The Evolution of Indiscriminate Altruism in a Cooperatively Breeding Mammal

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abstract: Kin selection theory suggests that altruistic behaviors can increase the fitness of altruists when recipients are genetic relatives. Although selection can favor the ability of organisms to preferentially cooperate with close kin, indiscriminately helping all group mates may yield comparable fitness returns if relatedness within groups is very high. Here, we show that meerkats (*Suricata suricatta*) are largely indiscriminate altruists who do not alter the amount of help provided to pups or group mates in response to their relatedness to them. We present a model showing that indiscriminate altruism may yield greater fitness payoffs than kin discrimination where most group members are close relatives and errors occur in the estimation of relatedness. The presence of errors in the estimation of relatedness provides a feasible explanation for associations between kin discriminative helping and group relatedness in eusocial and cooperatively breeding animals.

Keywords: altruism, cooperation, cooperative breeding, kin selection, meerkats.

Introduction

Altruistic behaviors are actions that are costly to the altruist but increase the fitness of others. According to inclusive fitness theory, altruism is more likely to evolve when social partners are closely genetically related (Hamilton 1964, 1972; Gardner et al. 2011) or, more broadly, when they have a high degree of shared reproductive interest (Dyble et al. 2018). A high degree of relatedness between social partners can be achieved when individuals are able to recognize and preferentially cooperate with more closely related individuals (kin-discriminate altruism). Alternatively, when local genetic relatedness is uniformly high, selection may favor individuals who are indiscriminately altruistic toward their social part-

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ners. High local relatedness can result from either limited dispersal (Queller 1992; Taylor 1992; Cornwallis et al. 2009) or the sociosexual characteristics of a species, with traits such as polytocy, monogamy, and high reproductive skew associated with high group relatedness (Hughes et al. 2008; Boomsma 2009; Lukas and Clutton-Brock 2012, 2018; Davies and Gardner 2018).

Some of the most conspicuous instances of altruism come from eusocial or cooperatively breeding species (Wilson 1975; Koenig and Dickinson 2016). In many of these species, helpers appear to be indiscriminate altruists who help group mates regardless of relatedness (Wright et al. 1999; Legge 2000; Blatrix and Jaisson 2002; Canestrari et al. 2005; Friend and Bourke 2012; Vitikainen et al. 2017). In others, however, helpers appear to be kin-discriminate altruists, adjusting the amount of help provided according to their relatedness to the recipient (Richardson et al. 2003; Wright et al. 2010; Browning et al. 2012; Zöttl et al. 2013; Leadbeater et al. 2014; Green et al. 2015; Dias et al. 2017; Leedale et al. 2018). Comparative studies have suggested that kin-discriminate altruism is associated with living in groups of low mean relatedness and high variance in relatedness (Griffin and West 2003; Cornwallis et al. 2009).

In order to kin discriminate, organisms need to be able to correctly recognize kin. This can be achieved via visual (Kendrick et al. 2001; Van Dyk and Evans 2007), vocal (Sharp et al. 2005; Dowling et al. 2016), olfactory (Lihoreau and Rivault 2009; Caspers et al. 2017), or associative (Komdeur et al. 2004) cues that can allow for context-based associative learning, learned individual-specific cues, direct phenotypic matching, or allele recognition (Mateo 2004). None of these kin detection mechanisms are perfect, and like all animal signals they will be prone to errors (Johnstone 1997; Keller 1997; Agrawal 2001). In line with the comparative studies mentioned above (Griffin and West 2003; Cornwallis et al. 2009), modeling has suggested that indiscriminate altruism may be positively selected over kin recognition when kin recognition is prone to error (Hamilton 1964; Agrawal 2001). However, these models

assume that groups have a simple kinship structure consisting of a mixture of kin and nonkin. In reality, animal groups frequently contain kin of varying levels of relatedness as well as nonkin. As a result, errors may be continuous rather than binary, and individuals may either overestimate or underestimate their degree of relatedness to other group members rather than making binary errors in which nonkin are mistaken for kin or kin are mistaken for nonkin. Further work is required to incorporate the observed relatedness structure of animal groups into theoretical models for the evolution of indiscriminate altruism. Here, we explore empirical data on cooperation among cooperatively breeding meerkats (*Suricata suricatta*) and use data on the relatedness structure of meerkat groups to develop such a model.

