Individual differences and variation in the reproductive strategies of cooperative breeders

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ABSTRACT

Ecological differences are instrumental to the evolution of cooperative breeding, because they mean that the costs and benefits of forming a group and sharing reproduction differ between individuals and environments. Current evolutionary models do not fully explain the diversity of cooperative breeders' strategies, which suggests that these models neglect important ecological factors and are insufficiently complex. The goal of this PhD is to understand the factors that influence the evolution of cooperative-breeding strategies. My thesis incorporates some of the overlooked individual variation and uncertainty into models of skew, to get further insights into the reproductive games of cooperative breeders. I combine theoretical and empirical approaches, including a cross-species comparison and a dataset analysis.

We first develop a model which reveals that the link between subordinate outside options and their effect on group productivity shapes skew and group formation. Using a meta-analysis I find that relatedness correlates positively with skew within species, suggesting that kin forego reproduction because the indirect benefits of helping are sufficient. We then develop a theoretical model to explore the effect of uncertainty which predicts that dominants should evolve to acquire information about the outside options of subordinates, but not their relatedness to those subordinates.

Another key facet of variation is sex differences in life histories, which might select for different response rules for costly cooperative behaviours and reproductive strategies. While parental conflict and reproductive conflict both influence group productivity in theoretical models, my work shows that combining these two games does not change their predictions, which suggests that they can be studied separately. Using data from wild dwarf mongooses (*Helogale parvula*), I uncovered an interaction between sex and period in contributions to costly sentinel activity, with males contributing more than females in the second fortnight after individuals acquire dominance.

Empirical studies testing the predictions of this thesis are needed to determine whether their hold true. Future studies should investigate how variation and uncertainty about other factors influence evolutionary games, to define what influences animals’ strategies.

Table of Contents

List of Figures 6
List of Tables 11
List of Appendices 14
Acknowledgements 15
Author's declaration 17
Glossary 18
Chapter 1 – General introduction 20
  1. Cooperative breeders and their reproductive strategies 22
  2. Unrealistic assumptions of skew models: incorporating variation and uncertainty 28
  3. Empirical evidence of variation in cooperative breeders 38
  4. Theoretical and empirical approaches to determine which factors influence cooperative breeders' reproductive games 41
Chapter 2 – Tests of reproductive skew theory: a review and prospectus 45
  Abstract 46
  Introduction 47
  Predictions of reproductive skew models 49
  Review of empirical findings 58
  Discussion 64
    Relatedness. 64
    Competitive advantage. 65
    Subordinate quality. 66
    Group productivity. 66
Chapter 3 – Cooperative breeding and the selection for information sharing amongst groupmates 76
  Abstract 77

Introduction 78

The model 81

Results 89

Discussion 100

Chapter 4 – Adaptive levels of skew under sex differences and parental conflict 107

Abstract 108

Introduction 109

The model 113

Results 121

Discussion 129

Chapter 5 – Sex and period interact to influence sentinel contribution around dominance acquisition 135

Abstract 136

Introduction 137

Methods 142

Results 146

Discussion 152

Chapter 6 – General Discussion 157

1. Summary of thesis findings 158
2. Implications of individual differences 158
3. Effect of uncertainty 161
4. Limitations and future research 163
5. Cooperative breeders and behavioural plasticity 164

6. Cooperative breeders and environmental change 166

Conclusion... 167
REFERENCES 168
ANNEXES 212
ANNEXE 2.A: Supplementary figures and tables for Chapter 2 212

ANNEXE 2.B: Methodology for Chapter 2.. 219

ANNEXE 2.C: Predictions of the new models for Chapter 2 221

ANNEXE 3.A: Analyses of the effect of information about subordinate quality for Chapter 3 228

ANNEXE 3.B: Numerical model investigating unknown relatedness for Chapter 3 245

ANNEXE 3.C: Supplementary figures for Chapter 3 251

ANNEXE 4: Supplementary figures for Chapter 4....................................... 253

ANNEXE 5: Supplementary tables and figures for Chapter 5 257

List of Figures

Figure 2.1 Direction of predicted association between skew and parameters of the skew models: (a-e) concession, (f-j) restraint, (k-o) tug-of-war. Areas indicate a positive (dark purple), negative (white) or non-significant (yellow) difference in *y** for two values of: (a, f, k) relatedness *r*; (b, g, l) subordinate quality *x*; (c, h, m) dominant's competitive advantage *b;* (d, i, n) group benefit *m* when outside option and group productivity are not associated *a*=0, *m*=*k*; (e, j, o) group benefit *m* when outside option and group productivity are positively associated *a*=0.5. Each area is the comparison between two values for a given parameter: *r*=0, 0.5, *x*=0.35, 0.65, *m*=0, 0.5. The difference was considered non-significant if its absolute value was smaller than 10% of the skew at the lower value of each parameter: e.g. if $\frac{|y^*(r=0.5)-y^*(r=0)|}{y^*(r=0)}<0.1$. Horizontal dotted lines indicate *a*=0, so show the predictions of the original models, and *m*=0.6 – *a* as otherwise groups are always preferred (for any *y*) if *a* is large and never preferred if *a* is small……………….p57

Figure 2.2 Number of species showing a positive, negative or nil link between skew and relatedness, as a function of (a) sex, (b) group and (c) taxa. N=45…p59

Figure 2.3 Effect (mean Hedge's g ± 1 SE) of the link between skew and relatedness as a function of (a) sex (females dark red, males: light blue), (b) group and (c) taxa (insects: dark green, vertebrates: yellow). N=16…………………p60

Figure 2.4 Number of species showing a positive, negative or nil link between skew *y* and (a) subordinate quality *x*, (b) dominant's competitive advantage (quality) *b* (N=17) and (c) group productivity *k* (N=19) in insects and vertebrates (N=7)…………………………………………………………………………p61

Figure 3.1 Optimal concession (a-d), dominant inclusive fitness (e-h) and subordinate inclusive fitness (bottom row) for some representative values of *a*

and *m* (columns) under perfect information P, no information N, and when alone A. The dotted lines in (a-d) indicate y=0. The dominant fitness depends on whether the dominant wants the subordinate to stay (d_P, $d_N > d_A$) and whether the subordinate chooses to stay (d_N, $s_N > s_A$). The dominant always does at least as well as no information when they have perfect information, whereas the opposite is true of the subordinate. Other parameter values: r=0.5, b=1 ……………………………………………………………………………………..p91

Figure 3.2 Effect of perceived quality of subordinate on the optimal concession y^* (black lines) for four levels of knowledge: (a) no knowledge ω=0, (b) some knowledge ω=16, (c) high information ω=512, (d) perfect information ω=∞. The colours show the areas of perceived quality by dominant (horizontal axis) and actual quality of subordinate (vertical axis) where for the optimal y both dominant and subordinate would do better in a group (green); only the dominant would do better in a group (yellow). Other parameter values: a=0.5, m=0.35, r=0.25…p92

Figure 3.3 Effect of information about x on the prediction of cooperative breeding for various QPC (a) and relatedness (r). The colours show the areas of dominants' level of information about x (horizontal axis) and actual quality of subordinate (vertical axis) where for the average decision across all perceived subordinate qualities was: to stay for both dominant and subordinate (green); only the dominant wants to breed cooperatively (yellow); only the subordinate wants to breed cooperatively (cyan); or neither wants to breed cooperatively (blue); for 3 values of quality-productivity coefficient a (columns) and four values of relatedness (rows); values shown on panels…………………………………..p94

Figure 3.4 Effect of information about x on decisions and fitness outcomes. (a-c) optimal concession (y*); (d-f) average dominant inclusive fitness and (g-i) average subordinate inclusive fitness, as a function of the quantity of information about the subordinate's outside option. Columns show different values of quality-productivity coefficient and synergy effect (a, m) (columns: left a=−0.5, m=0.85; middle a=0.5, m=0.35; right a=1.5, m=−0.25). Lines indicate gradually increasing

information (solid line), and analytical solutions for perfect information (dash line), no information (dotted line), fitness alone (dot-dash line). Other parameter values: *b*=1, *r*=0.5…………………………………………………………………………p95

Figure 3.5 Optimal amount of information about relatedness for dominants and subordinates of three different qualities (lines) for three values of the quality-productivity coefficient a (rows). Lines indicate dominant (solid lines), low-quality subordinate (*x*=0.2, dot-dash lines), average subordinate (*x*=0.5, dotted lines), high-quality subordinate (*x*=0.8, dashed lines)…………………………………p97

Figure 3.6 Value of information about relatedness as a function of subordinate quality (horizontal axes) for 4 values of *a* (lines). The vertical axis is the difference in realised inclusive fitness between the perfect information (*r* known) and the no information case (*r* could be any value). Panels show values of information (a) to the dominant and to the unrelated (b) or related (c) subordinate……………..p99

Figure 4.1: Conflict trait as a function of (a,b,c) probability to find a nest and (d,e,f) subordinate competitive ability. Subordinate competitive ability is (a) low, (b,e,d,f) medium and (c) high. Probability to find nest is (d) low, (a,b,c,e) medium and (f) high…………………………………………………………………………………p122

Figure 4.2: Subordinate share as a function of (a,b,c) probability to find a nest *NF, NM* and (d,e,f) subordinate competitive ability *bF, bM*. Synthetic and classic models for (a) low, (b) medium and (c) high subordinate competitive ability, and (d) low, (e) medium and (f) high probability to find a nest. Models: synthetic (violet line), concession (green dash-dot), restraint (blue dot) and tug-of-war (red dash). Grey boxes show where there is less than 10% probability males form groups (i.e., breed cooperatively), so male subordinate share is not under selection…………………………………………………………………………p123

Figure 4.3: (a,b,c) Parental efforts and (d,e,f) subordinate share as a function of parental effort costs for (a,d) low, (b,e) medium and (c,f) high parental effort benefit. Models: synthetic numerical (violet line), parental effort (yellow line), concession (green dash-dot), restraint (blue dot) and tug-of- war (red dash). Grey boxes show where groups do not form and subordinate share is not under selection (drift). Constant variables are $b_F = b_M = 0.7$; $N_F = N_M = 0.05$………p124

Figure 4.4: (a,b,c) Parental trait and (d,e,f) subordinate share as a function of dominant maximal productivity ϕ for (a,d) low, (b,e) medium and (c,f) high probability to find a nest. Models: (a,b,c): parental (yellow line) and synthetic numerical model (red line); (d,e,f) synthetic numerical (violet line), concession (green dash-dot), restraint (blue dot) and tug-of-war (red dash). Grey boxes show where groups do not form and subordinate share is not under selection (drift). Constant variables are $b_F = b_M = 0.7$; $N_F = N_M = 0.05$…………………………p125

Figure 4.5: Probability to form a group as a function of (a,b,c) probability for males to find a nest N_M and (d,e,f) subordinate male competitive ability b_M. Synthetic and classic models for (a) low, (b) medium and (c) high male subordinate competitive ability, and (d) low, (e) medium and (f) high probability males find a nest. Grey boxes show where probability that males form a group falls below 10%...p126

Figure 4.6: Conflict trait as a function of (abc) male probability to find a nest and (def) male subordinate competitive ability in the synthetic model. Male nest availability is (d) higher, (e) equal to and (f) lower than females' N_F=0.05. Male subordinate competitive ability is (a) higher, (b) equal to and (c) lower than females' b_F=0.5. Grey boxes show where probability that males form a group falls below 10%...p128

Figure 4.7: Subordinate share as a function of (a,b,c) probability to find a nest N_M and (d,e,f) subordinate competitive ability $b_{M,}$ in the synthetic model for (a) low, (b) medium and (c) high male subordinate competitive ability, and (d) low,

(e) medium and (f) high male probability to find a nest. Female: dark blue line and male: green line. Grey boxes show where males do not form a group and their subordinate share is not under selection (drift). Variation in male N_M and b_M; female N_F=0.05, b_F=0.5……………………………………………………….p129

Figure 5.1 Sentinel contribution (Mean ± 1 SD) as a function of sex and period. Females in yellow and males in dark blue in the four periods. Period A: 4-3 weeks before, B: 2-1 weeks before, and C: 1-2 weeks and D: 3-4 weeks after becoming dominant. N=9 females, 11 males……………………………………………p149

Figure 5.2 Duration of full grooming bouts as a function of sex and period (divided by Standard Deviation) (Mean ± SD). Females (left) are shown in yellow and males (right) in blue. Period A: 4-3 weeks before; B: 2-1 weeks before becoming dominant; C: 1-2 weeks and D: 3-4 weeks after dominance change………p150

Figure 5.3 (a) Grooming proportion per sex and period in good environments (Mean ± SD, non-weighted). Females in yellow (n=3) and males in blue (n=8). Periods: 4-3 weeks before (A), 2-1 weeks before (B), and 1-2 weeks (C) and 3-4 weeks (D) after dominance acquisition. (b) Grooming proportion as a function of season and environmental quality (Mean ± SD). Bad environments are shown in brown and good environments in light blue …………………………………p151

Figure 5.4 Body mass (in grams, +/- SD) as a function of sex, in the four periods around focal dominance acquisition. Females are shown in yellow and males in dark blue. Individuals were weighted in the evening. N=7 females, 4 males…………………………………………………………………………p152

List of Tables

Table 1.1: Predictions of the effects of biological factors on helpers' quality-productivity coefficient (QPC)……………………………………..………… pp34-35

Table 2.1 Parameters used in the models of reproductive skew and the range of values; baseline values……………………………………………………………….p49

Table 2.2 Assumptions and predictions of the three main models of skew: concession, restraint and tug-of-war. Predictions of the effect of variables on skew are adapted from Liebert & Starks (2006), Reeve & Ratnieks (2001) and Nonacs (2006). Sources are listed inside brackets and are the original models of skew: (1) Reeve & Ratnieks, (1993); (2) (Johnstone & Cant, 1999); (3) (Reeve et al., 1998a); (4) (Reeve & Keller, 2001)……………………………………….p54

Table 2.3 Sample sizes of the effects empirically tested in insects and invertebrates. Studies with data for males and females were shown as two data points. Unclear results are not displayed (n>1 studies per group, N=111 total with all links and unclear results.)…………………………………………………p61

Table 2.4 Empirical tests of our new predictions (species with ≥2 different factors tested). Models are the skew models whose predictions fit with the empirical tests once the QPC is incorporated…………………………………………………p68-70

Table 3.1 Variables and parameters in the model with their baseline and explored values……………………………………………………………………………p86-88

Table 3.2 Predicted effects of subordinate’s quality-productivity coefficient (QPC, *a*) on the reproductive strategies of cooperative breeders. Optimal concession *y** is the reproductive share that maximises inclusive fitness………………..p89-90

Table 4.1 Factors present in each game, with the baseline values and ranges……………………………………………………………………………..p114

Table 4.2 Variables used in the models, with their baseline values and the range explored……………………………………………………………………………p116

Table 5.1 Number of observations for sentinel scans, grooming proportion of the observed grooming in the group and full grooming bouts per status and sex in the four two-week periods around dominance acquisition. The analysis focused on individuals with data on sentinel contribution, and/or grooming proportion, in each period. However, due to the small sample size, all complete grooming bouts from incoming/recent dominants were included. N: number of individuals. One group grooming proportion was calculated per period and per individual…………………………………………………………………...p143-144

Table 5.2 Summary of the best mixed models for each prediction with effect sizes and AICc……………………………………………………………………………p147

Table 5.3 Summary of the best model for sentinel contribution with status (Predictions 1a and 3a)…………………………………………………………..p148

Table 5.4 Summary of the best model for sentinel contribution with period instead of status (Prediction 1b). The reference levels are period C and females……………………………………………………………………p148-149

Table 5.5 Summary of the best model for grooming duration (Predictions 2a and 3b)……………………………………………………………………………..p150

Table 5.6 Summary of the best model for group-grooming proportion (Predictions 2b and 3c)……………………………………………………………………….p151

List of Appendices

Each chapter comprises appendices that provide further information but are not essential, or are too lengthy to be included in the chapter.

ANNEXE 2.A: Supplementary tables and figures for Chapter 2

ANNEXE 2.B: Methodology for Chapter 2

ANNEXE 2.C: Predictions of the skew models for Chapter 2

ANNEXE 3.A: Analyses of the effect of information about subordinate quality for Chapter 3

ANNEXE 3.B: Numerical model investigating unknown relatedness for Chapter 3

ANNEXE 3.C: Supplementary figures for Chapter 3

ANNEXE 4: Supplementary tables and figures for Chapter 4

ANNEXE 5: Supplementary tables and figures for Chapter 5

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Chapter 1. AH provided guidance on the initial structure of the chapter. AH, TF and AR provided input on the writing.

Chapter 2. AH and I co-conceived the ideas and co-designed methodology. I and AH co-developed the models, which I used to generate predictions. I conducted the meta-analysis and analysed the data. AH provided guidance on analysing the predictions and on drafting the manuscript.

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Glossary

Alloparental care: post-hatching/birth behaviours towards the offspring, done by individuals that are not the parents, that improve the fitness of the parent and/or its offspring. Behaviours include for instance food provisioning and nest defence.

Asymmetric costs: costs of individuals of two types are not equal. For instance, mammal females typically have higher physiological reproductive costs than males.

Biological markets: concept based on partner choice and the fact that potential partners differ in their values, but also that partner availability varies. According to biological market theory, individual behaviour changes with the number and quality of partners available. For instance, in *Polistes* wasps, increasing the outside options of the subordinate helpers means that more helpers will leave the group to establish nests, and thus helper availability will decrease; the remaining helpers can reduce their helping efforts because the dominant has less partner choice and will tolerate it.

Cooperative breeding: phenomenon by which conspecific individuals form a group to raise offspring.

Dominant: breeding individual in the group, at the top of the hierarchy of same-sex group members.

Errors: decisions that are not optimal for the circumstance, which can result from imperfect decisions systems and/or imperfect information.

Floaters: individuals without a breeding site, living outside of breeding groups.

Helper: any non-parent individual that is in a group and does alloparental care. In this thesis ‘helpers’ is used interchangeably with ‘subordinate’.

Inclusive fitness: sum of the direct and indirect fitness to an individual.

Indirect fitness: direct fitness of all relatives of an individual multiplied by the relatedness of the focal individual to them.

Information: “fitness enhancing resource” about the state of the environment that enables an animal to predict the costs and benefits of its actions and that of others.

Outside option: independent breeding potential outside the group of the subordinate. Outside options can depend on intrinsic factors to the individuals such as reproductive maturity, and on environmental factors such as mate and breeding site availability.

Quality: intrinsic and extrinsic properties of an individual, that influence its reproductive success. Quality is a broad term and for subordinates it can refer to outside option and subordinate efficiency.

Quality-productive coefficient: associations between the subordinate's outside option and group productivity; If high subordinate quality is associated with being a good helper, for instance if both help and quality improve with age, the QPC would be positive.

Reproductive skew: share of the group productivity (e.g. number of offspring) between the dominant and the subordinate(s) of one group. Skew is calculated within one sex. Complete skew means that only the dominant breeder reproduces.

Subordinate: individuals of lower status than dominants; in cooperative breeders, subordinates often are helpers as they provide alloparental care.

Subordinate efficiency: relative ability to reproduce compared to a dominant (1-dominant’s competitive advantage).

Transactional model: models of reproductive skew that assume that the subordinate and the dominant only form a group when the inclusive fitness is higher in the group than alone. In the concession model the dominant has full control over the reproductive share, whereas in the restraint model the subordinate. In both models the subordinate can leave.

Uncertainty: the fact that individuals do not have perfect information and thus cannot perfectly know the state of the world (environmental and social). In modelling, an animal faces uncertainty about a certain factor when it has limited information about it.

Negotiation: the fact that individuals observe their interaction partner and adjust their own behaviour (e.g. parental efforts) as a function of partner’s behaviour. Evolutionary stable strategies are negotiation strategies if individuals evolve response rules instead of fixed efforts.

Chapter 1 – General introduction

Alpine marmots *(Marmota marmota)*

In a variety of social species, certain individuals provide care to young that are not their offspring (Emlen, 1995). These helpers engage in alloparenting whilst forming a group with the dominants (see Glossary for definitions). This phenomenon, known as cooperative breeding, has puzzled researchers for decades, as the genetic advantage of such a behaviour is not obvious. The ubiquity of cooperative breeding sparked lines of research that investigated its evolution and mechanisms (Clutton-Brock, West, Ratnieks, & Foley, 2009; Clutton-Brock, Hodge, Flower, Spong, & Young, 2010; Downing, Cornwallis, & Griffin, 2017; Oi, Wenseleers, & Oliveira, 2021; Shen, Kern Reeve, & Vehrencamp, 2011; Taborsky, Frommen, & Riehl, 2016). Research has established that subordinates receive some direct benefits from taking care of dominants' offspring, as helping can sometimes allow them to reproduce themselves, even if only on rare occasions. From the point of view of a dominant, allowing subordinate to breed reduces their own breeding success. As a result, dominants sometimes have evolved to constrain the reproduction of subordinates, based on subordinate quality and therefore the risk they potentially represent in terms of usurpation and leaving dominants.

In the following review I describe the most prominent theories to explain the evolution of cooperation and reproductive skew (Section 1a), discuss the diversity of cooperative breeders (Section 1b) and outline their different strategies (Section 1c) and the body of theory about them, namely reproductive skew theory (Section 1d). After reviewing the empirical tests of the models of skew (Section 1e), I discuss which assumptions might limit the ecological validity of the current theory. Specifically, models typically lack of variation between individuals (Section 2a) and in environmental conditions (Section 2b), as well as the perfect information (Section 2c), and assume helpful subordinates have high independent breeding options (Section 2d). I show how variation can create uncertainty for the animals when information is limited (Section 2e), which can influence the fitness consequences of decisions in reproductive games (Section 2f). Then, I review the evidence in cooperative breeders for the influence of variation in relatedness (Section 3a), sex differences (Section 3b) and the interaction between sex and status (Section 3c) on reproductive strategies. Finally, I discuss the strengths of combining theoretical (Section 4a) and empirical work to provide insights (Section 4b), before outlining the thesis contents in detail (Section 4c).

1. Cooperative breeders and their reproductive strategies

a. Cooperation and Hamilton's rule

A cooperative behaviour increases the fitness of its recipient (Bergmüller, Johnstone, Russell, & Bshary, 2007). Cooperation occurs in a wide variety of animal groups and even between species (Caves, Green, & Johnsen, 2018; Rasa, 1983; Sharpe, Joustra, & Cherry, 2010). Cooperation is so ubiquitous because it presents many advantages to fitness, such as increases in fecundity and/or survival (Rodrigues & Kokko, 2016). A commonly used measure of fitness is inclusive fitness, defined as the effect of an animal's behaviour on group fecundity weighted by relatedness (Glossary, Grafen, 1984) (although see critiques of inclusive fitness: (Allen & Nowak, 2016; Birch, 2017)).

Inclusive fitness is composed of direct fitness and indirect fitness (Hamilton, 1964a, 1964b). Direct fitness is the animal's reproductive success (Korb & Heinze, 2008) which means the contribution of the individual to the future gene pool. Indirect fitness consists of the direct fitness benefit to all relatives as a result of the help given by the individual, multiplied by the individual's relatedness to them (Mumme, Koenig, & Ratnieks, 1989). Hamilton theorised that relatedness influence when animals should act altruistically, since evolution selects individuals whose phenotype maximises the transmission of all copies of their genes (Grafen, 2009; Hamilton, 1964a). Hamilton's rule predicts that altruism should emerge when the benefit to the recipient multiplied by their relatedness are greater than the costs suffered by the donor.

The evolution of cooperation between non-relatives must be driven by factors other than relatedness (Field & Leadbeater, 2016; Queller et al., 2000; Zöttl, Heg, Chervet, & Taborsky, 2013). If dominants can punish unhelpful subordinates, cooperation can evolve among relatives and non-relatives (Quiñones, Van Doorn, Pen, Weissing, & Taborsky, 2016). Cooperation between non-relatives can also evolve through reciprocity (Barta, McNamara, Huszar, & Taborsky, 2011; Brandl & Bellwood, 2015).

b. Cooperative breeders

In a cooperatively breeding group, subordinate helpers engage in alloparental care, while dominants are the main breeders. Cooperative breeding is widespread in the animal kingdom, observed in 9% of birds (Jetz & Rubenstein, 2011), 1% of mammals (including humans (Kramer, 2010)), 2% of insects, as well as some shrimp (Koenig & Dickinson, 2004; Lukas & Clutton-Brock, 2017; Rubenstein & Abbot, 2017) and fish (Wong & Balshine, 2011). In many species cooperative breeding is facultative, so individuals can either breed solitarily and cooperatively (Du & Lu, 2009; Holman, 2014). For example, carrion crows (*Corvus corone*) form cooperatively breeding groups with a pair and helpers in Spain where territories are held year-round, but only monogamous pairs in Scotland, Germany and Switzerland (Baglione, Marcos, Canestrari, & Ekman, 2002). Cooperative breeding is also facultative in female wood mice (*Apodemus sylvaticus*) and should occur only in harsh environments, with daughters as helpers (Gerlach & Bartmann, 2002). Eusociality is an extreme form of obligatory cooperative breeding with division of labour into fixed castes (Boomsma, Huszár, & Pedersen, 2014), where helpers are typically sterile (Abbot et al., 2011).

