness, a simplification allowing for the evolution of a simple rule to adjust helping and dispersal strategies to the likelihood of becoming a breeder. Age has been shown to be a good proxy of rank in a range of species (17, 33, 81), even if it is not universal (82). Nonetheless, other life-history traits related to RHP and rank are likely to produce similar reaction norms based on these alternative traits (e.g., size). If a territory has no breeder or helpers remaining, then it is open for takeover from floaters in the same way. Therefore, subordinates may inherit the dominant position within their group (9, 50, 56, 81, 83), but they may also gain a breeding position elsewhere after dispersing to another group (54, 83–85). While floaters may be at a disadvantage compared to helpers due to higher mortality, they enjoy the advantage of being able to sample a larger number of territories in which a breeding vacancy may have opened up (80).

## Strategies

To assess the rules that govern the evolution of philopatry and the consequent emergence of help, as well as their interaction, we first outline a basic model in which individuals show a fixed strategy for the likelihood to disperse and for the level of help provided throughout their life. We then incorporate age-dependent plasticity by letting dispersal and help to be determined by reaction norms. The coevolution of the reaction norms, determining philopatry and help, will be driven by the likelihood of obtaining a breeding position.

### Fixed strategies of help and dispersal

We first model the coevolution of philopatry and help in which individuals express a fixed strategy throughout life. Help levels and dispersal propensity are quantitative phenotypic traits in the basic model, the values of which are solely determined by different alleles of a gene locus. In this basic model, the phenotypic dispersal propensity equals the allelic value of the gene β applying boundaries between 0 and 1. Likewise, the phenotypic value of help equals the allelic value of the gene α. If α takes negative values, then help = 0. In addition, to assess the influence of the evolution of help on philopatry, the mutation rate μ is initially set to 0 for α during the first 25,000 generations until the population reaches an equilibrium for the dispersal propensity and then μ is reset to allow for the evolution of help (Table 1). Initial values of α = 0 and β = 1.

### Reaction norms of help and philopatry

In addition, we construct a model in which the coevolution of help and philopatry is governed by behavioral reaction norms that allow individuals to express different levels of help and dispersal depending on their age. The dispersal likelihood $D$ takes a logistic function with boundaries between 0 and 1 as given in Eq. 1

$$D = \frac{1}{1 + \exp(-\beta_t t - \beta_0)} \quad (1)$$

The dispersal propensity is, therefore, conditioned by the age $t$ of the individual, the gene $\beta_t$ that modifies the strength and direction of the effect of age on the likelihood to disperse, and the gene $\beta_0$ that acts as the intercept (Table 1). The level of help $H$ is conditioned by the age of the individual, the gene $\alpha_t$ that modifies the strength and direction of the effect of age on helping levels, and the gene $\alpha_0$ that is the baseline in the linear function for the levels of help provided as given in Eq. 2

$$H = \alpha_0 + \alpha_t t \quad (2)$$

If the level of help resulting from the function is negative, then the phenotypic level of help = 0. As in the model of the fixed strategies for dispersal and help previously described, the mutation rate μ is initially set to 0 for $\alpha_0$ and $\alpha_t$ during the first 25,000 generations until the population reaches an equilibrium for the dispersal propensity and then μ is reset to allow for the evolution of help. Initial values are $\alpha_0 = \alpha_t = \beta_t = 0$, and $\beta_0 = 1$.

## Survival and reproduction

In each cycle, some individuals die, according to baseline mortality ($m_0$), group membership, and help provided to dominants. Higher values of $m_0$ indicate higher overall mortality for all individuals in

the population, where $1 - m_0$ is the maximum survival likelihood of the individuals in the population. In addition, the survival probability of breeders ($S_B$) and subordinates ($S_H$) depends on group size $N$, while the survival probability of a helper also depends on the cost of the amount of alloparental care $H$ provided. Dispersers survive with probability $S_F$ that depends on $m_0$ and an additional mortality attained to dispersal $m_d$, since several studies demonstrated higher mortality for dispersers by several orders of magnitude (76, 86). These survival probabilities are given by the logistic Eqs. 3.1 to 3.3

$$S_B = \frac{1 - m_0}{1 + \exp(x_0 - x_n N)} \qquad (3.1)$$

$$S_H = \frac{1 - m_0}{1 + \exp(x_0 + x_h H - x_n N)} \qquad (3.2)$$

$$S_F = \frac{1 - m_0 m_d}{1 + \exp(x_0)} \qquad (3.3)$$

where $x_n$ is a scaling parameter that quantifies the effect size of the benefit of group size in survival, $x_h$ is the effect size of the cost of helping, and $x_0$ is an intercept.

Reproduction in a territory is monopolized by the breeder, and it is asexual. We assume that the breeders' fecundity is a random value drawn from a Poisson distribution with mean $K$. $K$ depends on the baseline fecundity ($k_0$) and the cumulative level of help provided by the helpers in the group, assuming that diminishing fecundity returns as given in the Eq. 4

$$K = k_0 + \frac{k_h \sum_{i=1}^{i=n} H_i}{1 + \sum_{i=1}^{i=n} H_i} \qquad (4)$$

where $k_h$ is a scaling parameter that quantifies the effect size of the cumulative help of subordinates on the fecundity of the breeder.

Offspring inherit the alleles from their parent unless mutations occur. Mutations occur independently at each of the loci, at a low rate ($\mu = 0.05$) per locus and reproduction event. Mutations change slightly the value of an allele inherited from the parent by adding a value drawn from a normal distribution with mean 0 and an SD of $\sigma_\mu = 0.04$ (Table 1); hence, the allelic value in the offspring is similar to the parental allele.

## Relatedness
To calculate the coefficient of relatedness between the breeder and subordinates in a group, we track the evolution of another locus that changes exclusively by genetic drift. As in the phenotypic loci, alleles in this neutral locus represent different numerical values that are inherited from parent to offspring and modified by mutational processes. Relatedness between breeders and helpers in a group is calculated as the coefficient of a linear regression between the allelic values of the breeders and helpers for the neutral gene (87).

To distinguish the effect of kin selection from group augmentation, we created a parallel model for comparison in which individuals just born (i.e., age = 1) that decide to stay in the natal group as subordinates (Fig. 1, step 2) are shuffled to another group of the same size without passing through a dispersal phase, thereby removing relatedness from the model without interfering with dispersal patterns or group sizes. Although this implementation removes the effect of relatedness on the evolution of alloparental care, there might be a selective force to be philopatric at age 1 that involves indirect fitness

benefits, as the decision to refrain from dispersing will affect the effective group size of the related breeder positively. To assess this potential effect, we implemented a model in which the shuffling of the newborn helpers was done to random groups regardless whether they also produced offspring while blocking the evolution of helping. Effects of the potential cryptic kin selection influence on selection for philopatry as outlined above were mainly restricted to environments with medium mortality rates at low group size benefits and, therefore, do not greatly affect the conclusions of our model (see fig. S9).

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