The meerkats of the southern Kalahari Desert represent an ideal system in which to investigate altruism. Meerkats live in groups of up to 50 individuals within which reproduction is monopolized by a single dominant female and dominant male who are parents to more than 80% of all offspring born in the group (Hodge et al. 2008; Spong et al. 2008). Subordinate adults rarely successfully reproduce, but they exhibit a range of cooperate behaviors that benefit the offspring of dominant breeders (Clutton-Brock and Manser 2016). Helping has energetic costs to helpers, who experience reduced weight gain during periods of reproductive cooperation, although this rarely translates into long-term fitness costs (Russell et al. 2003). Although early research on meerkats found no evidence of kin-discriminate altruism in the expression of guarding (Clutton-Brock et al. 1999), babysitting (Clutton-Brock et al. 2000), or pup-feeding (Clutton-Brock et al. 2001) behaviors, a more recent analysis has suggested that the relatedness of a helper to a litter of pups is negatively associated with babysitting effort and positively associated with pup feeding (Nielsen 2012). Here, we use 25 years of longitudinal data on 1,347 individuals to achieve two aims: (1) to resolve previous inconsistencies and determine the extent to which meerkats are kin-discriminate altruists and (2) to use a model incorporating data on the kinship structure of wild meerkat groups to investigate the conditions under which different altruistic strategies would be selected, given varying levels of kin recognition error.

Empirical Methods

Study System

The empirical data analyzed in this study were collected in the southern Kalahari Desert, South Africa, between 1995 and 2016. Throughout the duration of the study, the number of groups habituated to human observers varied between five and 24 and the total population between 45 and 359. Animals were tagged with transponder chips and were individually recognizable by dye marks in their fur. Groups were visited and followed three to five times per week for 3 h in the morning from the time the group left the burrow and for 1 h before the group returned to the burrow in the evening. For the duration of group follows, behavioral data were collected ad lib. Data on group membership and individual life-history markers (such as pregnancy state and dominance relationships) were recorded for the duration of the study. The majority of the population were trained to be weighed on electronic scales, and individuals were regularly weighed during group visits. Our work was approved by the Animal Ethics Committee of the University of Pretoria, South Africa (EC010-13), and by the Northern Cape Department of Environment and Nature Conservation, South Africa (FAUNA 1020/2016).

Measures of Cooperation

Four cooperative behaviors were analyzed to measure the effects of relatedness on cooperative effort: (1) babysitting, where during the first 3–4 weeks of a pup's life, at least one adult will stay with them at the birth burrow throughout the day while the rest of the group forage; (2) pup feeding, where while foraging during the first 3 months of a pup's life, other group members will donate prey items to the pup; (3) guarding, where an individual will provide sustained vigilance for predators or other threats by assuming a bipedal position on raised ground or vegetation; and (4) digging, where individuals will excavate bolt holes and sleeping burrows for use by the whole group (fig. 1). Babysitting and pup feeding are litter-directed behaviors, whereas digging and guarding are group directed and of mutual benefit, providing benefits to all group members, including the altruist.

To quantify the cooperative contribution that individuals make in guarding and digging, their life span was split into 3-month periods. The total number of times that they were observed to engage in guarding or digging during each of these 3-month periods was collated ($n = 7{,}139$ periods from 1,347 individuals at 36 groups for both guarding and digging). Because the expression of babysitting and pup-feeding behaviors is limited to periods when pups were present in the group, we analyzed these data per litter, quantifying the contributions that individuals made to each litter. Pup-feeding data were restricted to the period of peak pup feeding (the first 45 days after the pups first started foraging; $n = 2{,}936$ periods of pup feeding for 329 litters from 1,164 individuals at 34 groups). During the babysitting period, groups were visited at least once a day and babysitters were identified. Individual contributions were quantified as total half days spent babysitting over the period ($n = 3{,}015$ periods of babysitting for 356 litters from 1,197 individuals at 35 groups). The frequency that digging, guarding, and pup feeding were expressed was recorded during behavioral observation sessions.

Figure 1: Photographs of the cooperative behaviors expressed by meerkats that are examined in this study: babysitting (*top left*), pup feeding (*top right*), guarding (*bottom left*), and digging (*bottom right*). Pup-feeding photograph copyright Dominic Cram.