The helpers benefit the offspring in a variety of ways (van Boheemen et al., 2019; Woxvold & Magrath, 2005), such as by providing food, baby-sitting and defending the group against predators (César et al., 2009; Konrad, Frasier, Whitehead, & Gero, 2019; Nam, Simeoni, Sharp, & Hatchwell, 2010). Helpers increase the dominants' reproductive success as their alloparental care often offers immediate benefits to the offspring (offspring number: Brand & Chapuisat, 2014; increased total provisioning: van Boheemen et al., 2019), and can also improve offspring's long-term survival (Brouwer, Richardson, & Komdeur, 2012). Helpers can also enable dominants to reduce their own parental care, therefore improving their survival and future reproductive success (Bruintjes, Heg-Bachar, & Heg, 2013; Crick, 1992; Hatchwell, 1999). In return, helpers can benefit from inclusive fitness benefits (Cockburn, 1998a). If helpers are related to the young and increase their fitness, then helpers receive indirect fitness benefits (Roux & Korb, 2004; Russell & Hatchwell, 2001). Helpers may also get direct fitness benefits by having a share in the group's reproduction (Groenewoud et al., 2018; Reeve, Starks, Peters, & Nonacs, 2000a) or eventually inherit the dominant breeding position (Duncan, Gaynor, & Clutton-Brock, 2018; Leadbeater, Carruthers, Green, Rosser, & Field, 2011).

Two key drivers of the evolution and maintenance of cooperative breeding are kinship and ecology (Shen, Emlen, Koenig, & Rubenstein, 2017). The kin selection hypothesis postulates that related helpers get sufficient indirect fitness benefits to stay with dominant breeders (Boomsma, 2009; Hamilton, 1964b; Lukas & Clutton-Brock, 2012b). However, while helpers are typically retained offspring, they sometimes are unrelated to the dominant’s offspring, and theoretical and empirical work has shown the importance of ecology in the evolution of cooperation (e.g., Korb & Heinze, 2008; Nowak, Tarnita, & Wilson, 2010). Individuals forego reproduction and help because such cooperative behaviour grants them benefits of resource defence and/or collective action (Shen, Emlen, Koenig, & Rubenstein, 2017). Subordinates can then get a share of the reproduction, improve their quality before their first independent breeding attempt and/or inherit the dominant’s breeding site. For instance, subordinate clownfish *(Amphiprion percula*) help without getting a reproductive share because dispersing is very risky and they inherit the anemone territory after several years (Buston, 2004).

The share of reproduction between helper(s) and dominants varies considerably between species, even within the same taxonomic family and for similar within-group levels of relatedness (Koenig & Dickinson, 2016). For instance within the Herpestidae, subordinate banded mongooses breed regularly whereas subordinate dwarf mongooses and meerkats rarely breed, despite the high group-level relatedness of these species (Cant, Vitikainen, & Nichols, 2013; Gilchrist, 2006; Griffin et al., 2003; Hamilton, 1964; Hodge, Bell, & Cant, 2011; Keane et al., 1994a; Rood, 1980). Skew sometimes also varies within a species (Keller, 1994). Long-term studies have revealed diversity in the identity and behaviour of the helpers of cooperative breeders (Koenig & Dickinson, 2016).

Depending on the species, dominant cooperative breeders have evolved a variety of proximate mechanisms to ensure high skew and helping. Dominants can punish non-cooperative subordinates with aggression (e.g. *Neolamprologus pulcher*: Fischer, Zottl, Groenewoud, & Taborsky, 2014a) or more extreme measures such as eviction (e.g. clown anemonefish *Amphiprion percula*: Rueger et al., 2018), infanticide (e.g. African wild dog *Lycaon pictus*: Fuller et al., 1992; Malcolm & Marten, 1982) or both (e.g. meerkats *Suricatta suricata*: Clutton-Brock et al., 1998). However, theory predicts the threat of punishment is typically sufficient to prevent subordinates from breeding or not helping sufficiently, so long as the threat is credible – sufficiently threatening to prevent an undesirable behaviour (Cant & Johnstone, 2009; McNamara & Houston, 2002). The threat of eviction causes subordinates to cooperate in at least two fish species (Rueger et al., 2018; Wong, Buston, Munday, & Jones, 2007), but it is not credible in banded mongooses because subordinate females breed (Cant, Hodge, Bell, Gilchrist, & Nichols, 2010). By contrast the threat of infanticide is credible in banded mongoose (Cant, Nichols, Johnstone, & Hodge, 2014). All these proximate mechanisms act to resolve the reproductive conflict between the dominants and subordinates.

c. Reproductive strategies

A strategy is a “genetically determined rule that specifies the action taken as a function of the state of the organism”, where state variable is “any aspect of physiology or any information” that the individual has (McNamara & Leimar, 2020, p14-15). In this thesis, the reproductive decisions of interest include 1) whether to breed alone or cooperatively, 2) whether to help or not, and 3) how to share the reproduction within the group between the dominant and the subordinate (reproductive skew). For cooperative breeding to occur, individuals must decide to form a group and there must be alloparental care. The benefits of cooperative breeding are known to differ between species, due to behavioural differences and environmental factors (Lin, Chan, Rubenstein, Liu, & Shen, 2019). Besides, the partitioning of reproduction varies within and between species of cooperative breeders.

In general, to decide whether to form a group, the animal has a strategy that has evolved to weigh the inclusive fitness of being in the group against the inclusive fitness of being alone. The survival and breeding success as a solitary individual of both dominant breeders and helpers are known as the outside option (Hellmann & Hamilton, 2018; Verhencamp, 1983). These outside options are important in the decisions of cooperative breeders. For instance, if breeding sites are readily available, the helpers may have higher expected inclusive fitness outside the group and thus be more likely to breed independently.

The subordinate decides whether to form a group with a dominant breeder and whether and how much to help the dominant’s offspring. Subordinates with experimentally increased outside options decrease their helping effort (Grinsted & Field, 2017b), but this link has not been considered in the standard models of skew. Dominant breeders will thus value the remaining helpers more, who can demand more to stay and who will be more likely to decrease their effort because their help is a rare supply in the “biological market” (Grinsted & Field, 2017b; Hammerstein & Noë, 2016).

The dominant breeder and subordinate helper decide how to share the reproduction, and the unequal sharing is defined as reproductive skew. Skew influences the benefits to stay, because as skew increases, the direct fitness of the subordinate decreases – but its indirect fitness increases if it is related to the dominant. Disentangling which factors of inclusive fitness, such as relatedness and the outside options, influence skew will help understand the diversity of cooperative breeders’ reproductive games.

d. The three types of reproductive skew model

Reproductive skew theory aims to understand between and within-species variation in the share of reproduction within groups (Verhencamp, 1983). Skew theory builds from kin selection theory and it assumes the dominant and subordinate maximise their inclusive fitness given the decisions of one another (Reeve & Shen, 2013). Models of skew relatedness and ecological constraints, to determine which factors influence group formation and skew (Johnstone, 2000). Transactional models assume that the reproductive share of the subordinate is a reward for the help given by the subordinate (Johnstone, 2000). Different power dynamics and order of decisions are possible. In concession transactional models, the dominant has full control over the reproductive share and “pays” the subordinate to stay and the subordinate decides whether the concession is sufficient to stay and help (Field & Cant, 2009). Conversely, the transactional restraint model assumes that subordinates can reproduce if they choose to and thus have full control over the allocation, and the dominant decides whether to evict the subordinate rather than tolerate the allocation (Johnstone, 2000). Both model types assume that the subordinate has an outside option that affects the decisions and so the skew. The tug-of-war model assumes dominants do not control fully the reproductive share, so both subordinates and dominants decide how much to invest into the competition over reproduction (e.g. aggressive behaviour, ornaments). Skew is determined by mutual competitive abilities and investment, instead of simply by status (Beekman, Komdeur, & Ratnieks, 2003; Hudson Kern Reeve & Shen, 2006).

e. Limitations of the models of skew

Empirical tests of the predictions of the models of skew found mixed within-species support for each type. For instance, in *Polistes* wasps the transactional models are not supported because skew does not correlate with relatedness, and aggression does not correlate with group productivity, relatedness or dominant's competitive advantage (size differences) (Nonacs, 2006).

Because of the complexity of social life, and the need to make models that are mathematically tractable, skew theory has developed in several directions, leading to a plethora of models which rely on different assumptions, with no consensus on which factors influence skew (Johnstone, 2000a; Kokko & Johnstone, 1999; Nonacs & Hager, 2011; Reeve & Shen, 2013; Sachs & Rubenstein, 2007; Shen & Reeve, 2010). Often when data match theoretical predictions, several mechanisms are possible (Magrath & Heinsohn, 2000). Current models may fail to make accurate predictions because of their over-simplification of animals' lives, prompting the need for more holistic, richer models (McNamara, 2013).

Whilst exploring the effect of different factors was informative (Reeve & Shen, 2013) the high number of models of skew has arguably contributed to the confusion over which predictions should be tested (Nonacs & Hager, 2011). Successive refinement and synthesis of skew theory that combines the concession, restraint and tug-of-war models, have been proposed (Johnstone, 2000b; Reeve & Shen, 2013; Shen & Reeve, 2010). However, claims that the tug-of-war is the only relevant model have persisted (Nonacs, 2010; Nonacs & Hager, 2011). A synthetic model predicts the occurrence of each type of model in different situations (Shen & Reeve, 2010) but requires as yet unavailable data to be tested (Reeve & Shen, 2013). Theoretical research focusing on the yet overlooked factors and their interactions, combined with detailed empirical studies that determine all the factors (and not only two predictors from the original models) will further understand social evolution with skew theory (Reeve & Shen, 2013).

2. Unrealistic assumptions of skew models: incorporating variation and uncertainty

Current models of skew (and cooperative breeding) might fail to generate useful predictions because they assume 1) identical individuals, 2) a fixed environment and 3) perfect knowledge.

The variation of the environment, both social and non-social, is a crucial feature of an animal's life and incorporating variability can dramatically alter model predictions (Kokko, 2003; McNamara, 2013). For instance, previously unexplained cognitive biases are predicted by theory incorporating complex environments with spatiotemporal heterogeneity and autocorrelation (Fawcett et al., 2014). Some of the empirical variation in female choosiness was explained by incorporating uncertainty about male quality influenced the level of choosiness, with an increase under high imperfect information and a decrease under low information compared to perfect information (Dechaume-Moncharmont, Brom, & Cézilly, 2016).

a. Identical Individuals

Individual variation refers to differences between animals of the same species. Individual variation occurs in traits that are typically fixed in models, such as sex, or variable, such as social status, age or hunger state. These traits can lead to differences in the costs and benefits of a given cooperative behaviour, which predicts that individuals may develop different evolutionarily stable strategies (McNamara, 2013). Evolutionary game theory can incorporate interindividual variability if individuals of a given type do not have identical fixed strategies. Theoretical research predicts that variation in behaviour leads to cooperation in a two-player game, the Prisoner's Dilemma (McNamara et al., 2004). Recent models suggested that variation between individuals may have played a major role in the evolution of cooperation (McNamara, Barta, & Houston, 2004b; McNamara & Leimar, 2010). Adding the richness of individual variation will therefore paint a more accurate picture of group dynamics.

Unexplained variation in cooperative behaviour may be understood if we investigate more closely different aspects and causes of individual variation (English, Kunc, Madden, & Clutton-Brock, 2008; Jeanson & Weidenmüller, 2014; Le Vin, Mable, Taborsky, Heg, & Arnold, 2011; McNamara, Barta, & Houston, 2004; Sih & Del Giudice, 2012). For instance, meerkat (*Suricata suricatta*) males and females differ in their cooperative behaviour (English et al., 2008), although there is still consistent interindividual variation (English, Nakagawa, & Clutton-Brock, 2010). In a cooperatively breeding cichlid and meerkats, individual identity predicted more than relatedness the quantity and type of cooperative behaviour (Clutton-Brock et al., 2001; Le Vin, Mable, Taborsky, Heg, & Arnold, 2011a). Interindividual variation in behaviour relies on proximate mechanisms and has ultimate consequences as variability in group members can influence group productivity (Jeanson & Weidenmüller, 2014b). Empirical research on the costs and benefits of interindividual variation in behaviour on group productivity is only beginning (for a review in insects, see Jeanson & Weidenmüller, 2014). While much is known of the causes of individual variation (Stamps & Groothuis, 2010), its consequences are less clear (McNamara, 2013).

b. Environmental conditions

Influences of the environment on cooperative breeders may include the biotic (e.g. mates, predators) and abiotic factors (e.g. temperature, rainfall) (Emlen, 1982). Harsh environments can reduce subordinates' outside options whilst decreasing dominant solitary fitness, consequently selecting for cooperative breeding. The ecological constraint hypothesis (Emlen, 1982) posits that limited subordinate outside options reduce the benefits of breeding independently, which selects for cooperative breeding. For instance, marmots' (*Marmota marmota*) maturation and dispersal are delayed in harsh environments (Blumstein & Armitage, 1999). Dominant meerkats are more likely to evict subordinates when food is abundant (Dubuc et al., 2017). When resources are scarce, dominant individuals may inhibit subordinates' reproduction and access to food (banded mongoose *Mongos mongo*: Nichols et al., 2012a), and nonbreeding individuals may decrease their investment in helping behaviour (Nichols et al, 2012b). Meerkat helpers buffer the reproductive success of dominants when food availability is low (Groenewoud & Clutton-Brock, 2021).

Variation in environmental conditions has been incorporated differently in various models of cooperative breeding, without being the main focus (Härdling, Kokko, & Arnold, 2003; Kokko & Lundberg, 2001; Kokko, Johnstone, & Wright, 2002; MacColl & Hatchwell, 2002). The environmental condition influences subordinates' outside options, and thereby their reproductive strategies. Several models incorporated variation in subordinate outside options as variation in the probability of successful solitary breeding (Kokko & Johnstone, 1999; Kokko, Johnstone, & Clutton-Brock, 2001), but also varied mortality rate as a function of status (Kokko et al., 2001). By contrast, Kokko & Lundberg (2000) and Nonacs (2019) compared environments with different territory density (breeding site availability) (Kokko & Lundberg, 2001; Nonacs, 2019). Another model also considered variation in the ecological constraints via habitat saturation and competitive abilities that depend or not on the status (Kokko & Ekman, 2002). The ecological conditions emerged in another model, as the number of individuals without breeding site ('floaters') evolved (Kokko & López-Sepulcre, 2006).

Theory predicts environmental stochasticity *per se* can drive the evolution of cooperation (Kennedy, Higginson, Radford, & Sumner, 2018; Shen et al., 2017). Cooperative behaviour appears to be a mitigating strategy that compensates for the less productive years, as animals shield their families from unpredictable environments – cooperative breeding enables to get the edge on competitors in harsh environmental conditions, even if it reduces competitiveness in favourable conditions (Kennedy et al., 2018). When food and breeding site availability are highly variable, cooperative breeding decreases the variation in breeders' reproductive success (Kokko, López-Sepulcre, & Morrell, 2006; Rubenstein, 2011). Spatial and temporal environmental variation can select for cooperative breeding in different types of environments. Indeed, empirical proof is establishing the specific role of environmental variation in the evolution of cooperative breeding (Koenig & Dickinson, 2016; Lin et al., 2019; Sheehan et al., 2015).

c. Perfect information

Incorporating variation modifies theoretical predictions regarding cooperation. Previous models predicted that under perfect information and no individual variation, cooperation should not evolve. In a repeated prisoner's dilemma game varying the number of rounds to cooperate, adding a probability of mutation low mutation probabilities select for defection, but above a threshold of high mutation probability, cooperation evolves (McNamara et al., 2004a). Besides, variation can create uncertainty. When individuals make errors regarding their own contribution creates individual variation in cooperative effort (Ito, McNamara, Yamauchi, & Higginson, 2016). When animals make errors, negotiation can select for runaway evolution of very high levels of cooperation (Ito et al., 2016).

Adding complexity to skew models is necessary to gain further insight into the evolution and mechanisms of cooperative breeding, as current conflicting theories fail to account for the diversity within- and between species (Akcay, Meirowitz, Ramsey, & Levin, 2012; McNamara, 2013; McNamara & Leimar, 2010; McNamara, Stephens, Dall, & Houston, 2009; Nonacs, 2019b).

d. Association between subordinate outside option and their help: quality-productivity coefficient

Subordinate individual quality is their independent breeding success outside of the group (i.e. outside option). Potential helpers can vary in their quality, but also in their effect on group productivity (Table 1.1). Tug-of-war models of skew implicitly assume that subordinate quality and their potential as breeders correlate positively with the benefit they provide to the group (Reeve, Emlen, & Keller, 1998). In transactional models of skew, subordinate quality is independent from their effect on group productivity (Verhencamp, 1983), but variation in the link between these variables has to my knowledge not been thoroughly explored. Subordinates with high outside options can be good *or* bad helpers. Indeed, while in most species subordinate size or age increase both outside options and helping effect, some cooperatively breeding species show divergent ontogenic trajectories whereby an individual becomes a helper or a breeder (Fischer, Bohn, Oberhummer, Nyman, & Taborsky, 2017; O'Riain, Jarvis, & Faulkes, 1996). In this case, the subordinate's outside option may correlate negatively with their helping contribution. This may explain the failure of models to predict the diversity of skew. Individual quality is the outside option in transactional models and the relative efficiency of subordinates in the competition in tug-of-war models.

Since in the tug-of-war model any competitive effort to increase one’s reproductive share reduces group productivity, we hypothesise it may be useful to explore variation in the link between the subordinate help and quality. This may help to bridge the gap between the original predictions of skew and diversity of cooperative breeders’ reproductive strategies. Shen et al (2011)'s model explores the effects of dominant and subordinate asymmetric costs of producing young on skew, where the parental care efforts are independent from the reproductive effort and the parental care costs are shared. Contrarily to what was expected from previous “costly young” models, individual care to the offspring is not necessarily positively correlated with reproductive share. These findings suggest some variation in the link between the cooperative efforts and reproductive share. The link between the effect of subordinate on group productivity and their outside option is likely to depend on social and environmental factors (Table 1.1).

Differences between taxa in the link between subordinate quality and help might underpin their behavioural differences (Table 1.1). A recent study (Lin et al., 2019) found support for two evolutionary pathways to cooperative breeding. In starlings (Sturnidae) cooperative breeding evolved through year-round defence of a valuable territory in favourable stable environments. In hornbills (Bucerotidae) cooperative breeding evolved through delayed dispersal in a harsh unstable environment. Depending on the way a species uses its environment to reproduce, helpers may be more or less beneficial (or detrimental) in a favourable stable environment. This shows that between-taxa variation in cooperative breeders can be explained by biological and behavioural differences, and suggests that an ecological factor in the same state (e.g., favourable environment with high food availability) can select or not for the evolution of cooperative breeding (i.e., shape differently the reproductive strategies). This difference in response to a same environmental condition may be associated with differences in the benefits and costs of breeding cooperatively. For instance, hornbill subordinates might provide little or no benefit to the group productivity in good environments, whereas starlings might be good helpers. Indeed, starling helpers do give multiple benefits, as superb starlings mothers with helpers get higher survival and reproductive success and reduce their caring efforts (Guindre-Parker & Rubenstein, 2018).

Table 1.1: Predictions of the effects of biological factors on helpers' quality-productivity coefficient (QPC). Factors correlate (+) positively or (-) negatively with QPC.

Biological factor	***QPC***	**Explanation**	**Species known to display this variation**
Food abundance	**+**	Lower competition, so low quality individuals can access the energy and resources required to help (Bruintjes, Hekman, & Taborsky, 2010a).	Carrion crow *(Corvus corone)* (Canestrari, Chiarati, Marcos, Ekman, & Baglione, 2008) ; Daffodil cichlid (*Neolamprologus pulcher*) (Bruintjes et al., 2010a) ; Meerkats (*Suricata suricatta)* (Clutton-Brock et al., 2001)
Food acquisition difficulty (skill)	**-**	High quality subordinates are more skilled and thus have more energy to help.	Within-species *S. suricatta* (Clutton-Brock et al., 2001). Between-species, test if higher effect of helpers in social insects and meerkats than species like herbivores where foraging requires less skill.
Nest availability	**-**	Less incentive to help, since breeding is more available. Dominants can choose among fewer subordinates (Grinsted & Field, 2017).	Paper wasp *(Polistes dominula)* (Grinsted & Field, 2017b)
Predation risk in pay-to-stay species	**+**	Higher investment in helping since the benefit of group security is more valued (Dutour, Lena, & Lengagne, 2016; Sandoval & Wilson, 2012), although better quality individuals may survive better (Kokko & Lundberg, 2001).	*N. pulcher* (Heg & Taborsky, 2010)

Rank (Short time before dominant breeder status)	**-**	Decrease helping when their outside options increase (Zöttl, Chapuis, Freiburghaus, & Taborsky, 2013).	*N. pulcher* (Zöttl, Chapuis, Freiburghaus, & Taborsky, 2013).
		Lower ranking helper should work harder (Cant & Field, 2005).	*S. suricatta* (Cant & Field, 2005).
Specialisation into helper or breeder	**-**	Dominants prefer helpers with low outside options linked to high helping quality.	Among different social insect species with varying specialisation (Dall, Bell, Bolnick, & Ratnieks, 2012). Specialised phenotypes in vertebrates: *N. pulcher* (Fischer et al., 2017); Naked mole rats (*Heterocephalus glaber*) (O'Riain et al., 1996)
Group size	**-**	Less help per individual as group size increases since effort is split among subordinates (Härdling et al., 2003; Savage, Russell, & Johnstone, 2015) (Härdling et al., 2003). Resource depletion and reproductive competition (Komdeur, 1994).	*S. suricata* (Clutton-Brock et al., 2001); Paper wasps (*Polistes dominula*) (Grinsted & Field, 2018a). Seychelles warblers (*Acrocephalus sechellensis*) (Komdeur, 1994).
Strength of behavioural syndromes	**+**	Bolder individuals show faster growth, higher reproductive rates and engage in riskier cooperative behaviours (e.g., cooperative defence).	*N. pulcher* (Le Vin et al., 2011b).

e. Variation in the world can create uncertainty

As individual and environmental variation affect the costs and benefits of actions, it is necessary to acquire information which has been defined as a “fitness enhancing resource” (McNamara & Dall, 2010, p231). Animals rarely have perfect information as their world is complex and changes spatially and temporally. Natural selection thus shapes cognitive systems to make decisions based on limited information. Variation produces uncertainty, which typically select for a sub-optimal strategy(McNamara, 2013). Empirical evidence abounds about the errors that animals make (Chittka, Skorupski, & Raine, 2009; Preece & Beekman, 2014), which can stem from imperfect decisions systems (errors even with accurate information) but also from imperfect information (McNamara, Webb, Collins, Székely, & Houston, 1997; Mesterton-Gibbons & Heap, 2015).

Any parameter used to assess some information about a conspecific will be subject to a certain amount of error (McNamara et al., 1997). The probability of making an error is likely to be negatively correlated with its fitness cost, due to natural selection acting to minimise costs (McNamara et al., 1997). Incorporating imperfect information can be done by allowing a certain proportion of the decisions to be suboptimal from the perspective of the focal individual (errors), or letting the information to be imperfect (Trimmer et al., 2008).

Theory predicts that information modulates behaviour in several contexts (Dall & Schmidt, 2010). A theoretical study examined how predator-prey population dynamics are influenced by imperfect information about predation risk and flexible prey behaviour (Luttbeg & Schmitz, 2000). For instance, if preys had perfect information about predation risk, both the prey and the predator survived more seasons than if preys learnt about predation risk through experience. Uncertainty also changes the predictions of the ideal free distribution because imperfect information decreased the attractiveness of high-quality patches when foragers did not have to always move between patches (Matsumura, Arlinghaus, & Dieckmann, 2010). In a social game, adding individual variation led to two different evolutionary stable outcomes, depending on the amount of individual variation, instead of a frequency-dependent (unstable) prediction (McNamara et al., 2004a). Indeed, between-individual variation in the number of rounds of the repeated prisoner’s dilemma selects for high levels of cooperativeness above a threshold in variation (probability of mutation). With low variation, however, cooperation does not evolve because the optimal strategy is to defect in the first round.

f. Imperfect information in models of skew and cooperation

Theory has shed light on the effect of individual quality on the reproductive strategies, but typically focused on the individual and environmental traits and overlooked the perceptive mechanisms through which individuals assess these traits (McNamara & Houston, 2009). Most models of reproductive skew and cooperative breeding implicitly assume perfect information about other individuals (e.g. relatedness, competitive abilities, reproductive investment, helping effect) and the environment (e.g. own and others' outside options, breeding site availability). For instance, the subordinate efficiency tug-of-war model predicts that the optimal reproductive skew should depend on the relative competitive advantage of the subordinate and the dominant, but it implicitly assumes that both individuals have perfect information about this relative competitive ability (Reeve, Emlen, & Keller, 1998). Transactional models predict skew varies with relatedness, but implicitly assume perfect kin recognition and perfect information about outside options (e.g. Verhencamp, 1983). Cooperation only evolved when individuals could use this information (Holman, 2014). As it is unrealistic to assume perfect information (Fawcett et al., 2014), new models where individuals can make errors are more likely to predict strategies more accurately (Higginson, Fawcett, Houston, & McNamara, 2018).

Two models predicted that imperfect information about the benefit of staying in the group (inside option) (Kokko, 2003) and the outside option of the cooperative partner (Akcay et al., 2012) prevent the evolution of cooperation. Kokko (2003) found that if subordinates lack perfect knowledge about their benefit of staying in the group in a transactional model of skew, there is no evolutionary stability. Changes in subordinates' reproductive strategies may occur over evolutionary times, and not behavioural times (Kokko, 2003). This means subordinate's threshold of departure should not respond to any particular dominant, which implies that a dominant may cheat by sharing less reproduction than is required by the subordinate. Akcay et al (2012) modelled uncertainty in the outside options of the potential partner, and assumed symmetrical information for the two roles. However, it is not well-understood how asymmetric information about the outside options of the subordinate may influence the reproductive games of cooperative breeders, and more specifically the predictions of a model of skew. It remains unclear which key factors provided sufficient benefits to individuals to select for cooperative breeding, as theoretical models of imperfect information have to my knowledge not explored this.