Measures of Relatedness

We tested for associations between our four measures of co-operation and three measures of relatedness. These measures represented both direct measures of the relatedness of the helper to the recipient and indirect measures that could represent cues used by individuals to assess their relatedness to the recipient. These measures of relatedness were as follows: (1) mean relatedness to the litter, a direct measure of r for the

two pup-directed behaviors (pup feeding and babysitting); (2) mean relatedness to the group, a direct measure of r for group-directed behaviors (digging and guarding) and possible indirect cue for litter-directed behaviors; and (3) relatedness to the dominant female, a possible indirect cue for all behaviors. There were strong positive correlations between our indirect and direct measures of relatedness (fig. A1; figs. A1–A7 are available online). As such, the possibility of them representing indirect cues of recipient relatedness are reason-

able. To produce these measures of relatedness, a relatedness matrix was generated for our entire population, and pairwise relatedness values were calculated between the helper and recipient(s). Relatedness was established from a multigenerational pedigree generated using the kinship2 package in R (Therneau et al. 2014) and based on parentage established through genetic analysis of 18 microsatellites derived from small tissue samples removed from the tail tip of individuals (Griffin et al. 2001, 2003; Nielsen 2012), supplemented with observational field data on maternity where genetic data were missing.

Statistical Analyses

Statistical analyses were performed in R3.4.3 (R Development Core Team 2017), and all data sets used in these analyses are available in the Dryad Digital Repository (https://dx .doi.org/10.5061/dryad.r01cq00; Duncan et al. 2019). Generalized linear mixed models fitted with the package glmmTMB (Magnusson et al. 2017) were used to investigate the factors influencing subordinate contributions to cooperative activities. To account for pseudoreplication, random effects for individual and group identifiers were included in all models and for litter identity in models of pup-directed behavior. All random effects included accounted for a significant amount of variation, as confirmed by likelihood ratio tests with adjusted P values for testing on the boundary (Zuur et al. 2009). Quadratic terms were fitted in models when preliminary diagnostic plotting revealed the presence of quadratic relationships. Where there were a priori expectations of the existence of interactions, these were also fitted. Collinearity for all fixed effects was tested using variance inflation factors with a threshold value of 3 (Zuur et al. 2009).

Contributions to babysitting were modeled using a binomial error distribution and a logit link with the proportion of half days babysat fitted as the response variable. Contributions to pup feeding, sentinel duty, and digging were modeled separately using negative binomial error distributions with a log link and the frequency that the behavior was expressed during the sample period fitted as the response variable. For the negative binomial models, the total duration (in minutes) that the individual was observed during the sampling period was included in the model as an offset to account for variation in sampling duration. Before testing the effect of relatedness on cooperative effort, models of best fit were created for each behavior, including variables that previous studies had revealed exert a significant influence over cooperation (Clutton-Brock et al. 2000, 2001, 2002). The following fixed effects were included in maximal models for all four behaviors: age, mean residual morning weight (standardized against age), mean group size, mean foraging rate, sex, litter size (for litter-directed behaviors), and whether the individual was living in their natal group. All continuous and two-

level categorical fixed effects were scaled to allow for relative effect size comparison (Gelman 2008). Model selection was guided by the Akaike information criterion to reduce maximal models to a model of best fit. The different measures of relatedness were included in the models of best fit to test their influence on cooperative effort. Each metric of relatedness was modeled separately because of collinearity between the measures. Only model outputs for the terms of relatedness are reported here; full model outputs with accompanying forest plots are available in figures A1–A4.

Empirical Results

The contributions of helpers were related to the size of their group and varied with their sex, age, and condition (figs. A2–A5). Across all four cooperative behaviors, the contributions of helpers to all cooperative activities declined with increasing group size; this effect was quadratic and, as group sizes increased, the strength of this effect decreased. Contributions to helping also differed between the sexes. Females invested relatively more than males in pup-directed behaviors (babysitting and pup feeding; figs. A2, A3), while males invested more than females in guarding and digging (figs. A4, A5). As individuals matured, their expression of cooperative behavior changed, and they showed increased investment in babysitting and guarding and a marginal decrease in investment in pup feeding and digging (figs. A2–A5). The contributions of helpers to the behaviors that benefit all group members were also related to their condition: heavier individuals contributed more to digging and guarding than lighter ones, and individuals with greater daily foraging success (measured by daily weight gain) contributed more than those with lower success (figs. A4, A5). Contributions to pup-directed behaviors were not as closely associated with variation in weight and foraging success as those to collective actions. While significant, their effects were small relative to other variables that exerted considerably more influence over cooperative effort (figs. A2, A3).

Across the four forms of cooperation, there was either a nonsignificant or a significant but very small association between relatedness and the amount of help expressed. For the two pup-specific behaviors (pup feeding and babysitting), we tested whether relatedness to the pups, to the whole group, or to the dominant female was associated with the amount of help provided. There were no significant relationships between the amount of babysitting expressed by an individual and their relatedness to the pups being babysat, to the group, or to the dominant female (table 1; fig. 2). While there was no significant association between an individual's mean relatedness to the group and their expression of pup feeding, there was a small significant positive association between dominant female relatedness and pup-feeding expression (table 1;

Table 1: Influence of different metrics of relatedness on an individual's contribution to cooperative behavior

Variable	Coefficient	SE	P	95% CI	Interpretation of effect sizes in a biological context
Babysitting:					
Litter r	−.049	.037	.190	−.121 to .024	An increase in relatedness from .25 to .5 reduces the probability of babysitting on a half day by .5%
Group r	.028	.046	.528	−.063 to .118	An increase in relatedness from .25 to .5 increases the probability of babysitting on a half day by .4%
Dominant female r	.076	.042	.071	−.006 to .158	An increase in relatedness from .25 to .5 increases the probability of babysitting on a half day by .74%
Pup feeding:					
Litter r	.024	.033	.465	−.041 to .089	On average an increase in relatedness of .25 to .5 increases the number of prey items fed to a litter by .46
Group r	.032	.037	.385	−.041 to .105	On average an increase in relatedness of .25 to .5 increases the number of prey items fed to a litter by .75
Dominant female r	.087	.032	.007**	.024 to .150	On average an increase in relatedness of .25 to .5 increases the number of prey items fed to a litter by 1.64
Digging:					
Group r	.167	.033	<.001***	.106 to .228	On average an increase in relatedness of .25 to .5 increases the number of digs performed in a 3-month period by 2.25
Dominant female r	.119	.031	<.001***	.031 to .150	On average an increase in relatedness of .25 to .5 increases the number of digs performed in a 3-month period by 1.36
Guarding:					
Group r	.054	.050	.278	−.06 to .11	On average an increase in relatedness of .25 to .5 increases the number of guards performed in a 3-month period by .53
Dominant female r	.023	.048	.633	−.78 to .90	On average an increase in relatedness of .25 to .5 increases the number of guards performed in a 3-month period by .15

Note: Generalized linear mixed model results. Each measure of relatedness was modeled separately; full model outputs and forest plots of effect sizes are in figures A1–A4 (available online). Interpretations of the practical effect of the various measures of relatedness were derived from model predictions with all other continuous explanatory variables held constant at the mean and the categorical variables sex set to female and group status to natal when included. CI = confidence interval.

** $P < .01$.

*** $P < .001$.

fig. 2). This effect equates to an individual increasing their pup-feeding effort by 5.8% should their dominant female be a full sibling ($r = 0.5$) as opposed to a half-sibling ($r = 0.25$). However, this effect does not appear to translate into individuals discriminating their pup-feeding effort in relation to their relatedness to the actual recipients because there is no significant association between the expression of pup feeding and relatedness to the litter being helped (table 1; fig. 2).

Variation in rates of guarding among subordinates was not significantly associated with either their average relatedness to group members or their relatedness to the dominant female (table 1; fig. 3). Rates of digging were significantly associated with an individual's relatedness to both their group

and their dominant female, although these effects were again very small. An increase of relatedness to the group of $r = 0.1$ and to the dominant female of $r = 0.25$ was associated with an increase in digging effort of 4.7% and 6.9%, respectively (table 1; fig. 3).