3. Empirical evidence of variation in cooperative breeders

a. Variation in relatedness

In most cooperatively breeding species, helpers typically stay in their natal group (Boomsma, 2009; Koenig & Dickinson, 2016; Wikberg et al., 2022), which means dominants' offspring are their siblings. However, not all helpers are relatives (Kaiser, Martin, Oteyza, Armstad, & Fleischer, 2018; Koenig & Dickinson, 2016), and variation in relatedness might influence helping efforts and skew. In Arabian babblers (Timalidae: *Turdoides squamiceps*) the only male subordinates that reproduce are those unrelated to the dominant, showing an interaction between status and relatedness (Lundy, Parker, & Zahavi, 1998). Similarly in the chestnut-crested yuhina (*Yuhina everetti*) only unrelated helpers can breed, while variation in relatedness does not influence provisioning rates (Kaiser et al., 2019). Across thirty-six cooperatively breeding birds, between-species variation in relatedness between helper and the group's offspring explains variation in their provisioning rate (Green, Freckleton, & Hatchwell, 2016). Indirect fitness benefits seem to drive subordinates closely related to the offspring to provision at higher rates that less related subordinates (Green et al., 2016; Nam et al., 2010), which suggests that variation in relatedness drive subordinates closely related to the offspring to help more. For instance, an experiment showed that long-tailed tit *(Aegithalos caudatus)* failed breeders preferred to help kin than nonkin (Russell & Hatchwell, 2001). However, little is known about the reproductive strategies of potential subordinates with various relatedness to the dominants in other taxa, and mathematical models may provide theoretical insights.

b. Variation in reproductive strategies between females and males

Males and females can evolve sex differences in life history, such as dispersal (Clutton-Brock et al., 2002; Koenig & Dickinson, 2016; Torrents-Ticó, Bennett, Jarvis, & Zöttl, 2018) or the quantity of help given (Downing, Griffin, & Cornwallis, 2018). Sex differences in the costs of reproduction due to anisogamy (Iyer, Shukla, Jadhav, & Sahoo, 2020) and to unequal parental care may select for sex differences in the reproductive strategies (Scantlebury, Russell, McIlrat, Speakman, & Clutton-Brock, 2002). Sex is therefore an overlooked factor of variation for skew theory.

The impact of sex differences on skew has not yet been explored. A study combined field and theoretical work to focus on female meerkat reproductive strategies and conflict resolution (Cram, Jungwirth, Spence-Jones, & Clutton-Brock, 2019). It predicted that reproductive suppression of subordinate should evolve because dominant females have higher outside options and breeding potentials than the subordinate females. However, this study did not include the possibility that presence of another sex may change the predictions of the skew models where there are typically one dominant and one subordinate of one sex, because the tug-of-war in one sex may impact group productivity for both. Some species show sex differences in breeding site availability because one sex only has to find a site, whereas the other sex needs to find a site and partner (Arlt & Pärt, 2008). The amount of intrasexual reproductive conflict – competition between dominant and subordinates over reproductive share – can differ between males and females (Berger, Lemaître, Allainé, Gaillard, & Cohas, 2018; Clutton-Brock, 2009; Clutton-Brock et al., 2006; Nelson-Flower et al., 2013), prompting the need to study effect of sex difference in subordinate competitive ability on the reproductive strategies.

c. Variation in sex and status is linked to variation in cooperative behaviour

Due to sex differences in the reproductive costs, evolution can shape different male and female behavioural strategies and traits, such as parental care (Ewald, McNamara, & Houston, 2007). For instance, males can evolve signals of quality for sexual selection (e.g. gorilla chest drumming) (Andersson, Ornborg, & Andersson, 1998; E. Wright et al., 2021) whilst females evolve a specific means to care for the young (e.g. mammalian lactation) (McNamara & Wolf, 2015; Schai-Braun, Steiger, Ruf, Arnold, & Hackländer, 2021). Similarly, sex differences in cooperative behaviour may evolve if being a dominant breeder, or a subordinate, is associated with sex specific costs and benefits.

In most cooperative breeders, only one sex is philopatric (Koenig & Haydock, 2004), which creates sex differences in subordinate direct fitness in the natal group as a subordinate co-breeder or later as dominant breeder (Clutton-Brock et al., 2002; Woolfenden & Fitzpatrick, 1978). The sex who is less likely to breed is selected to help more, such as banded mongoose subordinate males (Cant, 2003). Cross-species comparisons in birds suggest that future breeding opportunities in the natal group are associated with sex differences in the benefits of cooperation, with the philopatric sex helping more (Downing et al., 2018); The stronger the sex difference in future reproduction, the stronger the sex difference in helping efforts (Downing et al., 2018). Furthermore, the sex with the lowest reproductive skew (i.e. where subordinates are more likely to breed) helped more, suggesting immediate direct fitness benefits are associated with cooperation (Downing et al., 2018). Only the philopatric sex may inherit the nest once the same-sex dominant dies, so only the philopatric sex benefits from future direct fitness. Overall, when there were sex differences in the direct benefits (either immediate or future) within the natal group, the sex with the highest potential benefit invested more helping effort (Downing et al., 2018).

Female and male may have evolved differences in dominance-specific traits due to sex differences in life history. Dominance status can be associated with a constellation of status-based differences, such as skew, hormones and aggressiveness (Abbott, 1984; Aubin-Horth, Desjardins, Martei, Balshine, & Hofmann, 2007; Awde, Skandalis, & Richards, 2020; Cohas et al., 2018; Liao, Rong, & Queller, 2015; O'Riain, Jarvis, Alexander, Buffenstein, & Peeters, 2000). High reproductive skew may be explained if the reproductive costs, benefits and power change when the individual becomes a dominant. In species where breeding is more costly in one sex than the other, and both sexes are as related to the young, cooperative behaviours may evolve specifically in the other sex, as predicted by the parental games (Houston & Davies, 1985). High skew might select individuals with high reproductive costs to contribute more to offspring care as helper than as a dominant breeders. Consequently, individuals may adjust rapidly their cooperative behaviours once they become dominant, but the temporal scale of such changes is yet unclear. It is not well-understood how status and sex contribute to shaping the cooperative contributions.

4. Theoretical and empirical approaches to determine which factors influence cooperative breeders' reproductive games

In order to study the influence of variation and uncertainty in different factors on the reproductive strategies of cooperative breeders, this thesis combines theoretical and empirical approaches.

a. The strength of modelling

In behavioural and evolutionary ecology, modelling consists of putting a research question about a phenomenon into equations, then solving them to predict which behaviours should evolve (Kokko, 2007). To build useful models, it is important to identify which of the innumerable factors matters more for the phenomena under study. The precise mechanisms underpinning behaviours are rarely included in models that focus on the evolution of strategies.

A key theoretical approach used to study the ultimate function of cooperation is evolutionary game theory (McNamara & Leimar, 2020). Evolutionary game theory considers that animals take optimal decisions to maximise their fitness and use strategies to respond to the phenotypes of others. Strategies are an evolving set of rules or phenotypes used as a function of the situation (state and environment). For instance, in a mate choice game, the strategy was the optimal choosiness and it varied with quality (Chevalier, Labonne, Galipaud, & Dechaume-Moncharmont, 2020). Natural selection drives the evolution and maintenance of the strategies that give the highest fitness in a given environment. When individuals with an alternative mutant strategy become more frequent than the resident strategy, the mutant strategy is said to invade the population. Evolutionary game theory thus captures the interactions and decision making that lead to Evolutionary Stable Strategies (ESS). An Evolutionary Stable Strategy (ESS) is the optimal strategy, in that it cannot be invaded by any other strategy, and it can invade other strategies (Smith & Price, 1973). Several ESS can exist, and their occurrence/evolution will depend on the values of different factors (i.e. parameter space), such as individual quality or relatedness.

Three main benefits of theoretical works are to 1) create new theories that generate surprising insights, 2) formalise verbal arguments which can show whether they make sense mathematically, and 3) make clear testable predictions to take to the field (Dornhaus, Smith, Hristova, & Buckley, 2022). These predictions can also help understand which factors influence the variable of interest, and which should be empirically collected. Theoretical findings can lead to paradigm shift – for instance Hamilton's rule helped understand the evolution of altruism (Hamilton, 1964).

b. *Combining theoretical and empirical studies to move the field forward*

Combining theoretical and empirical research offers many benefits and improves the understanding of biological phenomena (Dornhaus et al., 2022). Theoretical research provides a strong foundation upon which to ask research questions. Some questions are direct rigorous empirical tests of the predictions generated by the models. When empirical data does not support the prediction of the model, such as transactional models of skew in paper wasps *Polistes* (Nonacs, 2006), it refutes the processes of the model. These rejections of the prediction are particularly useful as they mean that the model fails to capture the biological phenomena, and new models can tackle the research question. Empirical studies can also improve biological realism, for example fitting evolutionary simulations to the data of two mongoose species with high and low skew enabled to predict that skew increases the rate of natural selection (Akman, Hrozencik, & Mowry, 2016). An integrative approach may clarify thorny questions regarding the reproductive strategies of cooperative breeders (Bshary & Bergmüller, 2008; Dornhaus et al., 2022).

c. *Thesis aims and outline*

This PhD project aims to investigate the function and diversity of cooperatively breeding behaviour and to integrate empirical evidence and theory on both vertebrate and invertebrate cooperative breeders (Fawcett et al., 2012; Higginson et al., 2018;

McNamara & Houston, 2009). The main goal is to understand which factors influence the reproductive strategies of cooperative breeders.

To better understand variation in skew and in cooperative behaviour in cooperative breeders, both within and between species, we incorporate different types of variation. First, we investigate the effect of the link between the help provided the subordinate and its outside option when subordinates vary (**Chapter 2 and 3**). Second, we conduct a meta-analysis to test the link between relatedness and skew (**Chapter 2**). Third, we focus on the effect of information by extending the concession model with uncertainty about relatedness and subordinate quality (**Chapter 3**). Fourth, we explore sex differences by developing a sex-based model of skew where investment into the intra-sexual reproductive conflict reduces group productivity (**Chapter 4**). We also test empirically the existence of a sex difference in a costly and non-costly cooperative behaviour (**Chapter 5**). The thesis ends with a discussion of the findings in light of the literature (**Chapter 6**). Below are more details.

Chapter 2 consists of simple models of skew and a meta-analysis. We extended the concession, restraint and tug-of-war models of skew, by varying the link between subordinate quality and group productivity (QPC), which showed that the predictions differed between QPC>1 and QPC<1. This finding suggests that the link between group productivity and subordinate quality influences the reproductive strategies. I conducted a meta-analysis to determine the effect size of the link between skew and relatedness and match the empirical tests to the new predictions.

Chapter 3 investigates how limited information about subordinate quality or relatedness might influence 1) the optimal reproductive skew, 2) the prevalence of cooperative breeding in the population, and 3) the characteristics of helpers accepted by dominants. Subordinates likely have better information than dominants about the fitness benefit the subordinate will get outside the group and provide to the group, leading to information asymmetry about subordinate quality. Therefore, this chapter investigates the effect of various levels of information about subordinate quality on the reproductive strategies. Relatedness shapes cooperation according to kin selection, and the concession model of skew predicts skew should decrease with the relatedness to the helper. Consequently, we systematically varied the level of dominant uncertainty about subordinate relatedness to predict its influence on the reproductive strategies.

The model predicts that high levels of information about subordinate quality, but high uncertainty about subordinate relatedness should evolve. Indeed, related subordinates are selected to not show their relatedness to get a higher reproductive share.

This introduction (**Chapter 1**) has highlighted the need to disentangle the different social and ecological factors that underpin variation in cooperative breeding. **Chapter 4** tests the effects of having two sexes and sex differences in nest availability and subordinate competitive ability on reproductive strategies, by combining the skew games with a parental effort game. This is important because the mixed findings and variation of skew might be explained by the existence of two parallel skew games and by individual variation due to sex differences in life history. Despite an increasing emphasis on the need to combine several games (McNamara, 2013), the predictions did not change, which suggests that male and female skew games can be studied in isolation.

As individuals become breeders and dominants, their expected fitness changes, and the benefits to invest in cooperative behaviour that benefit adult group members may vary. **Chapter 5** investigates empirically how females and males vary a costly and a non-costly cooperative behaviour just before and after becoming dominants. A detailed long-term data collection in a wild population of dwarf mongooses (*Helogale parvula)* explores the short-term and fine scale variation in behaviour, by analysing the interaction between sex, status and environmental quality. The study found a temporary difference in the costly cooperative behaviour in the second fortnight following dominance acquisition.

Chapter 6 summarises the key findings, puts them into perspective and highlights potentially fruitful avenues for research.

Chapter 2 – Tests of reproductive skew theory: a review and prospectus

Long-tailed tit (*Aegithalos caudatus*)

Abstract

Reproductive skew refers to the unequal partitioning of reproduction by same-sex members of a social group. The concession, restraint and tug-of-war skew models attempt to predict which social and ecological factors influence skew, whilst assuming different power dynamics and making contrasting predictions. The factors underpinning within-species variation in skew remain unclear, despite decades of research. Individuals vary in both the benefit of leaving the group to breed (outside option) and in the contribution they make to group productivity if they stay. Variation is likely among several aspects of individual quality, so that individuals and species may show different associations between the subordinate's outside option and group productivity. Yet, no existing skew models allow for variation in this association, here named the quality-productivity coefficient (QPC). If high subordinate quality is associated with being a good helper, for instance if both help and quality improve with age, the QPC would be positive. If, instead, there is a trade-off or other contrast between breeding ability and helping effect, then the QPC will be negative. Here, we incorporate the QPC and derive new predictions for the concession, restraint and tug-of-war models, that sometimes changed their predictions. We review the empirical tests of the association of skew with relatedness, dominant’s competitive advantage, group productivity and subordinate’s outside option. From 16 studies available to calculate an effect size, relatedness correlated positively with skew; yet overall most of 45 studies reported no association. The association of skew with the outside option was negative or null, fitting the restraint and tug-of-war models. The mostly non-significant effect of group productivity supported the three models. Our review highlights future fruitful avenues for the study of cooperative breeding, especially more work to assess the association between subordinates’ outside options and their effect on group productivity.

Introduction

Cooperative breeding is when the parents are not the only caregivers of infants (Cockburn, 1998b). Ecological and social factors shape the evolution of cooperative breeding (Boomsma, 2009; Dillard & Westneat, 2016; Field & Cant, 2009; Lin et al., 2019), as they influence the inclusive fitness associated with cooperation and solitary breeding (Johnstone 2000). In cooperative groups, dominant individuals tend to monopolise reproduction to some extent, leading to reproductive skew: the unequal partitioning of reproduction by same-sex members of a social group (Verhencamp, 1983).

Variation in skew and helping among cooperative breeders has long been a subject of research into how animals decide whether – and to what extent – to help and to breed (Koenig & Dickinson, 2016). Models of reproductive skew seek to understand how individuals should divide up reproduction (Johnstone, 2000; Verhencamp, 1983). Three main types of skew models have been developed: the concession, restraint and tug-of-war models (Table 2.2). In the two transactional models − restraint and concession models − individuals can leave the group and so subordinates could breed on their own (i.e. they have an "outside option"). In the concession model, the dominant concedes a certain amount of reproduction to the subordinate and the subordinate decides whether to stay and help, whereas in the restraint model the subordinate restrains themselves to a certain amount of reproduction and the dominant decides whether to evict them from the group. In the tug-of-war model, individuals engage in a competition over the share of reproduction which is determined by their investment in the competition and their relative competitive ability.

The concession model predicts that skew should correlate positively with the relatedness between the subordinate helper and the dominant's offspring, as subordinates get more indirect fitness benefits and therefore require a lower reproductive share to stay than unrelated subordinates (Reeve & Ratnieks, 1993) (Table 2.2). By contrast, the restraint model predicts that skew should correlate negatively with relatedness, as related dominants can afford to share a higher proportion with the subordinate since they will get higher indirect fitness benefits than with an unrelated subordinate (Keller & Reeve, 1994; Reeve & Ratnieks, 1993). The tug-of-war predicts no association between skew and relatedness (Reeve & Keller, 2001; Reeve, Emlen, & Keller, 1998) (Table 2.2).

To test the predictions of skew models using empirical data, researchers have focussed on three factors that influence the benefits and costs of cooperative behaviours (Hellmann & Hamilton, 2018; Ragsdale, 1999; Reeve & Emlen, 2000): (i) genetic *relatedness* between dominants and subordinates; (ii) subordinate's *outside option*, which may depend on intrinsic quality or environmental conditions such as nest site availability and (iii) the dominant's *competitive advantage* which may depend on relative individual qualities or a status-related factor such as coalitional support from others. We may discern patterns of skew by investigating a wide range of associations in empirical tests (e.g. Langer, Hogendoorn, & Keller, 2004; Lu, Wang, & Du, 2012), that include the critical factors included in models of reproductive skew (Johnstone, 2000; Verhencamp, 1983), in both within- and between-species tests.

Reviews of many tests have suggested that relatedness does predict skew across species, in birds (Riehl, 2017), *Polistes* wasps (Liebert & Starks, 2006; Nonacs, 2006), and other taxa (Nonacs & Hager, 2011). However, these reviews did not use effect sizes but relied on counting the number of positive, negative and null effects. The empirical tests of skew in all species were last reviewed 10 years ago (Nonacs & Hager, 2011) and despite numerous more recent empirical tests, within-species variation in skew is not well understood. A new review focussing on effect sizes would quantify, hence potentially clarify, the link between skew and relatedness.

Our review is non-exhaustive partly because the data are so patchy, so we do not aim to unambiguously assign each taxa to supporting one model of reproductive skew. We also acknowledge that it may not be possible in many cases given that the concession, restraint and tug-of-war models may actually represent different facets of a continuum of reproductive strategies (Johnstone, 2000).

That said, our aims herein are: (1) to provide an update and a summary of the three types of model of reproductive skew and their predictions, including predicting when there will be non-significant effects; (2) determine whether particular taxa support particular models which would indicate that we can understand the selective pressures; and (3) to identify gaps in the literature of empirical tests to help target future research.

Predictions of reproductive skew models

Incorporating the quality-productivity coefficient

Here, we introduced a link between the subordinate's outside option - assumed to perfectly correlated with intrinsic quality - and the benefit they provide to the group productivity, named the quality-productivity coefficient (QPC). A negative QPC means that a subordinate either has high outside option or is very helpful to the group. For a positive QPC, the higher the QPC, the more subordinate outside option shapes group productivity.

Here, we describe how we refined the standard three models. Note that we standardised the parameter symbols, so they do not all match those of previous presentations. The dominant and the subordinate share a symmetrical relatedness r, the subordinate quality is x, the proportion of reproduction that is by the subordinate is y, and k is group productivity (Johnstone, 2000), (Table 2.1). In the concession model, the minimum proportion of reproductive share that a subordinate will accept to stay in the group and not breed independently is defined as y_{min} (Johnstone, 2000). We extended the simple tug-of-war model (Reeve et al., 1998a). We used the subordinate efficiency in converting resources into reproduction as a proxy for subordinate outside options (quality) (Johnstone, 2000), whilst keeping the focus on the tug-of-war model by setting the minimal and maximal subordinate shares as 0 and 1, respectively. Group stability varied with subordinate outside option and the quality-productivity coefficient (Figure 2.A2).

Table 2.1: Parameters used in the models of reproductive skew and the range of values; baseline values.

Symbol	**Parameter**	**Baseline values**	**Range explored**
y	Subordinate reproductive share	Optimised	0 – 1
r	Relatedness between co-breeders	0.5	0 – 1
b	Dominant's competitive advantage	1	0 – 1
k	Group productivity (fecundity)	$k = b + m + a*x$; 1.8	-1 – 6
x	Subordinate quality	0.5	0 – 1
a	Quality-productivity coefficient	0.8	-1 – 2
m	Group benefit (synergy effect to group productivity of having a subordinate)	0.4	0 – 1

Concession

The dominant's quality is assumed to be unity, which is the maximal subordinate quality. Hence, the solitary breeding fitness of a subordinate is its quality (i.e. outside option) x plus its relatedness to the dominant r. The minimal reproductive share conceded to the subordinate by the dominant that will induce them to stay is the value of y (y_{min}) at which its inclusive fitness if it stays in the group (l.h.s.) and if it leaves to breed independently (r.h.s.) are equal:

$$k(y_{\min} + r(1 - y_{\min})) = x + r \tag{2.1}$$

By re-arranging equation (2.1), we find

$$y_{\min} = \frac{x - r(k-1)}{k(1-r)} \tag{2.2}$$

Restraint

In the restraint model the subordinate takes a maximum proportion p_{max} of the group reproduction, above which the dominant would do better by breeding alone and so evicts the subordinate from the group (Reeve & Ratnieks, 1993; Reeve, Emlen, &

Keller, 1998b; Verhencamp, 1983). The maximum subordinate's reproductive share is the value of *y* at which the dominant's inclusive fitness if it accepts the subordinate (l.h.s.) and if it evicts the subordinate and breeds alone (r.h.s.) are equal.

$$k((1-y_{\max})+ry_{\max})=1+rx \tag{2.3}$$

Rearranging equation (2.3) gives the maximum subordinate reproductive share

$$y_{\max}=\frac{(k-1-rx)}{k(1-r)} \tag{2.4}$$

Tug-of-war

In the tug-of-war model the dominant and subordinate compete over the share of reproduction by investing in the reproductive conflict with *d* and *s* effort, respectively. The dominant has a relative competitive ability, which here we assume to be equal to their relative quality (x/b). The decision is assumed to be simultaneous. The equilibrium levels of *d* and *s* (*d** and *s**) are those at which the dominant and subordinate can do no better by changing it. Following the derivation from Johnstone (2000), the subordinate's reproductive share will be

$$y_t=\frac{\frac{x}{b}s}{d+\frac{sx}{b}}=\frac{sx}{b(d+\frac{sx}{b})} \tag{2.5}$$

After joint maximisation and replacement with the optimal subordinate effort *s** and optimal dominant effort *d**, the optimal subordinate share for its optimal tug-of-war effort *s** is

$$y_t=\frac{s*x}{b(d+\frac{s*x}{b})}=1-\cfrac{d}{\cfrac{d+(x\frac{b(b+m+ax)}{2(b-x)}-\frac{b\sqrt{\frac{1}{(b-rx)(x-rx+br^2-r^2x)}}(x+br-2rx)(b+m+ax)}{2(b-x)}}{b}}$$

Incorporating the quality-productivity coefficient

We derived the predictions of the concession, restraint and tug-of-war models after including an association between subordinate quality and their helping effect (i.e. QPC, *a*) by assuming a linear relationship, and that the dominant's quality is added to the effect of the subordinate's quality

$$k = b + m + ax \tag{2.6}$$

where *b* is the dominants' quality, *m* is the baseline benefit cooperating, *x* is subordinate's quality and *a* is the QPC (Table 2).

We replaced *k* as given by equation (2.6) in equation (2.2) to get the optimal reproductive share in the concession model

$$y_{\min} = \frac{x - r(b + m + ax - 1)}{(b + m + ax)(1 - r)} \tag{2.7}$$

We replaced *k* as given by equation (2.6) in equation (2.3) to get the optimal reproductive share in the restraint model

$$y_{\max} = \frac{b + m + ax - rx - 1}{(b + m + ax)(1 - r)} \tag{2.8}$$

In the tug-of-war model, *k* is the multiplier of the payoff subordinate and dominants invest *s* and *d*, respectively, into the struggle for reproduction, which reduces group productivity. The optimal reproductive share in the tug-of-war model is

$$y_{tow} = \frac{(bd - \sqrt{-bd(r-1)(bd + bx - dx + mx + ax^2})}{\dfrac{(b(bd - (-bd(r-1)(bd + bx - dx + mx + ax^2)^{1/2}}{b}} + \frac{sx + \sqrt{-sx(r-1)(bm - bs + sx + b^2 + abx}}{b}$$

After simplification

$$\begin{aligned} y_{tow1} &= \frac{-bd - \sqrt{-bd(r-1)(bd + bx - dx + mx + ax^2}}{x} \\ y_{tow2} &= \frac{-bd + \sqrt{-bd(r-1)(bd + bx - dx + mx + ax^2}}{x} \end{aligned} \tag{2.9}$$

The optimal dominant and subordinate efforts are respectively

$$d^* = \frac{x(b+m+ax)}{\sqrt{r^2[(b-1)(x-1)-1]+4bx}}\left(1-\frac{r}{2}+\frac{2x}{2(b-x)}\right)-\frac{x(b+m+ax)}{2(b-x)} \tag{2.10}$$

$$s^* = \frac{b(b+m+ax)}{2(b-x)}\left(1-\frac{(2x+br-rx)}{\sqrt{r^2[(b-1)(x-1)-1]+4bx}}\right) \tag{2.11}$$

$$\frac{s^*}{d^*+s^*} = \frac{x\left(\frac{b(b+m+ax)}{2(b-x)}-\frac{b(b+m+ax)(2x+br-rx)}{2(b-x)\sqrt{b^2r^2-2br^2x+4bx+r^2x^2}}\right)}{\sqrt{\frac{b^2x^2(1-r)^2(b+m+ax)^2}{b^2r^2-2br^2x+4bx+r^2x^2}}} \tag{2.12}$$

Note that *m* and *a* have cancelled out and that when *b*=1 we recover the standard result (Reeve et al 1998).

$$\frac{s^*}{d^*+s^*} = \frac{\sqrt{-r^2+4bx}}{2(1-x)(1-r)}-\frac{(2x+r-rx)}{4(1-x)(1-r)} \tag{2.13}$$

Note that since *k* is only a multiplier, the subordinate share does not depend on *m* or *a*.

Original concession, restraint and tug-of-war models

The three types of models of skew are based on different assumptions about the mechanism of control and make different predictions (Table 2.2). One assumption in all three models is that the parameters are assumed to be fixed and independent from one another. This means that the models are not self-consistent (*sensu* Kokko, López-Sepulcre, & Morrell, 2006), as one factor does not dynamically influence the payoffs. However, in nature the factors are likely to interact. Differences in breeding ability, survival outside the group or other factors such as age might cause variation in subordinate outside options. These differences might also create variation in the contribution that the subordinate makes to group productivity via its helping. In this case, the subordinate's outside options may correlate with its contribution to group productivity.