Meerkats live in closely related groups with a mean coefficient of relatedness among group members of $r = 0.34$ (SD = 0.16). As such, helpers are often highly related to the recipients of their cooperative investments. Natal helpers, who make up more than 91% of all helpers, are full or half-siblings to 64.4% of pups born in their group and are on average related to pups by $r = 0.34$ (SD = 0.14). Therefore, our finding that meerkats are largely indiscriminate in their altruism fits with previously described relationships between
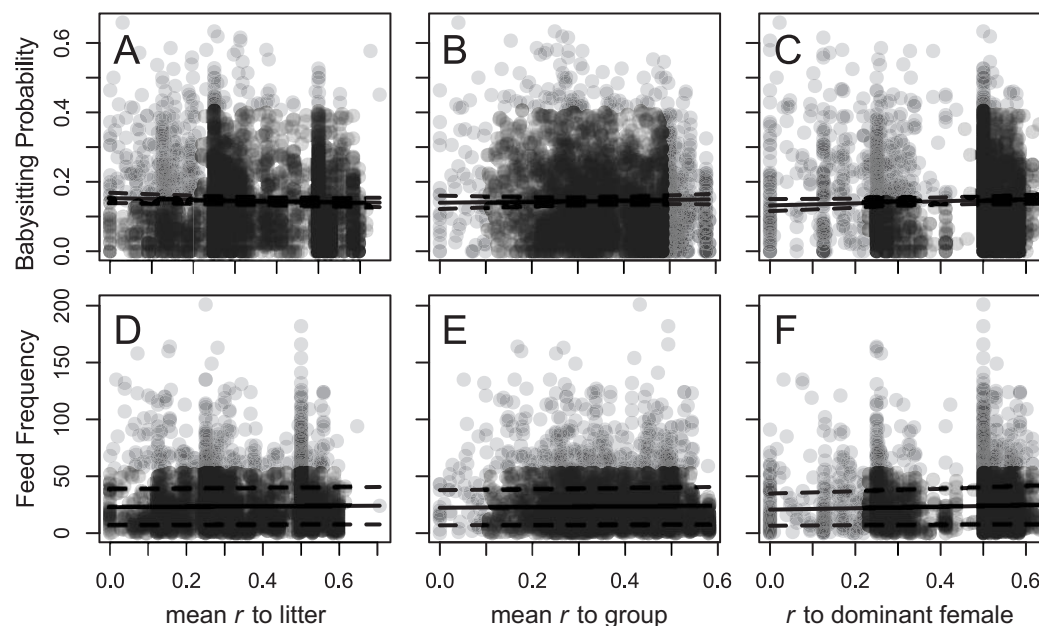
Figure 2: Association between an individual's relatedness to the litter (*A*, *D*), group (*B*, *E*), and dominant female (*C*, *F*) and the frequency of babysitting (*A*–*C*) and pup feeding (*D*–*F*). Raw data plotted as gray circles. Prediction outputs from generalized linear mixed models plotted as solid lines, with 95% confidence intervals plotted as dashed lines. All other continuous explanatory variables were held constant at their mean, and the categorical variables sex and group status were fixed at female and natal, respectively.

high group relatedness and indiscriminate altruism (Griffin and West 2003; Cornwallis et al. 2009, 2010).

Modeling Results

In order to explore the conditions under which indiscriminate within-group altruism might be positively selected, we constructed a model that incorporates observed data on the kinship structure of groups. We estimated the inclusive fitness payoffs that would result from three strategies: indiscriminate altruism (IA), where individuals act altruistically toward all group mates; selfishness (S), where individuals never act altruistically to group mates; and kin discrimination with error (KD), where individuals act altruistically toward others when they estimate that $rb - c > 0$ but where estimates of r are prone to error. To introduce error in the KD strategy, estimated r values are randomly sampled from a normal distribution with a mean of the true r value and with a standard deviation determined by parameter e (we also ran an extended model where b and c are also prone to error; see appendix). Sampling from observed coefficients of relatedness between group members, we can compare the mean fitness payoffs derived from social interactions under these three strategies (IA, S, and KD) across a range of b:c ratios and varying degrees of kin recognition error.

Given the observed kinship structure of meerkat groups, our model suggests that it can be advantageous to be an in-