Table 2.2: Assumptions and predictions of the three main models of skew: concession, restraint and tug-of-war. Predictions of the effect of variables on skew are adapted from Liebert & Starks (2006), Reeve & Ratnieks (2001) and Nonacs (2006). Sources are listed inside brackets and are the original models of skew: (1) Reeve & Ratnieks, (1993); (2) (Johnstone & Cant, 1999); (3) (Reeve et al., 1998a); (4) (Reeve & Keller, 2001)

Assumption	**Concession**	**Restraint**	**Tug-of-war**
Who decides the skew?	Dominant	Subordinate	Both
Can individuals leave the group?	Yes	Yes	No
Who decides if subordinate stays?	Subordinate	Dominant	N/A
Focus / type of model	Evolutionary / Ultimate	Evolutionary / Ultimate	Mechanistic / Proximate
Link between subordinate quality and group productivity	Implicitly, no link as group productivity is constant	Implicitly, no link as group productivity is constant	Implicitly, depends on their investment in the competition
Predictions			
Relatedness r	Positive (1)	Negative (2)	None (3)
Subordinate outside options x	Negative (1)	Positive (2)	None (3)
Group productivity k	Positive (1)	Negative (2)	None (3)
Aggression	Positive (4)	Positive (4)	Negative (3)
Dominant competitive advantage b	None (4)	None (4)	Negative (3)

Biologically, if high subordinate quality is associated with being a good helper, subordinates' quality would correlate positively with group productivity – this is a positive quality-productivity coefficient (QPC). A positive QPC may occur in apostle birds (*Struthidea cinerea)*, as older helpers contribute more than younger ones, and outside options are better for older individuals because the juveniles have poorer body conditions (10% less mass) (Woxvold, 2004; Woxvold, Mulder, & Magrath, 2006). Similarly, subordinate Seychelles warblers (*Acrocephalus sechellensis*) that do not help have lower body condition than helpers, and likely lower outside options (van de Crommenacker, Komdeur, & Richardson, 2011). Another example is the El Oro parakeet (*Pyrrhura orcesi*) because helper quality, measured as heterozygosity, correlated positively with clutch size and offspring body mass (Klauke, Segelbacher, & Schaefer, 2013). Heterozygosity is positively associated with individual condition and reproductive success (Seddon, Amos, Mulder, & Tobias, 2004; Wetzel, Stewart, & Westneat, 2012). With positive QPC, whether subordinates develop into helper or breeders will depend on the conditions (Tibbetts, Fearon, Wong, Huang, & Tinghitella, 2018a).

If instead subordinates either have high breeding ability *or* high helping effect then the QPC will be negative. This is the case in the paper wasps *Polistes dominula* where experimentally increasing subordinates' outside option decrease their cooperative foraging effort (Grinsted & Field, 2017b), which suggests a negative correlation between subordinate quality and helping effect.

Predictions of the modified models

Numerous empirical tests have found non-significant results for the association of most interest: the effect of relatedness r on reproductive skew y (Nonacs & Hager, 2011), which may be due to insufficient statistical power if the effects are weak. That is, any evolved response to be measured may be slight or the selective pressure may be too weak to cause the evolution of a response. It may be that there is no selection at all, with the selection to *not* respond. However, no study to our knowledge has *quantified* the predictions of the models of skew, so models have never predicted when there will be only a weak effect of included parameters. Here, we quantified the relative effect size and identified when the three models might predict a weak and so statistically non-significant effect (Annexe 2A, Table 2.A6, 2.A7). To do this, we chose two values for each parameter and calculated the difference in the skew y relative to its magnitude (i.e. standardised effect size). We then found when the standardised effect size is less than a value assumed to be empirically detectable. We chose 10% for the standardised effect size, but the insights are not sensitive to the particular value used.

Incorporating the QPC alters the predictions of the concession, restraint and tug-of-war models (Figure 2.1). All three models predict a positive or no association between relatedness and skew in some circumstances (Figure 2.1a,f,k). The concession model predicts that skew will correlate positively (purple areas) with relatedness when subordinate quality is high and the QPC is negative (Figure 2.1a), and when subordinate quality is low and QPC high. The concession model predicts skew correlates negatively with relatedness when the values of subordinate quality and QPC are equivalent (white area, Figure 2.1a). The restraint model makes the opposite predictions to the concession model about the effect of relatedness on skew (Figure 2.1f).

The concession model predicts a positive correlation between skew and subordinate quality, unless both relatedness and QPC are strongly positive, in which case x and skew correlate negatively (Figure 2.1b). Thus, there are situations where increasing outside options *increases* the dominant's share. The predictions of the restraint model about x also change if the QPC is positive, from greater skew to less skew if x increases (Figure 2.1g).

The three models predict dominant quality b should not influence skew (Figure 2.1c,h,m). Indeed, as a relatedness over 0.75 is not biologically realistic, the negative link between skew and b predicted by the concession model is deemed irrelevant.

The link between group benefit m and skew was different for each model but not sensitive to a nor x. The concession model predicts skew decreases (Figure 2.1d,e), whereas the restraint model predicts skew increases with group benefit m (Figure 2.1i,j). The tug-of-war model predicts no correlation between group benefit and skew.

Adding the QPC did not change the predictions of the tug-of-war model about the skew, that skew should increase with the dominant's competitive advantage b and decrease (or do not correlate) with relatedness r (Reeve & Keller, 2001;

Reeve et al., 1998a). This was despite their effect on the competitive effort (d* and s*; Eq. 2.10 and 2.11).

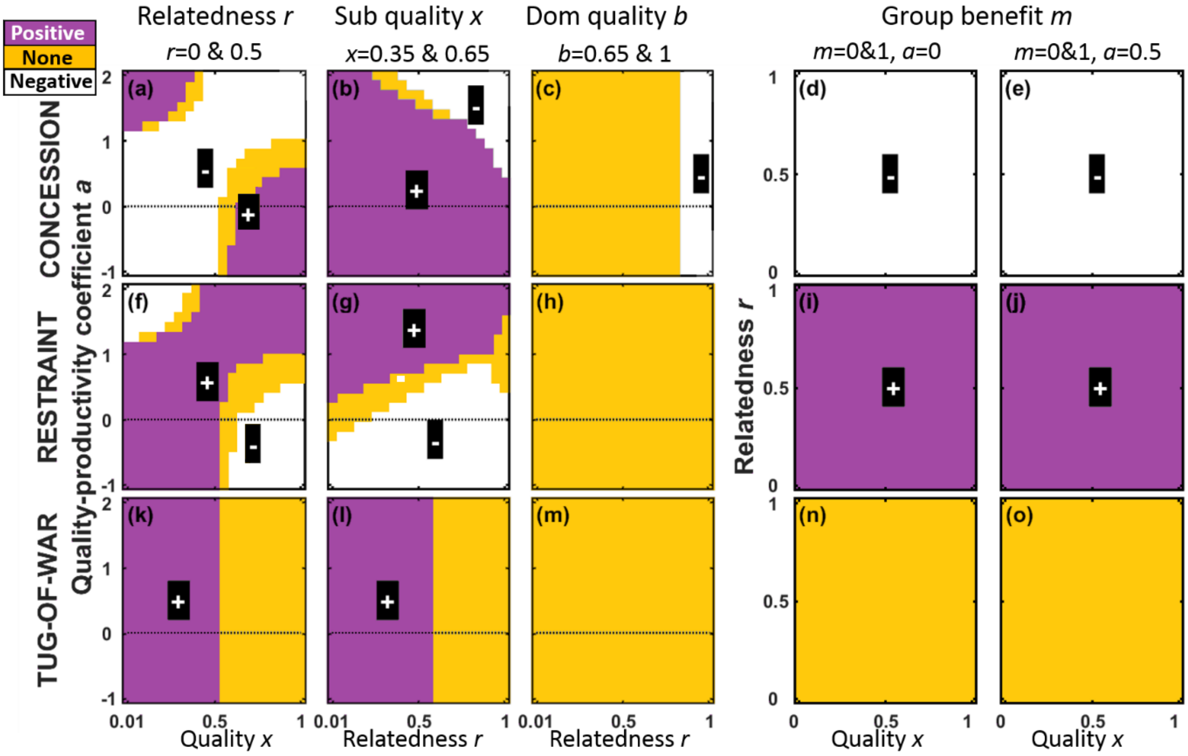

Figure 2.1: Direction of predicted association between skew and parameters of the skew models: (a-e) concession, (f-j) restraint, (k-o) tug-of-war. Areas indicate a positive (dark purple), negative (white) or non-significant (yellow) difference in *y** for two values of: (a, f, k) relatedness *r*; (b, g, l) subordinate quality *x*; (c, h, m) dominant's competitive advantage *b;* (d, i, n) group benefit *m* when outside option and group productivity are not associated *a*=0, *m*=*k*; (e, j, o) group benefit *m* when outside option and group productivity are positively associated *a*=0.5. Each area is the comparison between two values for a given parameter: *r*=0, 0.5, *x*=0.35, 0.65, *m*=0, 0.5. The difference was considered non-significant if its absolute value was smaller than 10% of the skew at the lower value of each parameter: e.g. if $\frac{|\,y*(r=0.5)-y*(r=0)\,|}{y*(r=0)} < 0.1$. Horizontal dotted lines indicate *a*=0, so show the predictions of the original models, and *m*=0.6 – *a* as otherwise groups are always preferred (for any *y*) if *a* is large and never preferred if *a* is small.

Review of empirical findings

Associations with relatedness

For studies for which we could find effect sizes we analysed the overall effects of parameters on skew. For many studies we could only get a direction of the effect (positive, negative, or non-significant), so for these we analysed counts.

Direction of effects

There were more studies on females than on males (Binomial test, p = 0.027, N=41). The sampling effort did not differ between insects and vertebrates (Binomial test, p = 0.471, N=45). Most studies reported no correlation between skew and relatedness (Binomial test, p = 0.011, N=45), which supports the tug-of-war model (Figure 2.1k).

The direction counts of the association between skew and relatedness was independent of sex (χ^2= 2.216, df = 2, p = 0.330, N=45, Figure 2.2a). The direction of the association between skew and relatedness did not differ between vertebrates and insects (Fisher's exact test, p = 0.520, N=45, Figure 2.2b, Table 2.A4) nor across taxa (χ^2= 10.977, df = 12, p = 0.531, N=45, Figure 2.2c).

Mammals showed no association between skew and relatedness (Binomial test, p = 0.031, N=6), which suggest mammals behave according to the tug-of-war model. No model was more supported than by chance in birds (χ^2= 0.464, df = 2, p = 0.793, N=17), bees (N=4, sample size was too low for statistical tests), wasps (χ^2 =0.792, df = 2, p = 0.673, N=12) and ants (χ^2= 0.32, df = 2, p = 0.852, N=5). However, birds, wasps, and ants all seemed to support more the tug-of-war model with mostly no association.

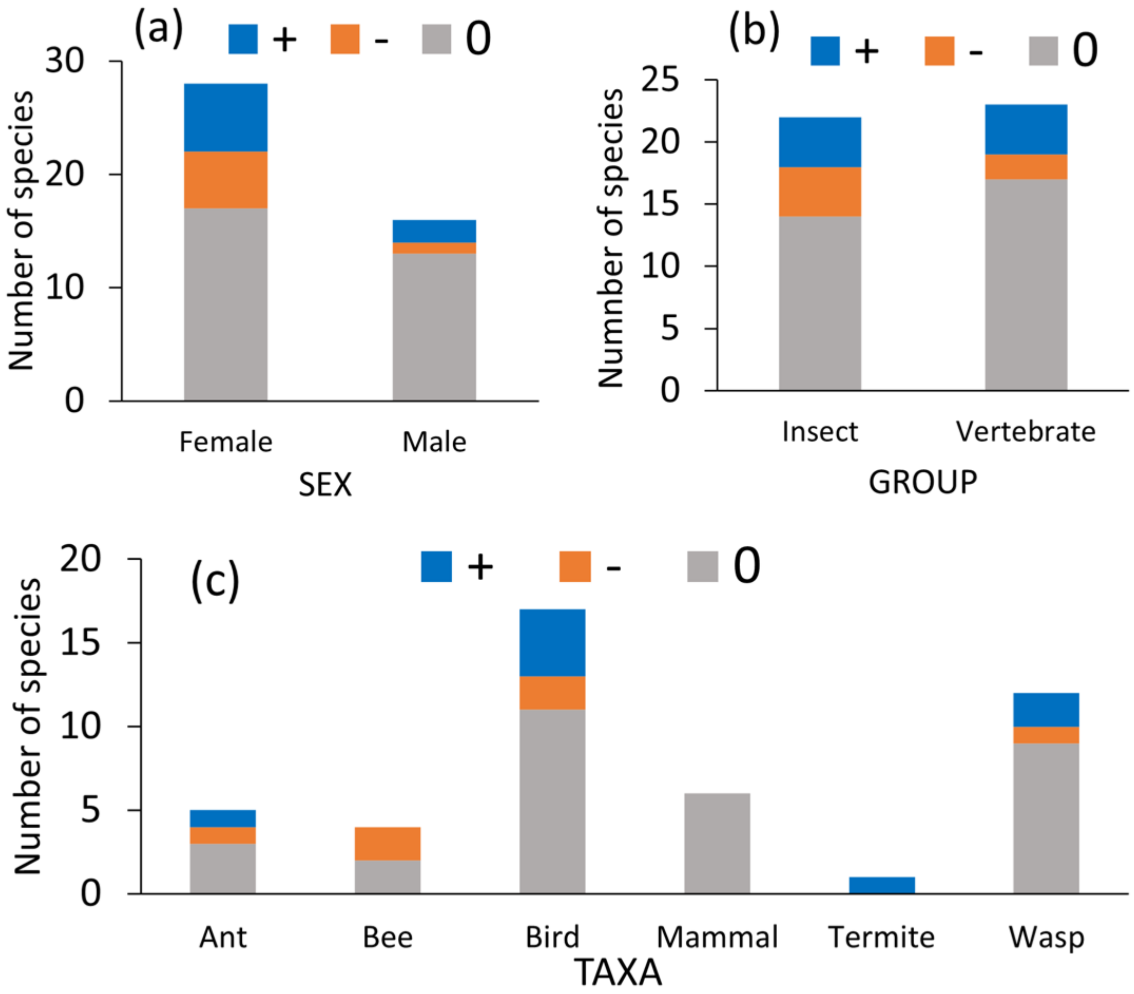

Figure 2.2: Number of species showing a positive, negative or nil link between skew and relatedness, as a function of (a) sex, (b) group and (c) taxa. N=45.

Size of effects t

We now consider studies of the association between skew and relatedness for which computing the effect size was possible (N=16) (Figure 2.A1, see Methods in Annexe 2.A). The average Hedge's g for all species (mean=0.533 ± SD 0.798) is significantly positive (one-sample t-test t16=2.85, p=0.011, N=16). The positive effect sizes averaged to 0.721 (± SD 0.622) and the two negative ones averaged to -0.780 (± SD 0.764). Removing the large effect sizes (>1 or <-1) does not change the results, as the average Hedge's g for all species (mean=0.382 ± SD 0.346) is still significantly greater than zero (one-sample two-tailed t-test t11=3.15, p=0.010, N=11). This suggests reproductive skew increases with relatedness (Figure 2.3), which is predicted by more of parameter space in the tug-of-war and concession models than the restraint model Figure 2.1a,f,k). The studies which reported no significant correlation between relatedness and skew still show a large positive effect (0.41± SD 0.441, N=10). A very large positive effect (1.41± SD=0.570, N=4) and a large negative effect (-0.600± SD=1.018, N=2) were found in studies that reported a positive and a negative effect, respectively.

The effect did not differ with sex (ANOVA $F_{14,15}$=1.11, p=0.311). However, female vertebrates and insects did not differ (ANOVA $F_{11,10}=2.27\times10^{-5}$, p=0.996), and no insect male data was available. Male insects might differ from female insects, so there may be a hidden sex difference (Figure 2.3a).

The effect did not significantly differ between vertebrates and insects (ANOVA $F_{15,14}$=2.09, p=0.171) (Figure 2.3b). Overall, all taxa had similar effect (ANOVA $F_{5,10}$=2.34, p=0.119) (Figure 2.3c). We tested if haplodiploidy, where helpers are highly related to their sisters, shaped the effect size, and found that the effects in Hymenoptera and non-Hymenoptera did not differ (ANOVA $F_{14,15}$=2.09, p=0.171).

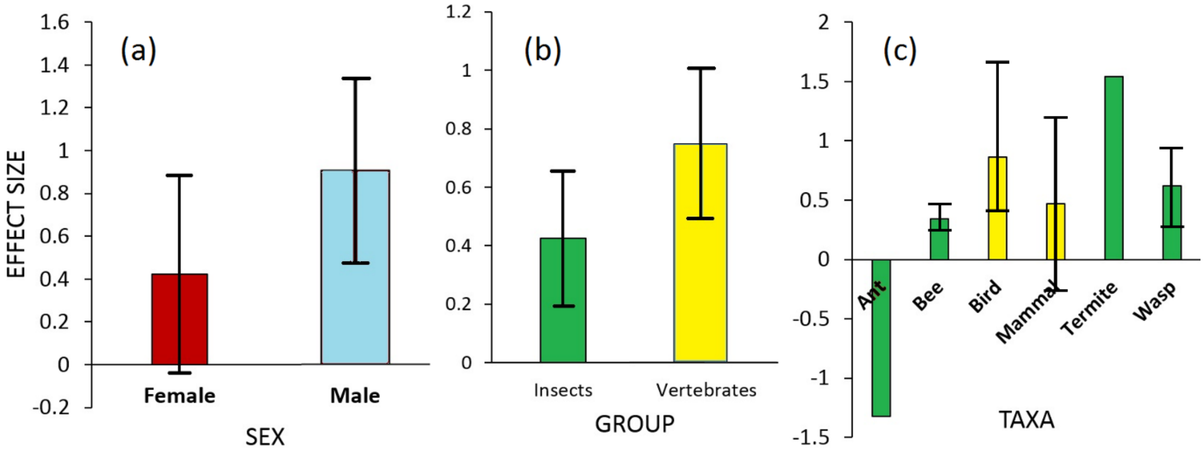

Figure 2.3: Effect (mean Hedge's g ± 1 SE) of the link between skew and relatedness as a function of (a) sex (females: dark red, males: light blue), (b) group and (c) taxa (insects: dark green, vertebrates: yellow). N=16.

Associations between skew and other factors

For factors other than relatedness there were insufficient data on effect sizes (Table 2.3), so we analysed direction data only.

Outside options and skew

The association between skew and outside options was examined in fewer insect than vertebrate studies although this was not significant (Binomial test, p = 0.125, N=7) (Table 2.3), and in as many female as male studies (Binomial test, p = *0.508*, N=9). Similar numbers of studies reported a nil, positive and negative, associations between outside options and skew (χ^2=1.273, df = 2, p = 0.529, N=9) (Figure 2.4a). The direction of the association between subordinate quality and skew was not biased by taxa (Fisher's exact test, p = 0.679, N=9) nor sex (Fisher's exact test, p = 0.740, N=9). Only one study examined haplodiploids.

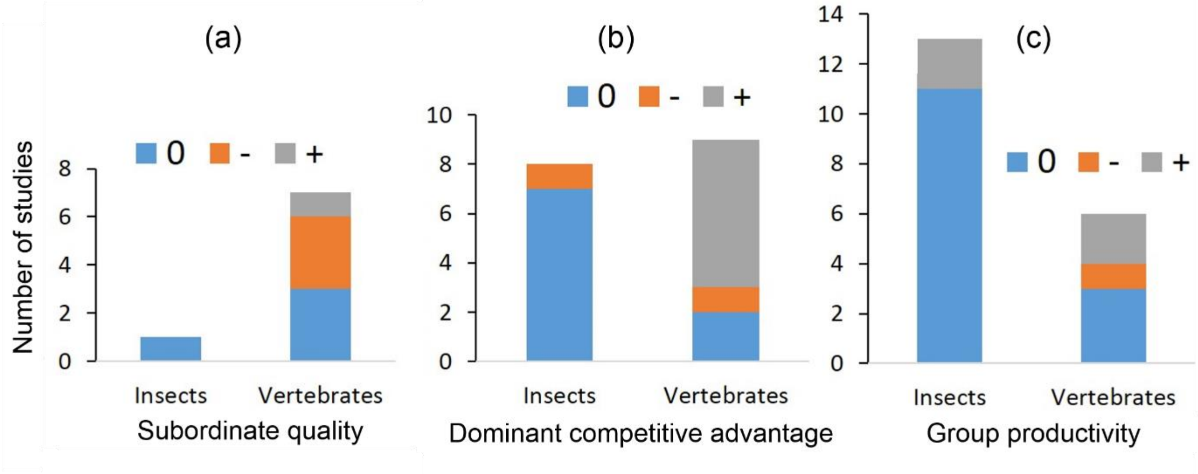

Figure 2.4: Number of species showing a positive, negative or nil link between skew (*y)* and (a) subordinate quality *x,* (b) dominant's competitive advantage (quality) *b* (N=17) and (c) group productivity *k* (N=19) in insects and vertebrates (N=7).

Dominant's competitive advantage and skew

The dominant's competitive advantage b was studied equally in vertebrates and insects (Binomial test, p = 0.647, N=15) (Figure 2.4b, Table 2.3), and in females and males (Binomial test: p = 0.263, N=20). More than half of the studies found no association (Figure 2.4c, Table 2.A1) and overall b and skew were not significantly positively or negatively correlated (χ^2= 4.35, df = 2, p = 0.113). Taxa varied in the direction of the link between b and y (Fisher's test: p = 0.021, N=17).

The direction differed between vertebrates and insects (both sexes: Fisher's exact test: p = 0.007, N=17, females: Fisher's test: p = 0.024, N=11), with insects showing mostly no significant correlation and vertebrates showing mostly a positive correlation. (Figure 2.4b). Haplodiploidy did not affect the direction (Fisher's test: p = 0.199, N=17). Sex did not bias the direction of this association (Fisher's test: p = 0.714, N=10).

Table 2.3: Sample sizes of the effects empirically tested in insects and invertebrates. Studies with data for males and females were shown as two data points. Unclear results are not displayed (n>1 studies per group, N=111 total with all links and unclear results.)

Link tested	**Symbols**	**Insects**	**Vertebrates**	**Total**
Dominant competitive advantage & skew	b & y	8	11	19
Group productivity & skew	k & y	13	7	20
Subordinate quality & skew	x & y	1	8	9
Quality-productivity coefficient & skew	a & y	1	1	2
Relatedness & group productivity	r & k	4	1	5
Relatedness & skew	r & y	22	23	45
Total all links		49	51	100

Group productivity and skew

There were equal numbers of studies of the association between group productivity k and skew was equal in insects and vertebrates (Binomial test: p = 0.316, N=19) (Figure 2.4c), but there were more studies of female than males (Binomial test: p = 0.0413, N=20) (Table 2.3). The direction significantly differed across species (χ^2 = 16.3, df = 2, p = 0.0003, N=20) as most studies found no association between group fecundity and skew (Table 2.A1, Figure 2.4).

The direction of the association between group fecundity and skew did not differ between vertebrates and insects (Fisher's test: females: p = 0.371, N=13; both sexes: *p* = 0.099, N=17) (Figure 2.4c), nor between diploids and haplodiploids (Fisher's test: *p* = 0.344, N=19). The direction of the association between skew and group fecundity was not biased by sex (Fisher's exact test, *p* = 0.278, N=20).

In summary, the dominants' competitive advantage *b* and group productivity *k* were not associated with skew in insects (Binomial test, *p* = 0.07, N=17) (Figure 2.4c), suggesting that other factors influence skew Figure 2.1c,h,m). In vertebrates, by contrast, the association between *b* and *k* on skew was not clear which may imply strong between-species differences in the selective pressures and current mechanisms to decide skew.

Test of co-occurrence of positive/negative associations

We tested the co-occurrence of different directions for the associations to detect potential patterns (N=24, Table 2.A3, 2.A5). No clear pattern emerged, as e.g. within birds no species showed similar directions for relatedness and skew nor for outside options and skew. The association between relatedness and skew was independent of the association between group productivity and skew (Fisher's test, *p* = 0.564, N=11). Similarly, the results of the association between relatedness and skew were independent to that of the association with outside options (χ^2= 5, *df* = 4, *p* = 0.287, N=11).

Empirical support for models of skew

We focused on the associations of skew *y* with: relatedness *r*, outside option *x*, dominant's advantage *b* and group productivity *k*, for which our new models makes clear predictions. Overall, for the baseline parameter values (dotted lines in Figure 2.1), 67.5% of empirical studies matched the predictions of the tug-of-war model, while 26.0% fit the predictions of the concession model and 18.2% of the restraint model (Table 2.A2). However, we have shown that the QPC may affect these predictions (Figure 2.1), making it essential to measure the QPC empirically.

Fewer insects (12.5%) than vertebrates (24.3%) studies supported the restraint model (Binomial test, *p* = 0.020, N=89), whereas they supported equally the concession and the tug-of-war (henceforth: TOW) models (Table 2.A2). The predictions of the concession model are supported in 25.0% of insect and 27.0%

of vertebrate studies (Table 2.A2). The concession model does not significantly match studies of dominant's advantage (Binomial test, $p = 0.549$, N=11). Studies of relatedness significantly did not support the restraint model (Binomial test, $p < 0.001$, N=45) nor the concession model (Binomial test, $p = 0.002$, N=45).