discriminate altruist rather than an error-prone kin discriminator across much of the parameter space (roughly when $e > 0.15$ and b:$c > 3$; fig. 4). In contrast, selfishness is favored only when the benefits of cooperation are small. These predictions are by no means an inevitable consequence of the setup of the model. If we substitute the empirical data from meerkat groups with hypothetical data on less closely related groups, we find that indiscriminate altruism is rarely favored. For example, if groups contain ~50% of unrelated individuals and ~50% kin of varying degrees of relatedness (a group composition similar to many old-world haplorrhine primate groups as well as human hunter-gatherer societies; Hill et al. 2011; Dyble et al. 2015, 2016), indiscriminate altruism is never favored. Instead, kin discrimination is favored for much of the parameter space (fig. 4). If we dilute group relatedness further, with ~90% of individuals being unrelated and ~10% being kin of varying degrees of relatedness (similar to the structure of a medium-sized herd of ungulates), we find that selfishness is favored for much of the parameter space (fig. 4). Similar results are produced when a discrete error structure is assumed (see appendix; fig. A6). As well as error in relatedness, it is also possible that an individual's estimation of the costs and benefits of an altruistic behavior is prone to error. Adding such errors to our model further reduces the payoffs of kin discrimination with error (fig. A7). In general, we predict that indiscriminate altruism will be favored over error-prone kin discrimination when the degree of error (*e*) in kin
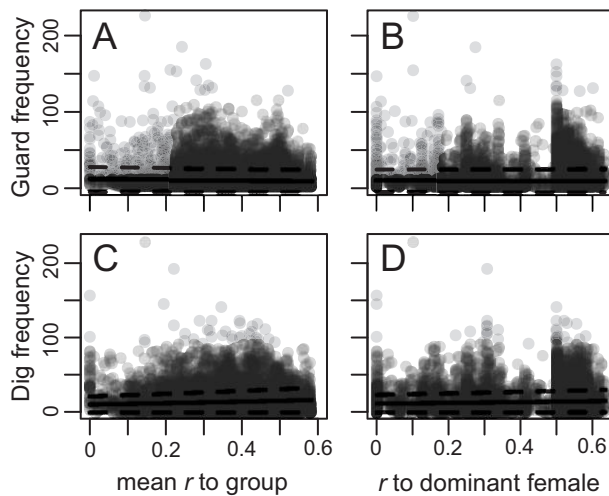
Figure 3: Association between an individual's mean relatedness to the group (*A, C*) and to the dominant female (*B, D*) on their expression of the cooperative behaviors guarding (*A, B*) and digging (*C, D*). Raw data plotted as gray circles. Prediction outputs from generalized linear mixed models plotted as solid lines, with 95% confidence intervals plotted as dashed lines. All other continuous explanatory variables were held constant at their mean, and the categorical variables sex and group status were fixed at female and natal, respectively.

recognition is greater than the standard deviation in relatedness among social partners and where the $b : c$ ratio is greater than the inverse of mean relatedness among social partners.

Discussion

Empirical Results

Our results show that the extensive cooperation seen within meerkat groups is largely indiscriminate with respect to relatedness. In line with some previous analyses (Clutton-Brock et al. 2000, 2001) but not with others (Nielsen 2012), we find that the frequencies of babysitting, pup feeding, and guarding in meerkats are not associated with the relatedness of helpers to the recipients. Although evidence of a significant association between the frequency of pup feeding and the relatedness of helpers to the dominant female could indicate kin-discriminate pup feeding via an indirect cue, this is inconsistent with the lack of association between pup feeding and relatedness to the litter of pups, the actual recipients of this help. For kin discrimination based on an indirect cue of recipient relatedness to be functional, it must also lead to an association between helping and relatedness to the true recipients, which—in the case of pup feeding—it does not.

Although digging is the only cooperative behavior where we find a significant relationship between the behavior and both direct and indirect measures of relatedness, the effects were very small and represented negligible variation in coop-

erative effort. We suspect that this observed association could be a statistical artifact driven by confounding variables associated with both kinship and cooperative behavior that our model has not accounted for. Moreover, in large data sets, such as the one analyzed here, there is a greater risk of effects lacking biological importance being assigned statistical significance (Nakagawa and Cuthill 2007; Lin et al. 2013). Ultimately, as we see no evidence of meerkats kin discriminating in cooperative behaviors where only indirect fitness benefits are derived (such as babysitting and pup feeding), we find it unlikely that there would be selection on meerkats to kin discriminate in their expression of cooperative behaviors that benefit all group members, including the altruist, such as digging.