We found 65.0% (N=41) of insect and 70.3% (N=37) of vertebrate studies support the TOW (Table 2.3, 2.A2, 2.A4). Empirical tests of relatedness and skew support the tug-of-war model (Binomial test, $p = 1.47\text{x}10^{-5}$, N=51). Studies of relatedness and skew significantly support the TOW model (Binomial test, $p = 0.004$, N=22), but not studies of outside option and skew (Binomial test, $p = 0.179$, N=6). Females and males vertebrates were as likely to support TOW ($\chi^2 = 0.106$, $df = 1$, $p = 0.744$, N=62). Taxa did not significantly differ in their support to the TOW ($\chi^2 = 9.92$, $df = 6$, $p = 0.128$, N=62), with no fish study and half of bird studies in line with TOW. TOW was not more supported than expected by chance in wasps (Binomial test, $p = 0.092$, N=23), mammals (Binomial test, $p = 0.180$, N=9), birds (Binomial test, $p = 0.108$, N=25), bees (Binomial test, $p = 0.453$, N=7) and ants (Binomial test, $p = 0.375$, N=5), although the sample size of bees and ants may be insufficient to rule out TOW.

Discussion

Summary of support for the models

A previous review found that 21 over 27 studies (78%) reported no correlation between skew and relatedness, and concluded that skew theory did not apply to within-species variation in skew (Nonacs & Hager, 2011). In our review, 31 over 45 studies (69%) showed no correlation between relatedness and skew. However, as we have shown, the models will sometimes predict non-significant effects, such as the concession and restraint models when subordinates are high quality and the QPC is medium (Figure 2.1a, f). By incorporating the QPC, we are in a position to better understand the variation in empirical findings.

Relatedness. The analysis of effect size indicated a positive association between relatedness and skew which supports the restraint model, or the tug-of-war model for low subordinate quality (or the concession model for high subordinate quality and low QPC) (Figure 2.1a,f,k). By contrast, the comparison of count data found that most studies showed no correlation, which supports, for high subordinate quality only, the tug-of-war model (or both concession and restraint models). The conflicting results are likely due to the methodological differences, as effect sizes capture not only the direction but the magnitude of the association (Haddaway et al., 2020). The conflicting results may also arise from the mere difference in sample size (N=16 versus 45), since few studies reported sufficient details to calculate the effect sizes. The meta-analysis is more reliable than ‘count voting’ (Haddaway et al., 2020), yet the small sample size may prevent from assessing if the association is nil or positive. However, neither method supported a negative correlation, so the concession model is overall not supported (except for specific cases where bad helpers have high outside options) (Figure 2.1a).

Relatedness and skew were not significantly correlated in any mammalian studies, but were positively correlated in several bird studies. Philopatric mammalian social groups are often highly related and subordinates may engage less in extra-pair mating than birds, potentially because the social groups are further apart and/or less tolerant (Beekman, Komdeur, & Ratnieks, 2003; Chen, Li, Liu, & Li, 2021; Kingma, Hall, & Peters, 2011; Sharp & Clutton-Brock, 2011). Consequently, individuals may have fewer opportunities to breed as subordinates (whilst avoiding inbreeding). Furthermore, mammalian helpers are seldom unrelated individuals (Isler & van Schaik, 2012) as they typically are the offspring or siblings of the dominants, so variation in relatedness may simply be insufficient to get significant effects. Since in several birds species good helpers also have good quality, and that some species showed a positive effect of relatedness and skew, the restraint or the tug of model may apply to avian systems (Klauke et al., 2013; van de Crommenacker et al., 2011; Woxvold et al., 2006).

Competitive advantage. The association between dominant’s competitive advantage and skew was positive in vertebrates, which does not match the new predictions for any of the models. By contrast, the lack of correlation between dominant’s competitive advantage and skew in insects fits with the three models. As dominant’s competitive advantage encompassed very diverse measures spanning from size difference to canine length, the studies may have not grasped fully the trait that characterises dominant’s competitive advantage. Indeed, measuring a range of traits may be needed to get data that accurately reflects how animals perceive the competitive advantage and make decisions.

Subordinate quality. The direction of the association between subordinate quality and skew was not significantly biased, overall, per sex nor per taxa. This may suggest that the data of subordinate quality are not based on equivalent measures of outside options, but may also reflect that each model makes a range of predictions and so species with different QPC and relatedness may make different predictions. Furthermore, the association between subordinate quality and skew may be more complex than a linear function.

Our results highlight the need to conduct meta-analyses (with standardised effect sizes) for as many empirical tests as possible. A definitive test would be to look at interactions between parameters. For example, measuring skew for high and low quality related and unrelated individuals would help distinguish between the models as they make differing predictions about this interaction.

Group productivity. While most of the examined studies reported no correlation between group fecundity and skew, taxa differed. This between-species variation may be linked to the two main evolutionary pathways to cooperative breeding, the defence of resources in a stable environment or the buffering of adverse variable environments (Lin et al., 2019).

Variation in the quality-productivity coefficient

Our review reveals a lack of empirical tests of the association between skew and the quality-productivity coefficient (QPC), despite the theoretical implications of including the dependence of quality on group productivity. The QPC is the parameter that transforms subordinate quality into its helping benefits. A high QPC means that the strong subordinates are very helpful. Variation in the value of the QPC may explain the inconclusive results regarding the association between skew and relatedness, as the predictions of the concession and the restraint models changed with QPC. Our findings suggest QPC is useful to disentangle subordinate’s quality from its effect on group productivity, and that empirical studies would benefit from assessing it (beyond helper’s effect). Further studies on QPC are needed to determine where in the prediction plot (Figure 2.1) the species is, and determine its association with skew.

As most of the species for which several tests have been conducted fit the predictions of two or three models (Table 2.4), it proves impossible to assign them to a model without further data on subordinate quality, relatedness and QPC. However, most of the wasp species seem to support the tug-of-war model, which is in line with a review that indicated that the concession and restraint models do not explain skew in paper wasps *Polistes* (Nonacs, 2006). One species of wasp fit with the predictions of the concession model in pairwise (but not between nest) comparisons of skew.

Table 2.4: Empirical tests of our new predictions (species with ≥2 different factors tested). Models are the skew models whose predictions fit with the empirical tests once the QPC is incorporated.

Species (taxa, sex)	**Source**	**Sample size**	***r&y***	***x&y***	***b&y***
Exoneura nigrescens (bee, females)	Langer et al., (2004)	r&y: 29, x&y: 16, k&y: 24 colonies	Negative Concession, restraint	Non-sig, restraint with high QPC and *r,* tug-of-war with high *x*	Not tested
Formica fusca (ant females)	Hannonen & Sundstrom (2003)	30 colonies	Negative (queens); Concession	Not tested	Non-sig; all models
Formica fusca (ant females)	Hannonen & Sundstrom (2003)	30 colonies	Non-sig (workers)	Not tested	Non-sig; all models
Leptothorax acervorum (ant females)	Walter & Heinze (2015), Hammond et al., (2006), Gill et al., (2009)	7 wild and 14 lab colonies, 17, 22 colonies	Positive and non-sig; concession and restraint	Not tested	Negative; none
Liostenogaster flavolineata (wasp females)	Sumner et al., (2002)	13 nests	Non-sig; all models	Not tested	Non-sig

Melanerpes formicivorus (bird males)	Haydock & Koenig (2003)	16 groups	Non-sig; all models. Mostly tug-of-war with high x and high r.	Non-sig; all models	Not tested
Parischnogaster mellyi (wasp females)	Fanelli et al., (2005, 2008)	15, 15 colonies	Non-sig. All models. Mostly tug-of-war with high x.	Not tested	Non-sig. All models. Mostly tug-of-war with high x.
Polistes carolina (wasp females)	Seppa et al., (2002)	30 colonies	Non-sig. All models. Mostly tug-of-war with high x.	Not tested	Non-sig. All models. Mostly tug-of-war with high x.
Polistes bellicosus (wasp females)	Field et al., (1998)	28 colonies	Non-sig (nest). All models. Mostly tug-of-war with high x.	Not tested	Non-sig. All models. Mostly tug-of-war with high x.
Polistes bellicosus (wasp females)	Field et al., (1998)	28 colonies	Negative(pairwise); Concession	NA	Non-sig

Suricata suricatta (mammal females)	Clutton-Brock et al., (2001), Cram et al., (2019)	B&y: 57, x&y: 112 subordinates, Cram: x&y:273 pregnancies from 192 subordinates in 22 groups.	Non-sig. restraint model medium-low QPC) or concession model (high QPC and relatedness).	Positive/Negative. restraint model medium-low QPC) or concession model (high QPC and relatedness).	Positive; None
Porphyrio porphyrio (bird females)	Jamieson (1997)	74 group-years	Positive. Restraint with medium and low QPC, high *x*.	Negative. Restraint with medium and low QPC, high *x*.	NA
Propithecux verreauxi (mammal males)	Kappeler & Shaffler (2008)	68 group-years	Non-sig. All models. Mostly tug-of-war with high *x*.	NA	Non-sig. All models. Mostly tug-of-war with high *x*.

Incorporating the QPC influenced the predictions of the tug-of-war model, as skew did not correlate positively with dominant's competitive advantage (Figure 2.1m). In line with the predictions of the original tug-of-war model, relatedness did not correlate with skew – although only for strong subordinates (Figure 2.1k). The tug-of-war model implicitly links subordinate quality and their contribution to group productivity, as the individual investment in the reproductive conflict decreases group productivity (due to an assumed trade-off). Unlike in our model, in the tug-of-war model group productivity does not influence skew, as individuals lack outside options. Indeed, in the tug-of-war model the quality did not refer to subordinate outside options, but to the subordinate's ability to fight or to invest in group productivity, which suggests that other models with QPC may be more comparable to our model.

In the general costly-young model, individuals can cooperate to raise the young by breeding cooperatively but compete over the share of reproduction (Shen, Reeve, & Vehrencamp, 2011). This model of cooperation explored the link between quality and group productivity. The dominant has lower costs to produce a young than the subordinate. The general costly-young model predicts that group productivity increases and skew decreases with subordinate investment into care (Shen, Reeve, & Vehrencamp, 2011). This prediction, contrary to the predictions of the tug-of-war model, suggests that subordinate quality correlates positively with group productivity.

Incorporating the QPC changed the predictions of the concession and restraint skew models concerning subordinate quality. In the presence of a positive correlation between skew and subordinate quality, as was found in meerkats (*Suricata suricatta*) (Cram, Jungwirth, Spence-Jones, & Clutton-Brock, 2019), we would have concluded that the restraint model applies without incorporating the QPC, but because of the QPC we conclude that this finding is not sufficient to determine which model apply (Table 4.1). Indeed, we cannot rule out the concession model as it predicts such positive correlation in their parameter spaces, and the restraint model predicts a negative correlation and no correlation in some of the parameter space. Consequently, variation in the QPC might explain the positive and negative correlations between female meerkats skew and subordinate quality (Clutton-Brock et al., 2001; Cram et al., 2019).

The QPC altered the predictions of the link between skew and relatedness, which changed the interpretations of empirical findings. For instance, in white-winged choughs (*Corcorax melanorhamphos),* where skew correlates positively with relatedness (Heinsohn, Dunn, Legge, & Double, 2000), we would have concluded that the concession model fits this species (and rejected the restraint and tug-of-war models) without incorporating the QPC. Yet, because of the QPC, the restraint and tug-of-war models are applicable in a larger portion of the parameter space than the concession model. We would need the value of the QPC, relatedness and subordinate outside options to determine whether the date supports the concession, tug-of-war and restraint models. In a nutshell, our new theoretical findings change the conclusions that can be drawn from the empirical literature, which highlights the importance of considering different aspects of individual variation as distinct and potentially correlated.

Which empirical tests do we need?

We did not find sufficient, good-quality evidence to judge whether one model of skew is the most applicable, and to which taxa. We showed here that making group productivity dependent on helper's outside options altered and complicated the predictions of the original model. Indeed, where one original model predicted a single direction, most of the new predictions vary with subordinate quality or relatedness. However, the predictions of the link between skew and benefit to group productivity of one subordinate (i.e. helping effect) give clear-cut distinctions between the concession, restraint and tug-of-war models. Importantly, the direction of the association between skew and group benefit should vary with the processes/strategies (i.e. model), but not depend on subordinate quality nor on how much help a subordinate provides as a function of their quality (QPC). These unambiguous predictions make it possible to test which model applies by measuring genetic data to determine skew and the increase in group productivity provided by one helper to determine group benefit. Future data collection of this group benefit, in a wide range of taxa, may be useful to understand diversity in cooperative breeding.

We suggest that unrecognised variation in factors such as the quality-productivity coefficient makes evidence support several models (i.e. one empirical association predicted by one model and another by another model). Hence, adding the quality-productivity coefficient might give more realistic predictions that may better match empirical data, and may especially explain sex differences in skew with sex differences in QPC or other factors. For instance, the bird *Porphyrio porphyrio* fits the original predictions of all models: male skew decreased with relatedness, supporting the restraint model, whereas female skew increased with relatedness supporting the concession model. The higher skew with higher constraints (lower *x* and lower *b*) fits with the concession and restraint models. *P. porphyrio* may behave following our new restraint model, if subordinate quality is associated with very high benefits (high QPC), and if females have higher subordinate outside option than males.

This review shed some light on the need to collect data for both males and females for each taxa. In the only taxa for which we were able to calculate the size of the association between relatedness and skew for both sexes, birds, females had a smaller effect than males. This may suggest that males are operating within the tug-of-war window of the synthetic model, whereas females sometimes operate within the restraint model window – conversely these results may stem from between-species variation. Sexual selection and the sex-specific costs of reproduction may drive females and males to make decisions based on different parameters when deciding whether to disperse and how much to help within a group (Boomsma, 2009; Creel & Creel, 2015; van Boheemen et al., 2019). Coalitions of brothers for instance may cause one male to monopolise reproduction and get related helpers (Gottelli, Wang, Bashir, & Durant, 2007; Krakauer, 2005), who can then become dominant more easily than if they were on their own (Schülke, Bhagavatula, Vigilant, & Ostner, 2010). To our knowledge no models of skew were tested on male insects, although sex-specific selection forces may be strikingly different in male and female insects due to haplodiploidy. We found only one study on female vertebrates (for 11 on males) which tested the association between relatedness and skew. Further empirical tests of the association between relatedness and skew of female vertebrates and male termites will help disentangle the potential taxa and/or sex differences. Empirical tests of females and males would strongly inform our understanding of social evolution across taxa.

Our review revealed the gaps in tests of the models of skew in some insects and in fish. Although some well-established study sites and species have provided good insights and built our understanding on particular species (e.g. *Polistes*), further tests of all cooperative breeders would ensure the veracity of the models on a range of taxa. To push the boundaries of this field we need empirical tests in termites where only one empirical test exist, in other insects and in cooperatively breeding shrimps.

Many studies reported “non-significant relationships”, but it may argued that the sample size was not sufficient to detect any effect, due to a confounding effect of a low statistical power (Cohen, 1992). Indeed, the studies we collected varied in their sample sizes (e.g. Table 2.4 for species where several links were tested). Positive or negative relationships between skew and factors may have been concealed by a lack of power, which further highlights the need to develop research with high sample sizes. For instance, data within a species can be combined across years. If some taxa benefit from higher sample size than others, the presence of significant relationships could be biased by taxa; however in the studies with sufficient details to calculate the effect sizes for the relationship between skew and relatedness, sampling efforts did not differ between insects and vertebrates.

The field of social evolution would benefit from precise tests of the theory of skew in species where long-term field work exists. Indeed, the genotypic data for calculation of the effect sizes on long-term field projects is not readily available yet, either because it was not measured or it is unpublished (Table 2.A5). Over the 45 studies reporting a (negative, positive or nil) association between skew and relatedness, only 16 provided sufficient data to calculate the effect (e.g. only the average skew was reported, not the skews for related vs unrelated). To test the predictions accurately with meta-analysis, studies should collect and report the reproductive skew for each category (average ± SD or standard error, e.g. related vs unrelated) along the sample size of each category, and detail the statistical tests. We need more information about the mating systems (who reproduces with whom) and the parental care systems (who takes care of the offspring) (Kappeler, 2019) to further advance our understanding of the factors that influence the diversity in skew and cooperative breeding (Makuya, Olivier, & Schradin, 2021).

The optimal skew has been shown to vary with environmental, social and individual factors, which combined with our updated predictions of the three models of skew suggests that instead of matching empirical results to a simple single prediction per model, we should aim to determine the parameter space in which species lie. Empirically, environmental quality such as food availability and the number of helpers significantly correlates with breeding success and skew in female meerkats (Field & Cant, 2009) and banded mongoose (Nichols, Bell, Hodge, & Cant, 2012). Harsh environments by contrast imply lower solitary breeding success (variation in dominant's competitive advantage *b*) and higher benefits by the helpers (variation in QPC and/or group benefit *m*). Rather than looking at a static image of reproductive skew in one (or several) population(s), and study reproductive skew in isolation, it may be fruitful to consider all the factors from the original models of skew, allowing for correlations among the parameters such as individual quality and group productivity.

Chapter 3 – Cooperative breeding and the selection for information sharing amongst groupmates

Black carpenter ant (*Camponotus pennsylvanicus*) by Egor Kamelev via Pexel

Abstract

Understanding variation in reproductive skew between and within cooperatively breeding species is a key aim. However, tests of reproductive skew models give equivocal results, potentially because of some of the theoretical assumptions. Most models assume that both dominants and subordinates are perfectly informed, but animals likely have asymmetric imperfect information, since individuals know better their own quality and subordinates are freer to explore breeding options outside the group. To explore effects of dominants' uncertainty, we extended the standard concession model of skew with an explicit focus on subordinate quality, which we assume determines their outside option and influences their contribution to group productivity. Depending on how quality influences group productivity, dominants should prefer low- or high-quality subordinates. When subordinate quality correlates positively and strongly with group productivity, skew decreases with quality, otherwise skew increases with quality. The average concession offered to subordinates is greatest when dominants have imperfect information and low when they have perfect information. In most cases dominants are selected to acquire information, whereas subordinates should restrict the information given to dominants, even though this may reduce the opportunities for cooperative breeding. Concessions always decrease with relatedness, so related subordinates would especially benefit from the dominant being uncertain about relatedness, which may explain why true kin recognition is rare in nature. Overall, the new predictions show uncertainty can influence evolutionary games and incorporating it in skew models may help explain the patterns of cooperative breeding observed between and within species.

Keywords: reproductive skew; outside option; concession model; private information; uncertainty; relatedness.

Introduction

Understanding variation in reproductive skew between and within cooperatively breeding species is a key aim (Koenig & Dickinson, 2016; Verhencamp, 1983). However, tests of reproductive skew models give equivocal results, potentially because of some of the theoretical assumption (McNamara, 2013). Models of skew typically assume perfect information, in that all individuals can base their decisions on all the influential factors such as subordinate's outside options and relatedness (Johnstone, 2000; Kokko & Ekman, 2002; Reeve & Ratnieks, 1993; Verhencamp, 1983). Here, we introduce uncertainty in a model of reproductive skew, since animals make decisions based on imperfect information, because their social and abiotic environments vary and they cannot be omniscient (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005).

How information about relatedness or subordinate quality influences reproductive skew has been little explored, despite some indications that incorporating uncertainty will affect predictions. For example, Kokko (2003) showed that when subordinates do not know perfectly the benefits of staying in the group, invasion by cheating dominants that concede nothing undermines the stability of cooperative breeding. Besides, limited information about one another's outside options can prevent cooperative breeding even when forming a group would be mutually beneficial, as shown in a model by Akcay, Meirowitz, Ramsey, & Levin (2012). In Akcay's et al. (2102) model, roles were asymmetrical: when forming a group, one individual gave up a share of reproduction (similar to a dominant) and the other gained a share of reproduction (similar to a subordinate). The uncertainty was symmetrical in that both individuals had limited information about the outside options of their potential partner (Akcay et al., 2012). These predictions suggest that the current models do not sufficiently capture the key factors that determine cooperative breeding, as animals achieve cooperation despite imperfect information. Because imperfect information can cause sub-optimal strategies compared to those in games where information is assumed to be perfect, models that integrate uncertainty about a subordinate's outside options and its relatedness to the dominant will improve our understanding of reproductive skew and cooperative breeding.

Instead of symmetric private information, it is likely that subordinates have more information than dominants about their outside options. First, individuals typically know more about their own abilities (e.g., body condition, size, strength) than those of others (Arnott & Elwood, 2009; Bridge, Elwood, & Dick, 2000). Second, the outside options (i.e., expected breeding success) of an individual are a combination of both its ability and the quality of the (potential) breeding sites. Dominant's outside options are here assumed to be solitary breeding in their current nest, whereas subordinate outside options entails breeding outside the group. Both dominants and subordinates know the breeding site quality of the dominant, therefore have high information about dominant's outside options. (Barve, Lahey, Brunner, Koenig, & Walters, 2020). Subordinates compare between breeding options (Young, Spong, & Clutton-Brock, 2007) and assess their qualities, whereas dominant cannot know which breeding site the subordinate would choose. Consequently, dominants have higher uncertainty about subordinate's outside option than subordinates. Third, dominants may all have similar outside options because individuals need to reach a threshold of quality (e.g., dispersal age) to become dominant and are then constrained by solitary breeding ability and limited resources at the breeding site (Creel & Rabenold, 1994; Stephens, Russell, Young, Sutherland, & Clutton-Brock, 2005; but see Boyd, 1992).

Skew models have also assumed that relatedness is known perfectly (Komdeur, Richardson, & Hatchwell, 2008). Cooperative breeders are commonly monogamous (Cornwallis, West, Davis, & Griffin, 2010; Hughes, Oldroyd, Beekman, & Ratnieks, 2008; Lukas & Clutton-Brock, 2012a), but there is great diversity in kin structure (Koenig & Dickinson, 2016). Some groups accept non-natal helpers and extra-pair paternity does occur, making help not exclusively kin-directed (Clutton-Brock et al., 2002; Cockburn, 1998; Kaiser et al., 2019; Kingma, Hall, & Peters, 2011b). Concession models predict dominants should concede less reproduction to more closely related subordinates (Hamilton, 1964; Verhencamp, 1983). Animals lacking perfect information about kinship may over- or underestimate how related they are to a subordinate, and therefore what degree of skew would be appropriate. Consequently, the decision to engage in cooperative breeding might depend on uncertainty about relatedness. Theoretical tests of the effect of uncertainty, assessing it independently for each individual, would help to assess the importance of information about relatedness in the evolution of cooperative breeding and optimal skew. However, models assume perfect information about relatedness (Holman, 2014; Kokko, Johnstone, & Clutton-Brock, 2001) between individuals, whether related or unrelated (Kuijper & Johnstone, 2018; Nonacs, 2019a). Because in cooperatively breeding groups, relatedness is not a binary, we systematically tested the effect of continuous various in 1) the amount of information and 2) the relatedness.

Depending on the species and the environmental conditions, having good outside options may correlate with high benefits to group productivity or with a low or negative effect on group productivity. For instance, subordinate quality is positively linked to young body condition in El Oro parakeets (Klauke et al., 2013), whereas in paper wasps (*Polistes dominula)* subordinates with experimentally increased nesting and partner availability reduced their helping efforts (Grinsted & Field, 2017b), which likely reduces group productivity. We refer to the link between an individual's quality and its impact on group productivity as the "quality–productivity coefficient" (QPC). If subordinate's QPC is negative, having better outside options is associated with a lower helping effect, which could happen when individuals specialise in breeding or helping. Naked mole-rats *(Heterocephalus glaber)*, where subordinates show distinct helper and disperser morphs (O'Riain et al., 1996), would be an example of negative QPC. Negative QPC might also occur if breeding success is underpinned by a mechanism that counteracts prosocial behaviour (e.g., testosterone: Vernasco & Moore, 2020). Therefore, subordinate quality (i.e., outside options) might have different effects depending on the QPC. Models of skew predict that subordinate quality should influence group formation, because it determines the fitness subordinates will get if breeding alone (Johnstone, 2000). Yet previous work has confounded subordinate quality and their QPC, by studying only the helper effect on group productivity (Doerr & Doerr, 2007; Grinsted & Field, 2018b; Jacobs & Ausband, 2019; Savage et al., 2015; Sparkman et al., 2011; Williams & Hale, 2006; Woxvold & Magrath, 2005). Such fine-scale variation in subordinate quality or QPC is not examined by studies that focus on the 'helper effect'.

Here, we investigate various scenarios to paint a fuller picture of the reproductive decisions of cooperative breeders. This work is conducted to respond to the need to understand the effect of varying the association between subordinate outside option and group productivity, and dominant's level of information about subordinate. We assume that subordinate intrinsic quality is equivalent to their outside option but that their contribution to group productivity may vary positively or negatively with the outside option, as indicated by the QPC. The model by Akcay et al. (2012) also focuses on information about the other's outside options. However, our model differs from theirs in that we explicitly assume dominants have less information than subordinates: subordinates know perfectly the outside options of the dominant (i.e., solitary breeding success estimated from breeding site quality), because they explore and collect more information about the environment, but not *vice versa*. We also examine the role of information about the subordinate's relatedness to the dominant.

Whilst different types of models of skew exist, the concession model is the most suitable for our investigation of the effects of information for two reasons. First, in the concession model the outside options of the subordinate for independent breeding are clearly and explicitly set as one factor, which we can vary. Second, in the concession model it is possible to study the effect of uncertainty about outside options while retaining perfect information about all the other factors separate, which is useful to factors to disentangle the interacting effects of a suite of social and ecological factors. In the tug-of-war model, the outside options are only considered to the extent that groups do not form if they exceed the payoff of cooperative breeding, which is why the concession is more appropriate here.

Our model reveals a strong impact of the QPC: when subordinate quality correlates positively and strongly with group productivity, skew decreases with quality; otherwise, skew increases with subordinate quality. The average concession offered to subordinates should be greatest when dominants have imperfect information. The concession should always decrease with increasing relatedness between the dominant and subordinate.

The model

We extended the transactional concession model of reproductive skew (Reeve and Ratnieks, 1993) by incorporating variation in subordinate quality.

Subordinate quality (x) affects both their outside options and group productivity (Table 3.1), and is equal to the subordinate's fitness payoff associated with the outside options. In our model, subordinate quality does not refer to the abilities of the subordinate to engage in the reproductive conflict (tug-of-war) or in dominance challenge, and is independent from within-group competition. The variables are described in Table 3.1.