Although our data suggest that meerkats do not strongly kin discriminate in cooperative behaviors, previous work has suggested that they kin discriminate in order to avoid inbreeding (Griffin et al. 2003) and that dominant females selectively evict less closely related subordinates (Clutton-Brock et al. 2010). Such inconsistencies in kin discrimination between behavioral domains are not unique to meerkats (Sanderson et al. 2015; Vitikainen et al. 2017). To avoid inbreeding, meerkats kin discriminate by distinguishing between (familiar) group members and (unfamiliar) members of other groups (Griffin et al. 2003), a mechanism seen in many cooperative breeders (Dickinson et al. 2014; Komdeur et al. 2014), with inbreeding generally occurring only between related individuals who have no prior within-group experience of each other (Nielsen et al. 2012). In contrast, kin-discriminate helping would require individuals to differentiate between group mates, a qualitatively different mechanism. Although within-group discrimination does appear to occur in the context of subordinate female evictions, with granddaughters and nieces more likely to be evicted than daughters or sisters, a more thorough analysis of this behavior across other possible kin categories is required to resolve the nature of this discrimination and whether it could be applicable in the context of helping. Furthermore, while scent presentation experiments suggest that meerkats may be capable of the fine-scale kin discrimination of unfamiliar individuals (Leclaire et al. 2012), this mechanism has not been tested among familiar individuals. Similar experiments on banded mongooses suggest that phenotype-matching mechanisms are not necessarily transferable between familiar and unfamiliar individuals (Mitchell et al. 2018).

Theoretical Results

Why do meerkats appear to be largely indiscriminate altruists? Our theoretical model suggests that indiscriminate altruism yields higher payoffs than kin discrimination where (1) kin discrimination is prone to error, (2) mean relatedness among social partners is high, and (3) the relative benefits of helping are large. This provides a plausible explanation not only for the evolution of indiscriminate altruism in meerkats
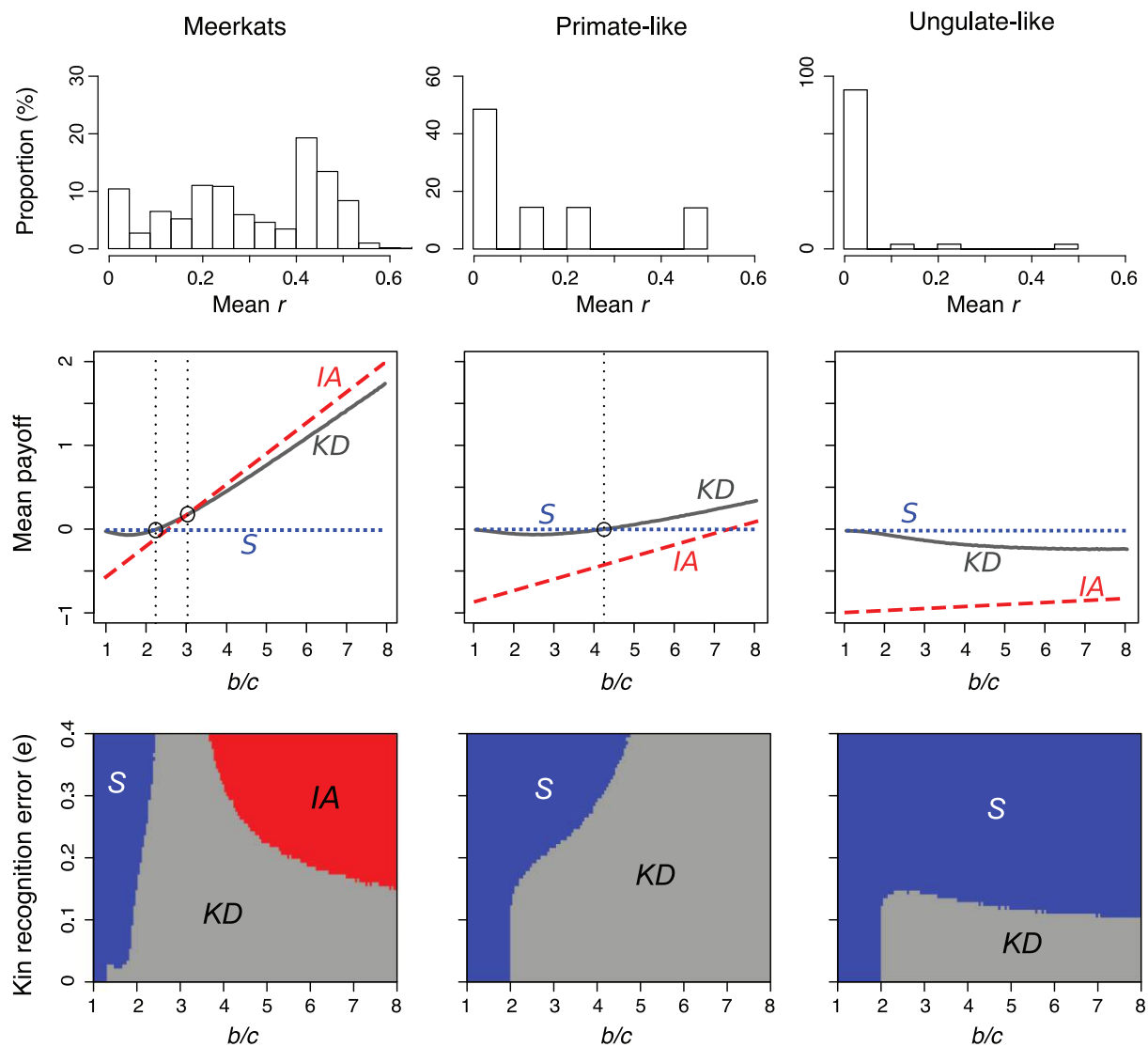
Figure 4: Kinship structure of meerkat groups may favor the evolution of indiscriminate altruism. *Top*, histograms of the relatedness among group mates. *Middle*, hypothetical payoffs of indiscriminate altruism (red dashed lines), selfishness (blue dotted lines), and kin recognition with error (gray solid lines) at $e = 0.25$. *Bottom*, strategy that yields the maximum fitness payoff across the $b : c$ ratio and kin recognition error. *Left*, predictions using empirical data from meerkats. *Middle*, predictions based on a old-world primate-like group structure. *Right*, predictions based on a large ungulate-like group structure. IA = indiscriminate altruism; KD = kin discrimination with error; S = selfishness.