The contributions to the inclusive fitness of a dominant (d_A) and subordinate (s_A) that share a proportion r of their genes by common descent if they do not cooperate (i.e. if the subordinate leaves or is evicted) are

$$d_A = b + rx \text{, and} \tag{3.1}$$

$$s_A = rb + x \text{, respectively,} \tag{3.2}$$

Where b is dominant's relative competitive ability. Without loss of generality (because all else scales), we assume that subordinate quality is uniformly distributed between 0 and 1, and that dominants have quality equal to the highest quality subordinate (b=1). In our model, subordinate has productivity x when it leaves, while the dominant has b. Each gets the sum of their own productivity (direct fitness), plus the other's productivity multiplied by their relatedness (indirect fitness).

The dominant's expected fitness for all subordinates is

$$D_A = b + \frac{r}{2} \tag{3.3}$$

We start from the baseline case in which the dominant has perfect information about subordinate quality x to explore the impact of the subordinate's QPC (denoted a) on the basic concession model. The subordinate provides a benefit h to the group as a helper, which increases linearly with its quality x, with slope a and intercept m (Table 3.1, equation 3.4).

$$h = ax + m \tag{3.4}$$

If $a < 0$, the subordinates with good outside options will be poorer helpers, whereas if $a > 0$ they are the better helpers. The additional group productivity from the subordinate staying is assumed to be the product of h and the dominant's quality b; thus the total group productivity G is

$$G = b + bh = b(1 + m + ax) \qquad (3.5)$$

Hence, if the subordinate stays to help, the direct fitness of a dominant who gives reproductive concession y_i is

$$d_I = (1 - y_i)G = b(1 - y_i)(1 + m + ax) \qquad (3.6)$$

and that of the subordinate is

$$s_I = by_i(1 + m + ax) \qquad (3.7)$$

So the dominant's inclusive fitness is

$$\begin{aligned} d_P &= d_I + rs_I = b(1 - y_i)(1 + m + ax) + bry_i(1 + m + ax) \\ d_P &= b[1 - y_i(1 - r)](1 + m + ax) \end{aligned} \qquad (3.8)$$

For $r<1$, the dominant's fitness decreases as y increases, so they should give the smallest concession that will induce the subordinate to stay, which by rearrangement of (3.8) is :

$$y_P* = \frac{x - br(m + ax)}{b(1 - r)(m + ax + 1)} \qquad (3.9)$$

We can get analytical results for the perfect and no-information extremes (Appendix 3.A). We use Bayes' theorem in a numerical model to explore the effect of increasingly accurate information on the decisions and inclusive fitness of both individuals. We assumed that information affects the distribution of possible subordinate qualities considered by the dominant, for a given true quality x. In brief (see Appendix 3.A for details), given an actual quality x, the probability distribution of the dominant's perception of this quality, *z*, follows a beta distribution

$$P(z \mid x) = \frac{z^{\alpha}(1-z)^{\beta}}{B(\alpha,\beta)} \tag{3.10}$$

where B(α,β) is the sum of the distribution in [0,1] and the error is controlled by the amount of information *ω*, with

$$\begin{aligned} \alpha &= 1 + x\omega \\ \beta &= 1 + (1-x)\omega \end{aligned} \tag{3.11}$$

such that higher values of *ω* give a narrower distribution. Note that if *ω* = 0 (no information) all *z* (0 ≤ *z* ≤ 1) are equally likely and if *ω* = ∞ (perfect information) then P(*z*|*x*) = 1 if *z* = *x*. The dominant should make its decision based on the probability of each actual quality *x* given its perception *z*, which we calculate using Bayes' rule

$$P(x \mid z) = \frac{P(z \mid x) \cdot P(x)}{P(z)} \tag{3.12}$$

The dominant finds the optimal concession given the inclusive fitness consequences for each *x*, which will influence whether the subordinate leaves or stays, weighted by *P*(*x*|*z*). Dominants and subordinates may be in conflict about the quantity of information (*ω*) that the dominant has about *x*. After finding the optimal concession *y**, we find the proportion of the population of subordinates for which the dominant and subordinate would choose to stay in the group and the fitness consequences for each *x* by using the weighting $P(x \mid z)P(x)$.

In the baseline concession model, relatedness is 0.25 to mimic the common situation where subordinates help half-siblings or cousins (Härdling et al., 2003; Rabenold, 1985). We developed a similar numerical model to explore how dominant's information about their relatedness (Ω) to the subordinate influenced the predictions (see details in Appendix 3.B). We considered relatedness values within the range [0,1]. Uncertainty about the subordinate's relatedness was expected to influence the reproductive decisions, because the dominant would not be able to compare accurately its expected inclusive fitness when breeding cooperatively and alone. Note that we show results for all possible z, but for $\omega > 0$ not all z are equally likely. Thus, calculating fitness outcomes must take the distribution of (x,z) into account.

Table 3.1 Variables and parameters in the model and their baseline and explored values

Symbol	Description	Baseline value	Explored values (figures)
Individual traits			
x	Quality and outside option of the subordinate (i.e. direct fitness if breeding independently) $0 > x > b$	0.5	0 – 1 (Figure 3.1, 3.3, 3.4, 3.A1, 3.A2, 3.A3)
x_i	Quality of individual i	0.5	0 – 1
x_c	Critical quality x above which subordinate will leave to breed alone	Solved	
y	Reproductive share offered to subordinate by dominant (i.e. proportion of group productivity)	Solved	0 – 1 (Figure 3.1, 3.2, 3.3a-c, 3.A4)
y_c	Critical share above which subordinate will stay and help	Solved	
y^*	Optimal reproductive share for range of subordinates	Solved	(Figure 3.3a-c)
y^*_P	Optimal reproductive share when dominants have perfect information about x	Solved	Equation 3.9
z	Perceived subordinate's quality when dominants have information ω	0.5	0 – 1 (Figure 3.2, 3.A1, 3.A2)
G	Group productivity (fecundity per breeding season)	$G=b(1+h)$	Equation 3.5
Group traits			
b	Direct fitness of a solitary dominant breeder	1	-

h	Effect of helping on group reproductive output	$h = ax + m$	Equation 3.4
m	Benefit of cooperation: Minimal effect of helping on group reproductive output	*0.35*	Equation 3.4 (Figure 3.1, 3.5, 3.A3)
a	Effect of quality x on group productivity: subordinate's quality-productivity coefficient (QPC)	0.5	-1 – 2 (Figure 1, 3, 4, 5, A4)
d_I	Productivity of a dominant (i.e. direct fitness)		Equations 1.6, 1.8
s_I	Productivity of a subordinate (i.e. direct fitness)		Equations 1.7, .18
Individual fitness			
d_P	Dominant inclusive fitness with no information (i.e. mean reproductive value of dominants)	Optimised	Equation 3.8 (Figure 3.1, 3.3d-f)
D_A	Dominant's expected inclusive fitness for all subordinates		Equation 3.3
v_A	General inclusive fitness of solitary dominants		Equation C1
v_P	General inclusive fitness of dominants with perfect information		
v_N	General inclusive fitness of uninformed dominants		Equation 3.A23
d_A	Dominant inclusive fitness when alone (i.e. mean reproductive value of solitary dominants per breeding season)		Equation 3.1

d_D	Direct fitness of a dominant who breeds cooperatively		Equation 3.A4
s_D	Direct fitness of subordinate who breeds cooperatively		Equation 3.A4
d_C	Inclusive fitness of a dominant when cooperatively breeding		Equation 3.A7
s_P	Subordinate inclusive fitness when dominants have perfect information (i.e. mean reproductive value of subordinates per breeding season)		Equation 3.2
s_N	Subordinate inclusive fitness when dominants have no information (i.e. mean reproductive value of subordinates per breeding season)		
r	Symmetric relatedness between the dominant and subordinate	0.25	0 – 1 (Figure 3.4, 3.6)
Information parameters			
ω	Dominant’s information about subordinate’s quality $0 > \omega > +\infty$	$2^4 = 16$	0, 2^0, 2^4, 2^{10}… ∞ (Figure 3.2, 3.4)
$P(z \mid x)$	Probability that quality x is perceived as quality z.		Equation 3.10
α, β	Parameters of the beta probability distribution $P(z \mid x)$		Equation 3.10
Ω	Dominant’s information about relatedness to the subordinate	$2^4 = 16$	0, 2^0, 2^4, 2^{10}… ∞ (Figure 3.A4)
θ	Beta-weighted distribution of what dominant infers from observation ω about x		
s	Mean reproductive value of the subordinate	Optimised	(Figure 3.1, 3.3g-i)

Results

Comparing perfect information and no information about subordinate quality

First, to understand the broad effect of information, we explored the interaction between the quality-productivity coefficient a and subordinate quality x in their effect on the optimal concession and fitness outcomes when the dominant has either perfect or no information. We could get analytical results for the effects of this absence of information (Figure 3.1, Table 3.2). We set the dominant's solitary breeding success at b = 1 throughout, to be equal to the highest-quality subordinate. To study the effect of a on the slope of fitness and optimal concession, but avoid changing the magnitude of the fitness with a, we kept h constant for the average subordinate (x = 0.5) by negatively linking m to a following $m = 0.6 - a/2$ so that the total group productivity for the average quality was always 1.6 (Figure 3.1, equation 3.4). Thus, the expected group productivity for the average subordinate is slightly higher than the sum of the solitary breeding productivities ($b + x$ = 1.5).

Table 3.2 Predicted effects of subordinate's quality-productivity coefficient (QPC, a) on the reproductive strategies of cooperative breeders. Optimal concession y^* is the reproductive share that maximises inclusive fitness

Effect	**Subordinate's quality-productivity coefficient *a***	
Reproductive behaviour	**Low (*a*<1)**	**High (*a* >1)**
*x on y**	positive	negative
Optimal concession y and information about x*	*y**Perfect lower than *y**NoInfo; *y** maximal at low information	*y**Perfect higher than *y**NoInfo *y** maximal at No Information
Optimal concession y with r*	decrease	decrease
Cooperative breeding	low *x*	high *x*
Solitary breeding	high *x*	low *x*

We show that having no information about subordinate quality affects the predictions of the basic concession model (Figure 3.1). The analysis predicts that when dominants have perfect information, concession should increase with subordinate quality *x* (Figure 3.1a–c) unless the effect of *x* on group productivity is very strongly positive ($a > 1$, Figure 3.1d), in which case higher-quality subordinates are willing to stay regardless of concession, so dominants can offer less. Dominants should breed cooperatively with low-quality subordinates when *a* is weak or negative ($a < 0.6$, Figure 3.1e,f) because for low-quality subordinates (but not high-quality ones), dominant fitness is higher with the subordinate than alone. However, as for strong positive *a*, retaining a high-quality (but not a low-quality) subordinate increases dominant fitness compared to solitary breeding, so dominants should breed cooperatively with high-quality subordinates (Figure 3.1g,h). These effects occurred when dominants had perfect and no information. Unexpectedly, the effect of *x* on payoffs and skew for average subordinates (around $x = 0.5$) is negative if *a* is small or negative and positive if *a* is large (Figure 3.1a-d,j-l).

Dominants with no information get lower payoff than those with perfect information across much of the range of *x,* but most strongly for intermediate values where they fail to breed cooperatively when they should (Figure 3.1e-h). Subordinates get higher inclusive fitness as a subordinate when *x* and *a* are either both high or both low (Figure 3.1i–l) because dominants offer more than they need to induce the subordinate to stay.

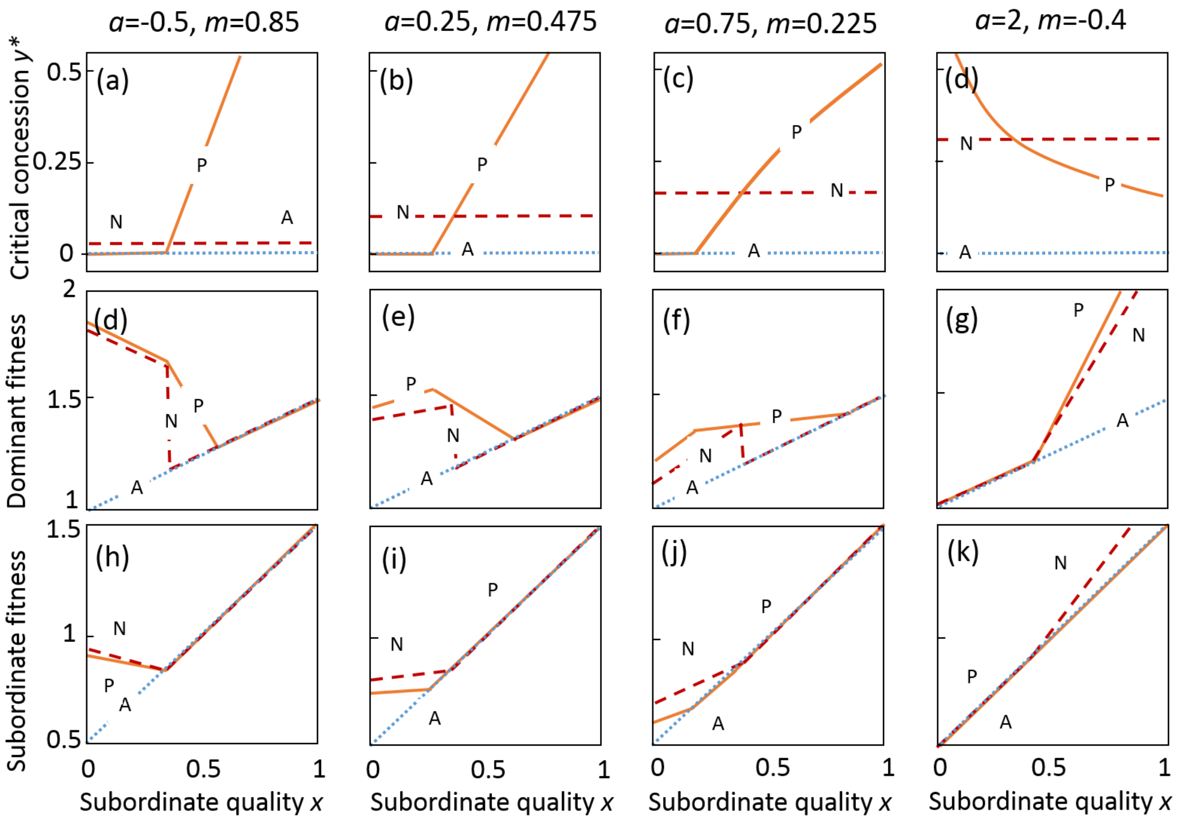

Figure 3.1 Optimal concession (a-d), dominant inclusive fitness (e-h) and subordinate inclusive fitness (i-k) for some representative values of *a* and *m* (columns) under perfect information *P*, no information *N*, and when alone *A*. The dotted lines in (a-d) indicate *y*=0. The dominant fitness depends on whether the dominant wants the subordinate to stay (d_P, $d_N > d_A$) and whether the subordinate chooses to stay (d_N, $s_N > s_A$). The dominant always does at least as well as no information when they have perfect information, whereas the opposite is true of the subordinate. Other parameter values: *r*=0.5, *b*=1

Responses to perceived subordinate quality

To understand the role of imperfect information, we explored group membership decisions given the dominant's optimal concession $y_M(z)$ for the range of perceived (z) and actual (x) quality: whether the subordinate wants to stay and whether the dominant wants them to stay (Figure 3.2, see Appendix 3.A for details). For moderate effects of subordinate quality and moderate relatedness (i.e. a = 0.5) (m = 0.35, r = 0.25), the dominant always wants the subordinate to stay given $y_M(z)$ (Figure 3.2), but the subordinate does not stay if the concession is too low.

In all cases, the range of actual subordinate qualities where groups fail to form increases as information decreases (height of yellow areas decreases right to left). Under no information (Figure 3.2a), y^* is constant (since there is no perceived quality z) and subordinates stay only if their actual quality is below a constant threshold. With $\omega > 0$, y^* increases with z and so this threshold also increases (Figure 3.2b-d). For good or perfect information (Figure 3.2c,d), there is a z above which the dominant perceives the necessary concession to be too great, so they offer nothing, but very low-quality subordinates would still stay due to the indirect fitness benefits of helping.

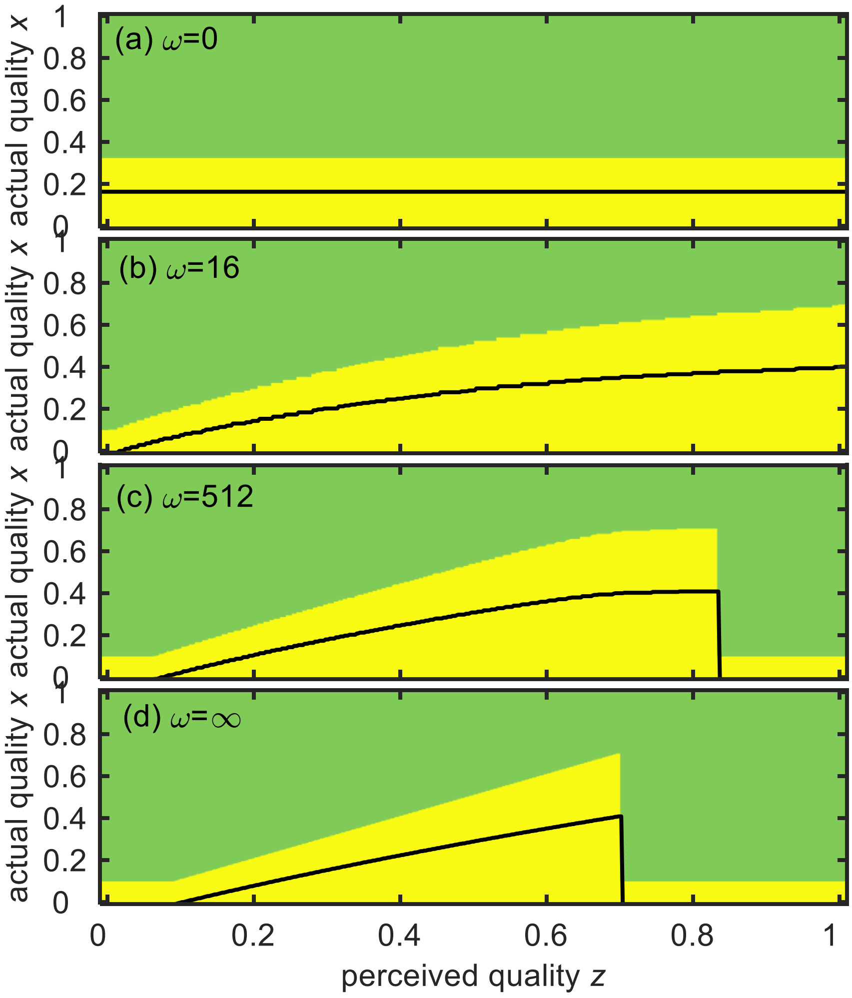

Figure 3.2 Effect of perceived quality of subordinate z on the optimal concession y^* (black lines) for four levels of knowledge: (a) no knowledge ω=0, (b) some knowledge ω=16, (c) high information ω=512, (d) perfect information ω=∞. The colours show the areas of perceived quality by dominant (horizontal axis) and actual quality of subordinate (vertical axis) where for the optimal y both dominant and subordinate would do better in a group (green)*;* only the dominant would do better in a group (yellow). Other parameter values: a=0.5, m=0.35, r=0.25.

The quality–productivity coefficient (a) strongly influences group formation. Dominants with no or imperfect information always would do better with a subordinate if $a = 0.5$ (Figure 3.2), but not for high perceived quality if $a = -0.5$ or 0.25 (Figure 3.A1). When a is low but positive, dominants prefer to form a group but subordinates prefer to breed alone if the concession is not higher than their quality x, as it is not sufficient to retain them (Figure 3.2). When $a < 1$, dominants with low information gave the highest concession (Figure 3.3a,b), due to the shape of the relationship between the (expected) quality and concession (Figure 3.2). When a is low (Figure 3.4 left and middle), there is a threshold of minimal subordinate quality below which groups are unlikely to form because on average subordinates prefer to breed alone (green and blue areas). When the effect of subordinate quality on group productivity is negative (left column), the regions of solitary breeding are larger because the group productivity is smaller. When group productivity strongly depends on subordinate quality (i.e. high a; Figure 3.4 right), dominants would breed cooperatively with subordinates of high, but not zero, quality (Figure 3.4c,f,i) and the threshold of minimal subordinate quality decreases with relatedness.

For higher relatedness (Figure 3.4h,k), there is a region of moderate information where both dominants and subordinates prefer to breed alone, because breeding separately increases the dominant’s inclusive fitness compared to the large concession the subordinate would require to stay. There is a region of low-quality and low information where moderately related subordinates want to stay, but the dominant does not want them because they would reduce group productivity to a potentially large degree.

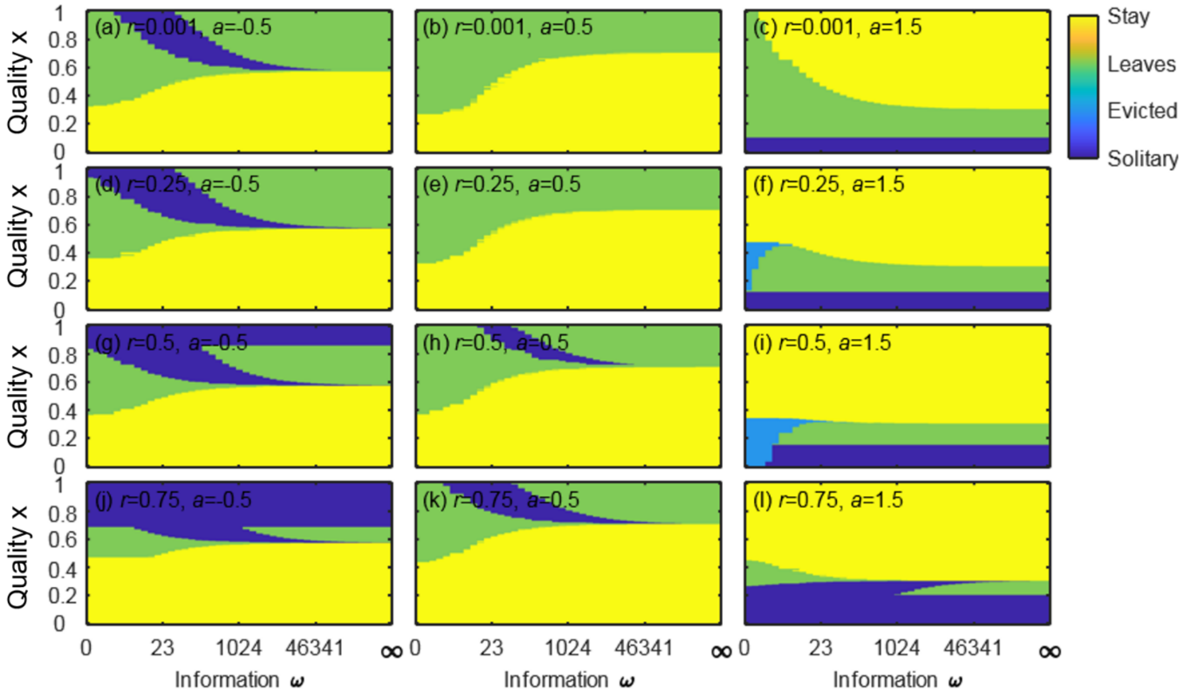

Figure 3.3 Effect of information about *x* on the prediction of cooperative breeding for various QPC (*a*) and relatedness (*r*). The colours show the areas of dominants' level of information about *x* (horizontal axis) and actual quality of subordinate (vertical axis) where for the average decision across all perceived subordinate qualities was: to stay for both dominant and subordinate (green); only the dominant wants to breed cooperatively (yellow); only the subordinate wants to breed cooperatively (cyan); or neither wants to breed cooperatively (blue), for 3 values of quality-productivity coefficient *a* (columns) and four values of relatedness (rows); values shown on panels

Effect of uncertainty about subordinate quality on mean fitness

When group productivity moderately increases with subordinate quality (*a* = 0.5, Figure 3.4 middle column), dominants with perfect information give a smaller concession than those with no information, but the effect of information on concession size is not monotonic, with a maximum at some intermediate information level (Figure 3.4b). This occurs because having some information may allow the dominant to know that subordinates are not very low-quality ones who should be offered zero because they only moderately increase productivity. Therefore, greater concessions can be given knowing that the investment will be worth it. At higher information dominants know that the subordinate is not high quality so can offer only what is necessary. Intuitively, dominant inclusive fitness increases with information (Figure 3.4e) but with diminishing returns as concessions and payoffs are similar for subordinates of similar quality. Due to the effect on concession, the effect of information on subordinate fitness is not monotonic (Figure 3.4h) but is always lowest when dominants have perfect information.

A decreasing effect of *x* on group productivity (*a* < 0, Figure 3.4 left column) has similar results to when 0 < *a*< 1. On the other hand, when *x* strongly positively affects group productivity (*a* > 1, Figure 3.4 right column), information always decreases the concession and so subordinates have highest fitness when dominants have no information.