but also for the negative relationship between kin discrimination and group relatedness reported for cooperatively breeding vertebrates more generally (Cornwallis et al. 2009). Living in moderately sized social groups of low mean relatedness that include a minority of close kin—as is characteristic of many primate groups, including humans (Dunbar 1998; Dyble et al. 2015; Lukas and Clutton-Brock 2018)—may favor the evolution of kin-discriminate altruism, advanced social cognition, and relational complexity (Dunbar 1998; Lukas and Clutton-Brock 2018).

Our assumption that kin discrimination is prone to error is consistent with empirical evidence of errors in kin discrimination among eusocial and cooperatively breeding species. For example, kin-discriminate altruists who use associative or familiarity-based mechanisms to recognize kin appear to be unable to discriminate variation in relatedness caused by extrapair mating (Dickinson et al. 2014; Komdeur et al. 2014). Additionally, rather than discriminating between kin and nonkin in a binary sense, there is evidence that several species can discriminate between various discrete categories of kin and

possibly even continuously discriminate fine-scale genetic differences among conspecifics in the expression of cooperative effort (bell miners [*Manorina melanophrys*]: Wright et al. 2010; long-tailed tits [*Aegithalos caudatus*]: Nam et al. 2010; Leedale et al. 2018; paper wasps [*Polistes dominulus*]: Leadbeater et al. 2014) and other behaviors (honey bees [*Apis mellifera*]: Getz and Smith 1983; German cockroach [*Blattella germanica*]: Lihoreau et al. 2016).

In addition to error-prone kin recognition and high group relatedness, the evolution of indiscriminate altruism may be promoted by a number of other factors (Keller 1997). First, the mechanism underlying kin discrimination may also incur a direct cost (e.g., in terms of the energetically demanding cognitive architecture required). Second, as extensions to our model demonstrate, the benefits of kin-discriminate altruism will be further diminished by error in the estimation of the costs and benefits of helping. Third, the payoffs of indiscriminate altruism may be increased by the direct benefits of group augmentation (Kokko et al. 2001; Kingma et al. 2014). Finally, although our theoretical model focuses on fixed errors in perception, animal signals may themselves be error prone, and both signals and perception are likely to be subject to selection (Johnstone and Grafen 1992; Johnstone 1997; Keller 1997).

Conclusion

In summary, we show that cooperatively breeding meerkats are largely indiscriminate altruists who do not substantially increase their cooperative effort when they are more closely related to the recipients of their help. Building on previous empirical and theoretical work, we suggest that indiscriminate altruism may evolve when group relatedness is high and when kin recognition is prone to error. Our work provides further support for the importance of group structure and relatedness in driving the evolution of cooperation and complex social organization.

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Newly born meerkat pup (*Suricata suricatta*) being babysat by a subordinate individual at the birth burrow. Photo credit: Chris Duncan.