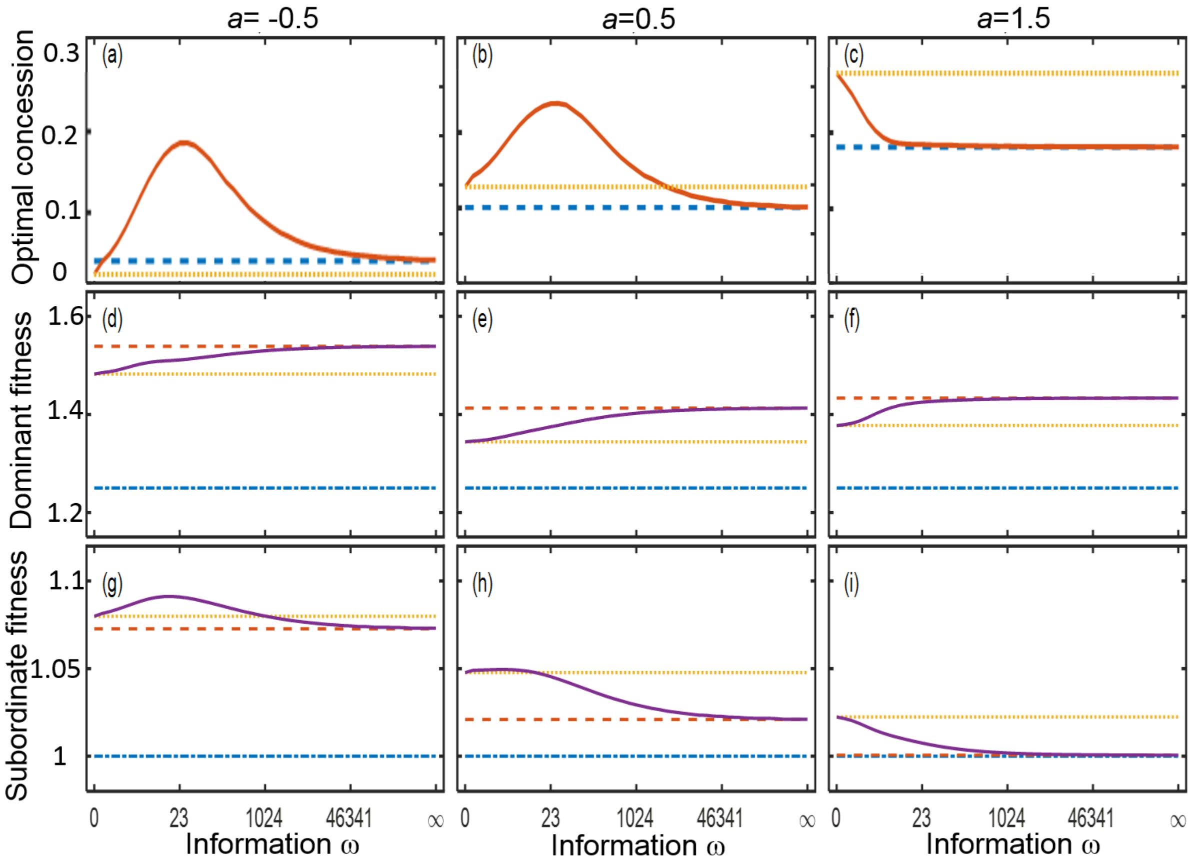

Figure 3.4 Effect of information about *x* on decisions and fitness outcomes for all possible subordinates. (a-c) optimal concession (*y*);* (d-f) average dominant inclusive fitness and (g-i) average subordinate inclusive fitness, as a function of the quantity of information about the subordinate’s outside option. Columns show

different values of quality-productivity coefficient and synergy effect *(a, m)* (columns: left $a=-0.5$, $m=0.85$; middle $a=0.5$, $m=0.35$; right $a=1.5$, $m=-0.25$). Lines indicate gradually increasing information (solid line), and analytical solutions for perfect information (dash line), no information (dotted line), fitness alone (dot-dash line). Other parameter values: $b=1$, $r=0.5$

Comparison to previous work on information and skew

To compare our results to those of Akcay et al. (2012), where helping effects do not vary with individuals' outside options, we set a constant group productivity ($a=0$, $m=\frac{1}{b}-1$) and altered the qualities of both the dominant (b) and the subordinate (x) (for details see Figure 3.C2). Cooperative breeding occurs when subordinate quality is high and dominant quality is low, since then the dominant benefits most and is willing to give a large concession (Figure 3.C2a, d). Uncertainty creates a large region of space in which the dominant would accept the subordinate but does not give a sufficiently large concession, and this area is partly in the space where groups would form under perfect information. Between these two regions of consensus where both either want to form a group or breed alone, dominants fail to retain subordinates (Figure 3.C2a-c). The zone of conflict over group formation is where the benefit of cooperation m and the subordinate's outside option x add up to a small positive value. Thus, the results of Akcay et al. (2012) are robust to departures from the assumption of symmetrical information.

Optimal information about subordinate's quality

Our model shows that information about the quality of a potential subordinate, as opposed to mere information about the probability distribution of this quality, increases dominants' inclusive fitness. However, dominant fitness does not increase linearly but is asymptotic (Figure 3.4d-f); therefore, if there are costs or constraints of acquiring or using information, then selection would not lead to perfect information. For illustration, we assume each unit increase in information ω costs an arbitrary 0.003 units of payoff, which allows us to find where the effect of gaining information is negligible; we refer to this as the 'optimal' information for dominants. By contrast, increasing dominant information has a non-monotonic effect on fitness for most subordinates in most situations (Figure 3.4h-i), so no costs are assumed when seeking the optimal information for subordinates.

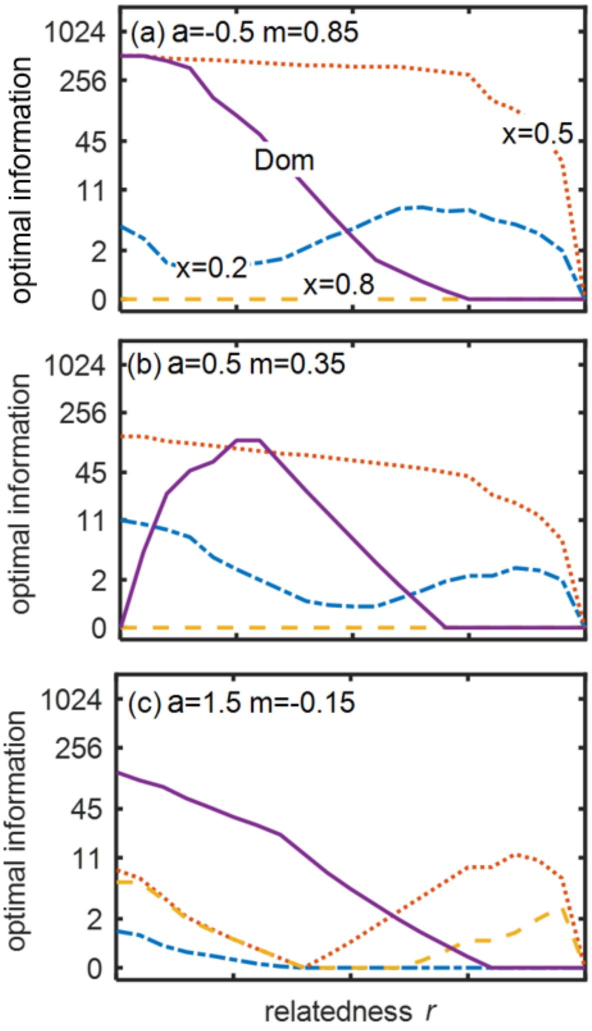

Figure 3.5 Optimal amount of information about quality for dominants and subordinates of three different qualities (lines) for three values of the quality-productivity coefficient *a* (rows). Lines indicate dominant (solid lines), low-quality subordinate (*x*=0.2, dot-dash lines), average subordinate (*x*=0.5, dotted lines), high-quality subordinate (*x*=0.8, dashed lines)

In general, the optimal information for dominants decreases as relatedness increases (Figure 3.5, solid lines), because necessary concessions are lower and have less effect on the dominant's fitness due to indirect fitness when the subordinate breeds. The exception is where *a* = 0.5 and relatedness is low (left of Figure 3.5b), when increasing relatedness increases the need for information because low-quality subordinates will stay even if they get zero concession, so it is worth identifying these subordinates.

The optimal information is very different for different qualities of subordinate, being in general greater for average-quality subordinates (Figure 3.5, dotted lines) because the optimal concession is greatest at intermediate *x*, so these subordinates want to be distinguishable from the others. This declines as relatedness increases because the concession approaches zero. The highest-quality subordinates (Figure 3.5, dashed lines) rarely get to stay, so it is better for them if dominants have less information, as then they will offer some concession.

Uncertainty about relatedness

Individuals may have uncertainty not only about quality, but also about relatedness. We ran similar analyses to those above but with *x* known perfectly to the dominant and varying and uncertain *r*. For all feasible values of parameters, the optimal concession decreases as relatedness and information increases (Appendix 3.B: Figure 3.B1). The magnitude of this varies with *x* and *a.* Consider a full offspring or sibling (*r*=0.5). If they are of low quality and quality strongly affects group productivity (Figure 3.B1b), or if they are of high quality and quality weakly affects group productivity (Figure 3.B1c), then the concession, and hence subordinate fitness, is only slightly reduced by information. By contrast if subordinates are of low quality and quality weakly affects group productivity (Figure 3.B1a), or if they are of high quality and quality strongly affects group productivity (Figure 3.B1d), then the concession is greatly reduced by information and so subordinate fitness would be greatly reduced.

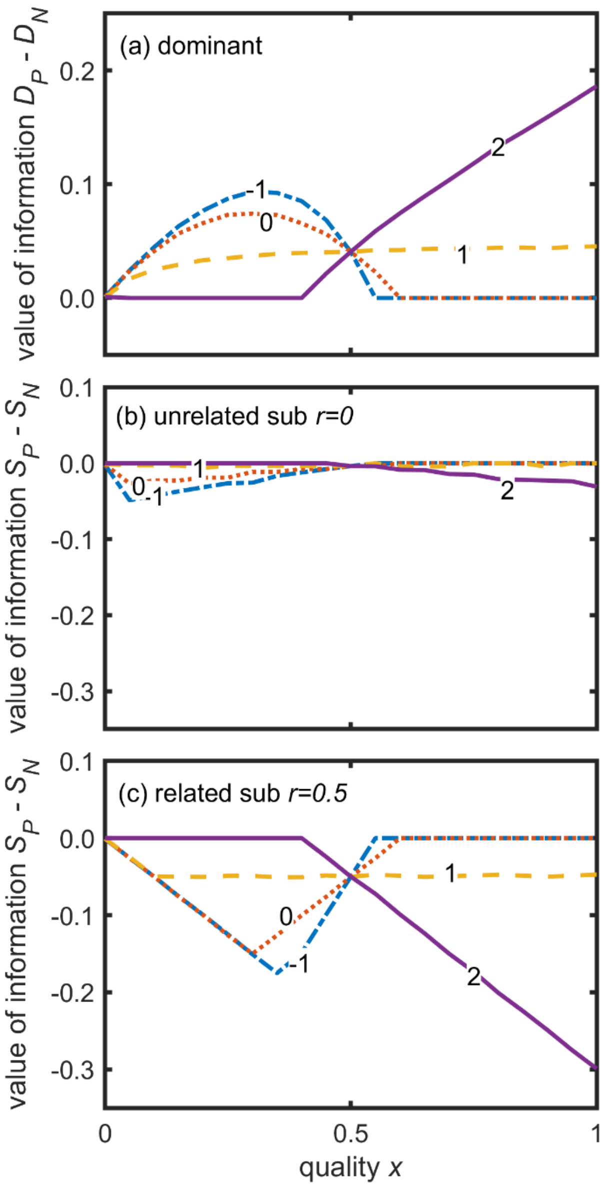

Figure 3.6 Value of information about relatedness as a function of subordinate quality (horizontal axes) for four values of *a* (lines). The vertical axis is the difference in realised inclusive fitness between the perfect information (*r* known) and the no information case (*r* could be any value). Panels show values of information (a) to the dominant and to the unrelated (b) or related (c) subordinate

The predictions about the value of information about relatedness reflects these differences (Figure 3.6). Here, we compare the actual fitness of the individuals for all perceived relatedness values (Figure 3.6). The dominant would greatly benefit from information about relatedness if the subordinate is of low quality (*x*) and the relationship between subordinate quality and group productivity (*a*) is weak or negative (dotted and dot-dashed lines), or if *x* is large and *a* is strongly positive (solid and dashed lines) (Figure 3.6a). Whilst unrelated subordinates are almost unaffected by the dominant’s information (Figure 3.6b), related subordinates show an opposite pattern to the dominant’s but of greater magnitude (Figure 3.6a,c): related subordinates get greater fitness if the dominant does not know how related they are.

Discussion

Using a transactional concession model of reproductive skew with explicit variation and uncertainty, we have shown that the direction of the associations between skew, subordinate outside option and relatedness is influenced by how subordinate quality affects group productivity (Quality-Productivity Coefficient). We have extended the theoretical framework for reproductive skew with two new realistic additions: (i) an association between the subordinate’s outside options and group productivity; and (ii) dominant’s uncertainty about their subordinates. Varying the level of uncertainty (i.e., quantity of information) of dominants about the subordinate’s outside options influenced the optimal concession and fitness outcomes.

The importance of the subordinates’ effect on productivity

Empirical tests of the models of reproductive skew have so far yielded inconclusive evidence, as subordinate share has been found variously to increase, decrease, or not significantly vary with subordinate outside options, relatedness and group productivity (Nonacs & Hager, 2011). Our model revealed that the subordinate’s quality–productivity coefficient (QPC) can alter the sign of the relationships amongst the optimal concession, subordinate quality, and relatedness. Dominants maximise their inclusive fitness by retaining low-quality subordinates when the QPC is negative (as those will provide more help), and high-quality subordinates when the QPC is strongly positive.

Our model predicts that information about kinship influences fitness only when the subordinate’s quality and how this quality translates into group productivity are both high or both low, which might explain the diversity of empirical test results. High-quality subordinates with a low QPC would not get a striking increase in their indirect fitness from helping. Conversely, subordinates who can greatly improve group productivity but have limited outside options may prefer to stay for a low reproductive share, regardless of their relatedness.

Our model shows that simply changing the link between subordinate quality and group productivity can switch on (and off) cooperative breeding. When the QPC is high, the optimal share decreases with the (perceived) subordinate quality, which supports the original concession model of skew (Verhencamp, 1983). This finding also matches the prediction of a recent tug-of-war model incorporating variation in the ratio of available breeding sites (comparable to the outside options in our model), in which subordinate share decreased with nest competition when subordinates had the choice between breeding sites (Nonacs, 2019). Conversely, when the QPC is low (or negative), the optimal share increases with subordinate quality, in line with the predictions of the restraint model (Reeve & Ratnieks, 1993) and suggesting that the QPC might actually determine which individual controls the allocation of reproduction within a transactional framework (Buston, Reeve, Cant, Vehrencamp, & Emlen, 2007). We expect the QPC to be high in conditions where subordinates have limited outside options and group living is favourable, such as harsh environments rife with outgroup conflict, because individuals would benefit from staying to help until their quality is sufficiently high to disperse and breed (Kokko & Ekman, 2002).

Separating the helping effect into the subordinate's quality and their QPC allows us to disentangle the effects of individual and environmental factors, which may partly explain the variation among and within species in the quality and relatedness of subordinates. Indeed, either high- or low-quality subordinates may be selected to help (Barclay & Reeve, 2012). Selection for helping by low-quality subordinates may give rise to two distinct developmental trajectories into helper or breeders (Fischer et al., 2017).

Conflict over information about subordinates' quality

A conflict over the optimal level of information about subordinate quality is predicted, as dominants maximise their fitness at a higher information level than subordinates. Having some information about the subordinate's quality increases the concession offered by the dominant, as dominants act as though they overestimate the benefits the subordinate will provide, and behave generously to retain the subordinate. Dominants should increase their concession as subordinate quality increases above a certain threshold. The maximal concession should occur when dominants have low levels of information about subordinate quality (unless the subordinate's QPC is large and positive), as dominants should concede higher reproductive shares. This conflict over the optimal quantity of information is somewhat analogous to models of chick begging, where offspring can conceal their true hunger state to increase parental feeding, in that information is asymmetrical (e.g. Godfray & Johnstone, 2000). However, in the parent–offspring signalling game, the parent will not desert the offspring and the aim is to find the optimal parental effort, whereas in our model of skew groups can break apart. This possibility to leave the interaction partner resembles game theoretical models of divorce strategies in birds, where individuals pair randomly without any information about their partner's quality (McNamara, Forslund, & Lang, 1999). However, in the divorce game, individuals gain perfect information about their partner's quality after the first breeding season and before deciding whether to stay or leave, whereas in our model the dominants' levels of information remains constant and individuals decide to form a group before the first (and only) breeding season. As in our model, in the divorce game both individuals can decide whether to leave and find a better option (i.e. divorce). High-quality individuals form stable bonds whereas low quality individuals divorce frequently (McNamara, Forslund, et al., 1999). When both sexes can divorce, high-quality individuals are choosier and divorce less commonly, because both sexes should be less choosy as their probability to be deserted by their partner increases.

An ability to obtain information about the subordinate's outside options is likely to be selected for when the expected breeding success of a solitary (dominant) breeder is low. This fits with phylogenetic data from taxa in which cooperative breeding is largely concentrated in harsh unpredictable environments (Lin, Chan, Rubenstein, Liu, & Shen, 2019; Rubenstein & Lovette, 2007), where dominants' expected solitary breeding success is low and subordinates may vary in quality (e.g. early-life effects: Taborsky, Arnold, Junker, & Tschopp, 2012). In such situations, dominants would benefit from information about subordinate quality to inform their own reproductive decisions. However, food scarcity could increase uncertainty by reducing the precision of the perceived information, potentially causing dominants in harsh environments to face higher uncertainty (McNamara, Forslund, et al., 1999; Padamsey, Katsanevaki, Dupuy, Rochefort Correspondence, & Rochefort, 2021). Dominants may then prefer to retain subordinates rather than breed alone, which could favour the evolution of cooperative breeding. Dominants may seek information about subordinates' quality by exploring the surroundings of the nest (to assess whether potential mates and breeding sites are available) and observing the subordinate to determine its condition (e.g., its size or sexual maturity: Young et al., 2006).

Counteracting this, subordinates may evolve strategies to increase dominants' uncertainty about their quality. Downplaying apparent quality (e.g. by reducing their helping effort) should be easier for subordinates than pretending to be stronger, because the evolution of honest signalling will tend to constrain the upper limit on work capacity (e.g. Weaver, Santos, Tucker, Wilson, & Hill, 2018; Wright et al., 2021). Subordinates may also conceal their mating, leading dominants to underestimate their outside options. Indeed, birds are sensitive to others' visual perspective and can adjust their mating behaviour to keep information private (Arnold, 2000). Evidence of this concealing strategy (i.e. sneaky mating) by helpers exists in mammals, birds and fish (Chen, Li, Liu, & Li, 2021; Creel et al., 1993; Hellmann, Stiver, Marsh-Rollo, & Alonzo, 2019).

Conflict over information about relatedness

In line with the original concession model of skew, our model predicts that skew should increase with relatedness, which suggests kinship influences reproductive games even when subordinate information and subordinates' quality vary (Verhencamp, 1983). While empirical data mostly do not support models of skew within species, skew does increase with average relatedness across species (Nonacs & Hager, 2011), at least in birds (Riehl, 2017) and social wasps (Oi et al., 2021). Kinship may shape – and hence predict – skew at the between-species level, but it is less clear whether it does so within species (Dugdale et al., 2008; Haydock & Koenig, 2003a; Kaiser, Martin, Oteyza, Armstad, & Fleischer, 2018; Widdig et al., 2004).

Our model predicts that dominants will seek information about relatedness that most subordinates are willing to provide, but only up to a point, and only if relatedness is low. A conflict in the optimal information about relatedness emerges with high relatedness. Dominants are selected to concede as little reproductive share as possible and can give less to related subordinates to match the outside option. As a consequence, related subordinates should be selected to withhold information about relatedness, to ensure dominants give them higher reproductive share. The majority of cooperative breeding occurs in family groups (Hatchwell, 2009; Rosenbaum & Gettler, 2018), which implies high and stable relatedness levels between the helper(s) and the dominant. This small variation in relatedness might be associated with little variation in dominant fitness which would not select for kin recognition. For instance, the choice between different breeding sites might be based on less information if there are fewer available breeding sites. Indeed, a model of cooperative breeding found that the difference in fitness across outside options decreases with breeding site saturation (Nonacs, 2019a). This indirect investigation of information suggests that the value of information about potential breeding sites is lower when fewer sites are available. Increasing information sampling might therefore only minimally increase fitness. The value of the information about one factor might decrease with the amount of the variance in fitness that this factor provides, suggesting that information about relatedness will not be highly valuable in most cooperative breeders (who live in family groups).

Subordinates' reproductive share decreases as dominants' information about their relatedness increases, while dominants' optimal level of information about relatedness decreases with relatedness. Taken together, these predictions reveal a lack of selection for true kin recognition, as subordinates should conceal relatedness and dominants are not strongly selected to acquire it. Perhaps, true kin recognition did not evolve in most within-species empirical studies where skew did not significantly correlate with relatedness (Nonacs & Hager, 2011). Kin-biased behaviour (i.e. kin discrimination) based on familiarity or stimuli in common such as location or nest odour to discriminate/recognise kin (Charpentier et al., 2020; Holmes & Sherman, 1983; Levréro et al., 2015) is well documented (e.g. Komdeur, Richardson, & Burke, 2004; Mitchell, Kyabulima, Businge, Cant, & Nichols, 2018). However, few studies have demonstrated true kin recognition (i.e.

phenotype matching) (American toads *Anaxyrus americanus*, pig-tailed macaques *Macaca nemestrina*, mandrills *Mandrillus sphinx;* Charpentier et al., 2020; Holmes & Sherman, 1983; Levréro et al., 2015; Rodrigues De Souza et al., 2017). Recent empirical work indeed found no evidence for kin recognition in House sparrow (*Passer domesticus*), as male breeders did not discriminate their own offspring from others in their parental care (Lattore, Nakagawa, Burke, Plaza, & Schroeder, 2019), which seems to contradict Hamilton's rule but is in line with our predictions. A recent model found that stable inaccurate recognition should evolve when the payoff to the interaction partner that benefits from this dishonest signalling is higher than the payoff to both interaction partners when kin recognition is accurate (Sheehan & Reeve, 2020). This prediction is in line with our findings that individuals who benefit from errors might select for high uncertainty. Non-discriminating kin may be adaptive if this "veil of ignorance" promotes the redistribution of help to the young that need it most, promoting equality and higher fitness of all group members (Marshall et al., 2021). Another model predicted that in closely related groups, animals would be selected to help without kin discrimination (Duncan, Gaynor, Clutton-Brock, & Dyble, 2019). By disentangling kin recognition from relatedness, our model allows us to detect a possible strategy of kin concealment by related subordinates.

Future tests of the predictions

Our model predicts that QPC changes the direction of the link between skew and subordinate quality. To test these predictions, future experiments could compare dominant's acceptance of related subordinates in periods of outgroup conflict (high subordinate QPC) and periods of good environmental quality but high within-group conflict (low subordinate QPC) in two situations: reproductively mature subordinates with several available mates (high quality) and reproductively immature subordinate with no available mates (low quality). Group size may correlate negatively with the QPC, as individuals with similar outside options (quality) help less in larger groups. Here, we predict that older (i.e. higher-quality) subordinates will more often leave the group than younger (lower-quality) subordinates when foraging requires high skill, in large groups and when breeding sites are available, since these conditions are likely associated with low subordinate QPC. In meerkats, both prey-catching abilities and outside options increase with age (Thornton, 2008; Thornton & McAuliffe, 2006), and the oldest subordinate females are more often evicted in large groups – where sneaky mating with unrelated males is likely more frequent – than in small groups (Clutton-Brock et al., 2010). Higher-quality subordinate meerkats therefore leave the group more often in conditions where QPC appears to be low, which matches our predictions. Further empirical studies should test the predictions by measuring QPC, subordinate quality and relatedness.

It is clear that information should influence the decisions of the individuals and should therefore be considered where possible in studies of social life. Future empirical studies could potentially test the effect of uncertainty about subordinates' outside options with experiments that manipulate the quantity of information. This might be feasible in certain species that will breed cooperatively in the laboratory, for example the cichlid *Neolamprologus pulcher*. For instance, a subordinate without a breeding position and a resident dominant could be placed in adjacent tanks in an observation phase. The subordinate, but not the dominant, would be able to see potential breeding sites (i.e. the subordinate's outside options) by using an occluder for the dominant. Different experimental treatments would vary the outside options of the subordinate and the visual access of the dominant to those outside options. The dominant and the subordinate would then be given the opportunity to form a group (or not) and breed, to measure skew and cooperative breeding. The dominant could also be given erroneous information, such as via a screen that displays a different number (or quality) of breeding sites, to test the effect of the quantity of information on skew and group formation.

Chapter 4 – Adaptive levels of skew under sex differences and parental conflict

Dunnock (*Prunella modularis*)

Abstract

Sexual reproduction often entails cooperation between the two parents, and in cooperative breeders additionally between helpers and parents. Models of reproductive skew focus on the conflict between the same-sex subordinate and dominant, whereas the parental effort game explores the conflict over maternal and paternal investment. Since these conflicts are studied in isolation, it is unclear how the presence of the opposite sex might affect skew and how subordinates might affect effort by the opposite sex. Here, we incorporate the parental effort game into a synthetic model of skew combining transactional and tug-of-war models of skew. The model predicted no effect of the skew in one sex on the other sex. Subordinate share decreased with parental effort benefit but did not vary with parental effort cost. Subordinate share also decreased with dominant solitary group productivity in the synthetic model, as predicted by the restraint model alone. Overall, nest availability did not influence reproductive strategies in the synthetic model, and dominant conflict trait and subordinate share increased with subordinate competitive ability while subordinate conflict trait decreased. The sex with the higher breeding site availability might evolve very high levels of intra-sexual conflict over the share of reproduction. Our findings suggest that models of skew and parental effort games can be studied in isolation without loss in biological realism, as factors in one sex did not affect the reproductive strategies of the other sex. Empirical tests with variation in nest availability would provide helpful indications regarding the applicability of the model.

Keywords: subordinate competitive ability; reproductive skew; parental effort; variation; outside option, cooperative breeding.

Introduction

Sex differences in cooperative breeders

Sexual reproduction entails cooperation between the two parents, and between helpers and parents in cooperative breeders. Yet, producing the next generation can also give rise to conflict (Trivers, 1972), as each parent strives to maximise its life-time reproductive success by letting the other parent carry out more of the offspring care (McNamara, Gasson, & Houston, 1999; McNamara, Houston, Barta, & Osorno, 2003). Similarly, in cooperative breeders, subordinates and dominants are in conflict over the share of reproduction (Verhencamp, 1983). While parental efforts increase group productivity, the reproductive conflict over the share of group productivity (skew) can decrease it if individuals inflict harm to offspring (e.g. infanticide (Creel, 2022; Mumme, Koenig, & Pitelka, 1983; Saltzman, Digby, & Abbott, 2009)) or incur body condition costs in intrasexual conflict (e.g., Barboza, Hartbauer, Hauer, & Blake, 2004; Nelson-Flower et al., 2013) which is linked to lower caring effort (e.g., Clutton-Brock, Russell, & Sharpe, 2003; Reeve, Emlen, & Keller, 1998). It is important to focus on both competition and cooperation (Croft, Brent, Franks, & Cant, 2015), as the costs and benefits shape animals' social decisions.

In cooperative breeders, foregoing reproduction is typical of helpers (Clutton-Brock et al., 2010; Hearn, Davies, & Schwarz, 2022), although not universal (e.g. (Cant et al., 2013; Keane et al., 1994a). Reproductive skew refers to how unequally the dominant and the subordinate(s) share the group reproduction (Verhencamp, 1983). Variation in skew is influenced by several factors, such as relatedness (*Euglossa melanotricha:* Andrade, Miranda, Del Lama, & Nascimento, 2016), competitive abilities (*Neolamprologus pulcher:* Heg & Hamilton, 2008) and the subordinate's outside option (*Suricata suricatta:* Clutton-Brock et al., 2001). Models of reproductive skew incorporate such factors to attempt to understand what causes variation in skew (Buston, Reeve, Cant, Vehrencamp, & Emlen, 2007; Johnstone, 2000; Shen & Kern Reeve, 2010). However, models of skew do not currently provide a complete explanation of the diversity of behavioural strategies of cooperative breeders (Nonacs & Hager, 2011; Nonacs, Reeve, & Starks, 2004), which suggests that important selective pressures have been overlooked.

Sex differences in reproductive skew have been documented in cooperative breeders. In dwarf mongooses (*Helogale parvula)* skew is higher in females than in males (Keane et al., 1994b). By contrast, skew is higher in males than in females in the social cichlid fish species (*Neolamprologus multifasciatus)* (Bose et al., 2022) and (*N. pulcher*) in which subordinate females produce 14.5% and males 4.5% of the group's offspring. While empirical studies have explored the proximate mechanisms of this difference (e.g. (Abbott, 1984; Keane et al., 1994b; Tibbetts, Fearon, Wong, Huang, & Tinghitella, 2018; Young et al., 2006)), the function of these sex differences in skew are not well-understood.

A potential approach to understand sex differences in skew is to combine the skew games with a game where females and males are present. Indeed, it is important to consider how different games are connected and interact (McNamara, 2013), as animals' decisions are not made in isolation from each other. The Houston-Davies (1985) parental effort game aims to predict the evolutionary stable strategies (ESS) levels of offspring provisioning of a male and a female (reviewed and extended in Ewald, McNamara, & Houston, 2007), when parents pay a cost to their future reproductive success. If offspring provisioning has diminishing returns, then each parent should reduce its effort if the partner increases their effort, unless the parents are in pairs with lifetime monogamy. A meta-analysis in birds supports the parental effort game as parents partially compensated for the reduced effort of their partner (Harrison, Barta, Cuthill, & Székely, 2009).

Incorporating sex differences in skew theory

In the parental effort game, any small difference between males and females in the costs or benefits of caring behaviour can select for sex differences in parental efforts and abilities (McNamara & Wolf, 2015), which shows the importance of the effect of differences. Sex differences in life history may similarly create sex differences in skew. Indeed, a sex difference in subordinate inside or outside options might influence the skew, because both sexes are affected by reduction in the total group productivity caused by the departure of any subordinate or high conflict between females or between males. The dominant male and female have fitness interdependence, suggesting reproductive strategies in one sex might vary depending on the strategies of the other sex (Bshary & Bergmüller, 2008). A recent model aimed at understanding the evolution of sex differences in skew and social dominance predicted that males face high (within-group) mating and foraging competition, whereas females face high global (between-group) competition (Leimar & Bshary, 2022).

The models of skew and the parental games have been developed independently, although both focus on cooperation and conflict over reproduction (Cant, 2006). Models of skew fail to explicitly consider offspring care as a trait independent to the investment into the reproductive conflict (as the tug-of-war model only assumes a trade-off between investing in the reproductive conflict and in offspring care). Typically, dominance and skew are studied in one sex. However, often both sexes contribute to group productivity, so that sex differences in offspring care and reproductive conflict may influence group productivity and consequently the fitness benefits of cooperative breeding. It is not well understood how the presence of males and females and sex differences in life history traits, may influence the ESS reproductive strategies. Consequently, it is important to combine the skew the parental effort games and asses how they affect one another's predictions.

In cooperative breeders where dominants get a higher share of the reproduction than subordinates, subordinates may have lower competitive ability than dominants. A sex difference in subordinate competitive ability might therefore underlie the observed sex differences in skew. For instance, sperm competition and sexual selection may reduce the reproductive success of subordinate males (e.g. *N. pulcher*: Koenig & Dickinson, 2016). In other species, the suppression of female reproduction is stronger in females than in males, implying higher subordinate competitive ability in males (e.g. dwarf mongoose: Keane et al., 1994a, common marmoset: Abbott, 1984). Subordinate competitive ability influences the reproductive share obtained for given subordinate and conflict traits and can thus impact the ESS conflict trait and group productivity. As such, it indirectly influences the fitness received by helping the dominant, which means that it affects the subordinate's 'inside option' (benefit of forming a group). Differences in the ability to compete over the share of reproduction might drive differences in skew, as sex differences in subordinate competitive abilities may select for sex differences in tug-of-war conflict and affect the fitness of the other sex via the total group productivity.

There are sex differences in the probability to find a breeding site. Indeed, sometimes females can breed as soon as they locate a breeding site, whereas males need to find a breeding site and a female (Berger-Tal & Lubin, 2011). In migratory birds by contrast, females need to find an occupied nest as males reach the breeding location earlier, and consequently have lower nest availability than males (Arlt & Pärt, 2008). In acorn woodpecker (*Melanerpes formicivorus*), females have better outside options but lower survival than males (Haydock & Koenig, 2003b). As individuals are expected to have evolve to behave like they compare their inside and their outside option before deciding whether to become a subordinate, there may be sex differences in the conditions required for breeding cooperatively. However, the dominants' outcomes are important too, as it determines their investment in competition and willingness to evict or tolerate the subordinate. The reciprocal nature means that a game theoretic model is necessary to understand these family dynamics.

Aims and objectives

Our synthetic model was used investigate the adaptive function of sex differences in skew. We combined the three models of skew and the parental game to see how this affects the predictions about evolutionary stable skew, competitive investment and parental effort, and the likelihood of cooperative breeding. The investment in the tug-of-war conflict can be conceptualised as a conflict trait which is the opposite of cooperation, since it decreases the common good of group productivity. We explored the effect of nest availability, subordinate competitive ability, dominant and subordinate breeding success if alone, and the costs and benefits of parental efforts in a synthetic model. The objectives are to investigate the effect on cooperative breeding and skew of i) the presence of the other sex and ii) sex differences in the probability to find a nest and subordinate competitive ability

The model

Skew games

The concession and restraint models do not allow group productivity to vary, as caring efforts are not considered and one individual controls the allocation of reproduction. It was important to incorporate the concession and restraint models, however, to study group formation, because – unlike in the tug-of-war model – the subordinate can leave or the dominant evict them if breeding alone has greater payoff than the payoff from cooperative breeding. The tug-of-war model, by contrast, focuses on the conflict over the share of reproduction between a dominant and a subordinate. Group productivity is reduced by the reproductive conflict, as investing in the conflict limits the potential for offspring care via the waste of parental energy or effort.

Parental effort game

The parental effort game focuses on the conflict over the caring effort between a male and a female who share equal relatedness to an offspring. The group productivity is increased by the caring efforts of both parents. Our model is based on the static Houston-Davies (1985) game, from the description in Ewald et al. (2007). Parental effort benefits offspring survival with a diminishing return at high provisioning rates, but reduces the parent's future reproduction. This predicts that an increase in partner's efforts lead to a reduction of own efforts (and vice versa).

The parental game resembles the tug-of-war model of skew in that both individuals choose how much to cooperate to contribute to the group fecundity, at the cost of their own fitness. However, the parental effort game focuses on a female and a male breeder and future costs, whereas the tug-of-war game focuses on same-sex subordinate and dominant and immediate costs. By combining the two games, we obtain a more accurate picture than if group productivity only varied with the parental or the reproductive conflict.

Table 4.1: Factors present in each game, with the baseline values and ranges

Factor	Synthetic	Concession	Restraint	Tug-of-war	Parental
Presence two sexes	Yes	No	No	No	Yes
Subordinates Present	Maybe	Maybe	Maybe	Yes	No
ESS level of conflict	Yes	No	No	Yes	No
ESS parental effort	Yes	No	No	No	Yes
Outside options	Yes	Yes	Yes	No	No

A Synthetic Model

To explore how the presence of another sex and sex differences influence reproductive strategies and skew, we combined the parental game with the three skew games in MATLAB2022b. Since group in our model productivity depends on both the level of reproductive conflict and the level of parental care, dominants can compensate their investment in the conflict with subordinates by investing more in parental care. A given total parental effort can therefore be associated with a range of group productivities, which changes the benefit to breed cooperatively. We assume that individuals have a fixed status, and thus are either subordinate or dominant and male or female. As in the concession and restraint models, individuals (of each sex) can breed alone or with a subordinate. Thus, groups may be of 2, 3 or 4 individuals.

Procedure

Two evolvable traits represent the parental and reproductive conflicts (Table 4.2). The ‘conflict trait’ ($c_{i,j,}$, where $i = M$ for males, F for female; $j = D$ for dominant, S for subordinates) determines what proportion of their effort an individual puts into competing for reproduction. Subordinates only have this trait. Dominants also have a ‘parental trait’ that is how much effort to invest in the current brood ($p_{i,}$). Conflict traits decrease group productivity if the subordinate is present (because of costly competition), while parental efforts increase group productivity but reduce their future fitness. Note that subordinates can have offspring without the ‘parental trait’ and that implies that dominants do ‘parental care’ towards unrelated young if subordinates get a reproductive share.

Each individual provides a fixed maximum contribution to group productivity of 0.5, so that one helper increases group productivity by half, and two helpers double the group productivity. Similarly to the tug-of-war model, subordinates’ alloparental care is considered indirectly as their competitive effort reduce their care. In the synthetic model, we include the parental effort game between the dominant, so variation in alloparental care is not examined in male and female. This assumption relies on the fact that either subordinates provide alloparental care or not, the mere presence of subordinate improve offspring survival through 'group augmentation benefits', or both.

As a synthetic model is not analytically tractable, we took a numerical approach and find the evolutionary stable strategy (ESS) of all four individuals by a sequence of best responses until convergence occurs. The best response for dominants is the combination of values of both their traits that maximises their fitness. The subordinates have just one trait in their best response.

The payoff is defined as the reproductive output during one breeding season. Individuals breeding cooperatively get their individual share of the group productivity, whereas solitary breeders get the solitary productivity (i.e. their outside options) (Table 4.2). Nest availability is operationalised as the probability that a subordinate finds a nest to breed. Subordinate competitive ability is the relative advantage of the dominant in the conflict over the share of reproduction.

All possible values of the conflict traits are explored, to determine which value gives the highest payoff to the individual (e.g. dominant female) given the resident conflict traits of the others (e.g. males and subordinate female). Each individual makes a decision regarding the ESS trait in turn, and this loop repeats until the best response doesn't change for all individuals (i.e. convergence).

Table 4.2: Variables used in the models, with their baseline values and the range explored.

Variables	**Definition**	**Initial value**	**Range**
$c_{M,S}$	Level of conflict for subordinate males	0.1	0 – 1
$c_{F,S}$	Level of conflict for subordinate females	0.1	0 – 1
$c_{M,D}$	Level of conflict for dominant males	0.1	0 – 1
$c_{F,D}$	Level of conflict for dominant females	0.1	0 – 1
p_F	Parental effort of dominant female	1	0 – 1
p_M	Parental effort of dominant male	1	0 – 1
Parameters			
σ	Cost of conflict	1	
ρ	Benefit of parental effort	1	0 – 0.5
μ	Cost of parental effort	0.5	0 – 1
ϕ	Dominant pair breeding potential (without effect of parental and conflict traits)	2	
δ	Amount of error	10	
ψ	Subordinate reproductive share		
b	Subordinate competitive ability (i.e. competitive abilities in the reproductive conflict)	0.7	0 – 1
N	Probability that subordinates find a nest	0.05	0 – 1

Calculating group productivity

For each type (status and sex) of individual, the group productivity is calculated when the individual stays and when it leaves the group. To match the classical parental game model (Houston-Davies, 1985), the productivity of the pairs of dominants is a quadratic function

$$\phi = \phi_B.(p_M + p_F - \frac{p_M \cdot p_F}{2}) \tag{4.1}$$

With p_M and p_F the parental efforts of dominant males and females, respectively, and ϕ_B dominant breeding potential (Table 4.2).

Group productivity is defined as a function of the reproductive conflict traits and the probabilities that the subordinates stay. Group productivity g is the sum of the group productivity with one subordinate G_1, two subordinates G_2 or none G_0. Since the conflict traits influence group productivity, it is G_F when the subordinate female stays, given the probability that the subordinate male stays, and G_M when the subordinate male stays and the subordinate female leaves. Being four individuals brings a benefit of 2 compared to a breeding pair, so being in a group of 3 with one helper gives a benefit of 1.5.

$$G_2 = S_F.S_M.\phi.(2-\sigma(c_{F,D}+c_{F,S}+c_{M,D}+c_{M,S}))$$
$$G_M = (1-S_F).S_M.\phi.(1.5-\sigma.(c_{M,D}+c_{M,S}))$$
$$G_F = S_F.(1-S_M).(\phi.(1.5-\sigma(c_{F,D}+c_{F,S}))$$
$$G_1 = (1-S_F).S_M.\phi.(1.5-\sigma.(c_{M,D}+c_{M,S}))+S_F.(1-S_M).(\phi.(1.5-\sigma(c_{F,D}+c_{F,S}))$$
$$G_0 = (1-S_F).(1-S_M).\phi$$
$$g = G_2+G_1+G_0 \tag{4.2}$$

Group productivity is g_2 if the subordinate of the focal sex stays, and g_1 if the focal sex subordinate leaves, given the probability that the other subordinate stays. Subordinate outside option is the group productivity with no subordinate g_0, if it tried breeding alone, given the success in finding a breeding site N.

Subordinate outside options are defined as

$$x_i = N_i.g_0 \tag{4.3}$$

with N subordinate's probability to find a nest (i.e. nest availability) and g_0 the group productivity of a solitary breeder (i.e. without any subordinate).

Dominant best response

The dominant's best response is computed based on the resident conflict traits and the group productivity in each situation. The dominant mutant response to the resident traits is calculated for a range of possible parental effort and conflict trait values, and depends on whether the subordinate stay.

The subordinate who stays receives the payoff

$$W_C{*} = g_2 \frac{b.c_S{*}}{b.c_S{*} + c_D} \tag{4.4}$$

The decision to stay is error-prone, which influences the probability to stay

$$S{*} = \frac{1}{1 + e^{\delta(N_i.g_0 - W_C)}} \tag{4.5}$$

with δ the amount of error (δ >0) following (McNamara et al., 1997).

If the subordinate stays, the dominant gets payoff

$$V_C = g_2.\frac{c_{F,D}}{b_F c_{F,S}{*} + c_{F,D}} \tag{4.6}$$

So, given the probability that subordinate stays, dominant's payoff is reduced by the cost of its investment in the reproductive conflict and in parental care

$$V_C = S{*}.W_C + (1 - S{*}).g_1 - \phi.\mu.c_D{}^2 \tag{4.7}$$

with μ the cost of parental effort and ϕ dominant's maximal productivity without subordinates.

The best decision is the conflict trait which maximises dominant payoff. The best mutant payoff is calculated at each iteration. Mutant conflict traits and parental efforts are compared to the resident traits. For the dominant mutant conflict trait, subordinate's reproductive share is

$$\varphi{*}_F = \frac{b_F c_S}{b_F c_S + c_D} \tag{4.8}$$

Group formation occurs in the synthetic model if both individuals want to stay. In the concession and the restraint model, the probability of the subordinate and the dominant, respectively, to form a group determines group formation.

Dominant ESS mutant traits (p_M, $c_{M,D}$ for males; p_F, $c_{F,D}$ for females) are stored and becomes the resident trait for the next type of individual: their subordinate. As previously, group productivity is calculated in each situation for subordinate trait optimisation.

Subordinate best response

Next we calculate the subordinate's best conflict trait value given the fact that the dominant has a probability of evicting them depending on their decision and the resident dominant strategies. We show the procedure for females and do the same for males.

The dominant payoff if the subordinate stays depends on group productivity and dominant reproductive share, and is

$$W_{F,C} = g_2 \frac{c_{F,D}}{b_F c_{F,S} + c_{F,D}} \tag{4.9}$$

The probability that the dominant evicts its subordinate is

$$E_F = \frac{1}{1+e^{(\delta g_1 - V_{F,C})}} \tag{4.10}$$

A subordinate who stays gets the payoff

$$W_{F,C} = g_2 \frac{b_F c_{F,S}}{b_F c_{F,S} + c_{F,D}} \tag{4.11}$$

Consequently, subordinate payoff as a function of dominant mutant conflict is

$$W_F = E_F . S_F + (1 - E_F) . g_0 . N_F \tag{4.12}$$

The subordinate ESS conflict trait maximises its payoff.

After the female dominant and subordinate best responses have been found, the best responses are found for the male dominant then the male subordinate.

Each model starts with a different set of initial values for subordinate competitive ability *b*, the cost *μ* and benefit of the parental effort ρ, the cost of the conflict trait σ, the probability to find a nest *N* and dominant outside option *y* (Table 4.2). The evolving subordinate conflict trait $c_{M,S}$ and $c_{F,S}$ and dominant conflict trait $c_{M,D}$ and $c_{F,D}$ are initialised at 0.1 (Table 4.2). We assume that individuals form a group at first, so the probability to stay is initialised at 0.5.

Individuals are unrelated since the kin selection model does not explain all cases of cooperative breeding, the tractability of the model is improved and kin selection is not the focus of this model.

The convergence speed and the speed of replacement of mutant strategy by resident strategy for the conflict and parental traits are both set at 0.01 to ensure convergence of the traits. The traits evolve to convergence.

To explore the effect of the added complexity, we first compared the predictions of the synthetic model to the classical ones when varying subordinate competitive ability, nest availability in a similar way in both sexes.

Next, to explore the effect of sex differences on the reproductive strategies, we kept a baseline/constant female trait whilst systematically varying male 1) subordinate competitive ability and 2) nest availability.

Recreating the classic models

To confirm that our procedure could recreate the predictions of the classic models, we changed some of the initial parameter space to match the mechanisms. For the concession model, subordinates have no power, so their conflict trait is set to a minimal value of 0.05. For the restraint model, dominants have no power in the reproductive conflict (0.05). For both transactional models, conflict is not costly (σ =0) and there is no dominant's competitive advantage so subordinate competitive ability b_F = b_M = 1. For the tug-of-war model, the nest availability was set to zero so subordinates cannot leave. Conflict is not costly (σ = 0) and the effort benefit (ρ) is 0.5. For the parental effort game, subordinates have a nil conflict trait whereas dominants have a maximal conflict trait, because the reproductive conflict is not considered. The breeding pair has no subordinates in the parental effort game, so subordinates never stay as they have no competitive ability in the reproductive conflict and as nest availability is high.

Results

Our numerical versions of the classic models make similar predictions to the analytical classic models (Appendix Figure 4.A1, 4.A2), which means our procedure was reliable. Subordinate share increased with nest availability in the concession model (Appendix Figure 4.A1) and with subordinate competitive ability in the tug-of-war (TOW) models (Figure 4.A2), and parental effort matched expectations from the parental effort game

Comparison of the synthetic model to the classic models

Dominants evolved higher conflict traits than subordinates for medium nest availability (Figure 4.1b) and most subordinate competitive ability (Figure 4.1e). Subordinate conflict traits decreased whereas dominants' increased with subordinate competitive ability when subordinate has medium and high probability to find a nest (Figure 4.1ef). Subordinates evolved higher conflict traits than dominants when they have no outside options (Figure 4.1a). Groups always form when the probability to find a nest is very low, so the conflict traits drift (right of Figure 4.1a,b,c). For medium and high probability to find a nest, subordinates evolved higher conflict traits than dominants if subordinate competitive ability is very low; dominant conflict trait is higher than subordinates' after a certain level of subordinate competitive ability (Figure 4.1ef). Subordinate conflict traits decrease with their competitive abilities (Figure 4.1de), unless nest availability is high (Figure 4.1f)

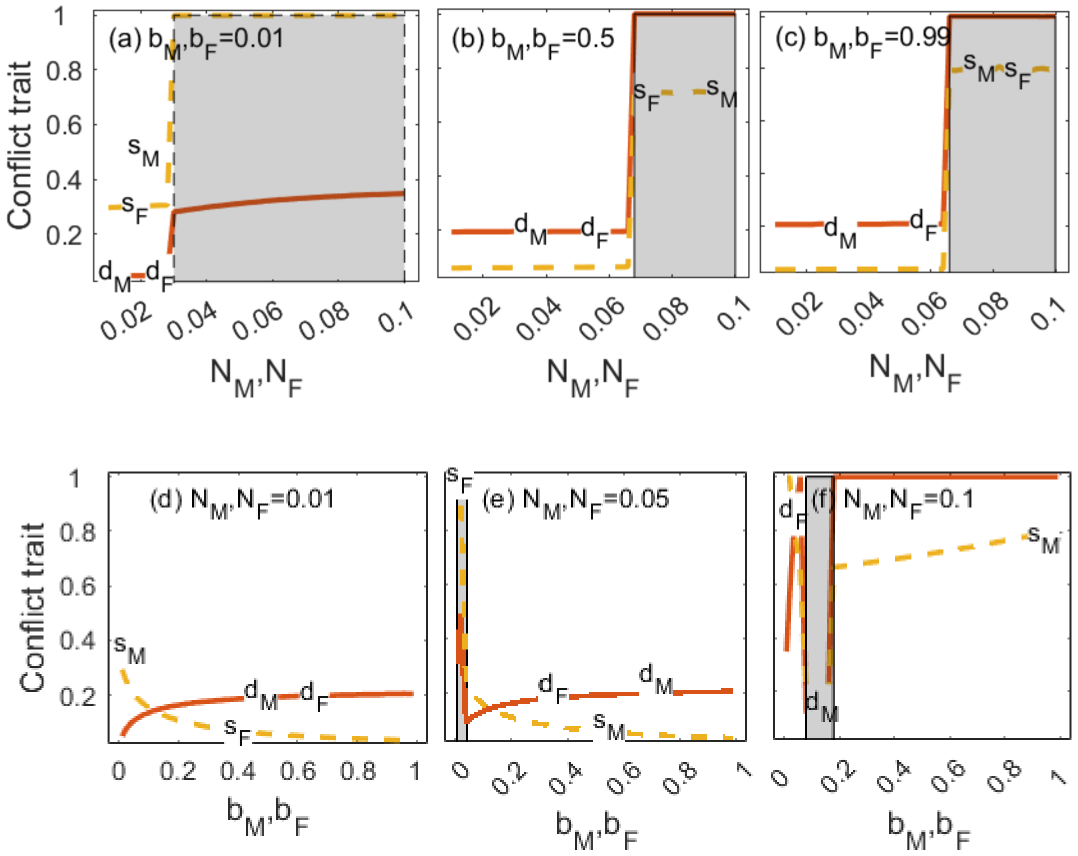

Figure 4.1: Conflict trait as a function of (a,b,c) probability to find a nest and (d,e,f) subordinate competitive ability. Subordinate competitive ability is (a) low, (b,e,d,f) medium and (c) high. Probability to find nest is (d) low, (a,b,c,e) medium and (f) high.

The synthetic model makes quite different predictions about skew to the classic models (Figure 4.2). When subordinate competitive ability and nest availability are small, the synthetic model predicts a similar reproductive share as the concession model (left of Figure 4.2a). When subordinates have at least some minimal competitive ability (Figure 4.2b,c), the subordinate share of the synthetic model is between those of the concession and the TOW models. The outcome is that the skew in the synthetic model is not as responsive to nest availability as in the concession model, and not as responsive to subordinate competitive ability as in the TOW model.

The subordinate share predicted by the synthetic model is almost always higher than that of the concession model when subordinate competitive ability is medium or high (Figure 4.2def), and always lower than that of the tug-of-war model (Figure 4.2). The possibility to evict or leave the group, present in the synthetic models, dampens the effect of subordinate competitive ability compared to the TOW (Figure 4.2 def). Subordinate share increases with subordinate competitive ability in the TOW but not with the probability to find a nest (Figure 4.2def). Subordinate share increases strongly as subordinate competitive ability comes from 0 to 0.1, afterwards the increase is less steep (Figure 4.2def). Subordinate share is higher in restraint than concession model (Figure 4.2).

Parental traits did not vary with subordinate competitive ability (Figure 4.A4a-c) nor with the probability to find a nest (Figure 4.A4d-f). Dominants evolved the maximum parental traits in our synthetic model, but not in the parental game (Figure 4.A4).

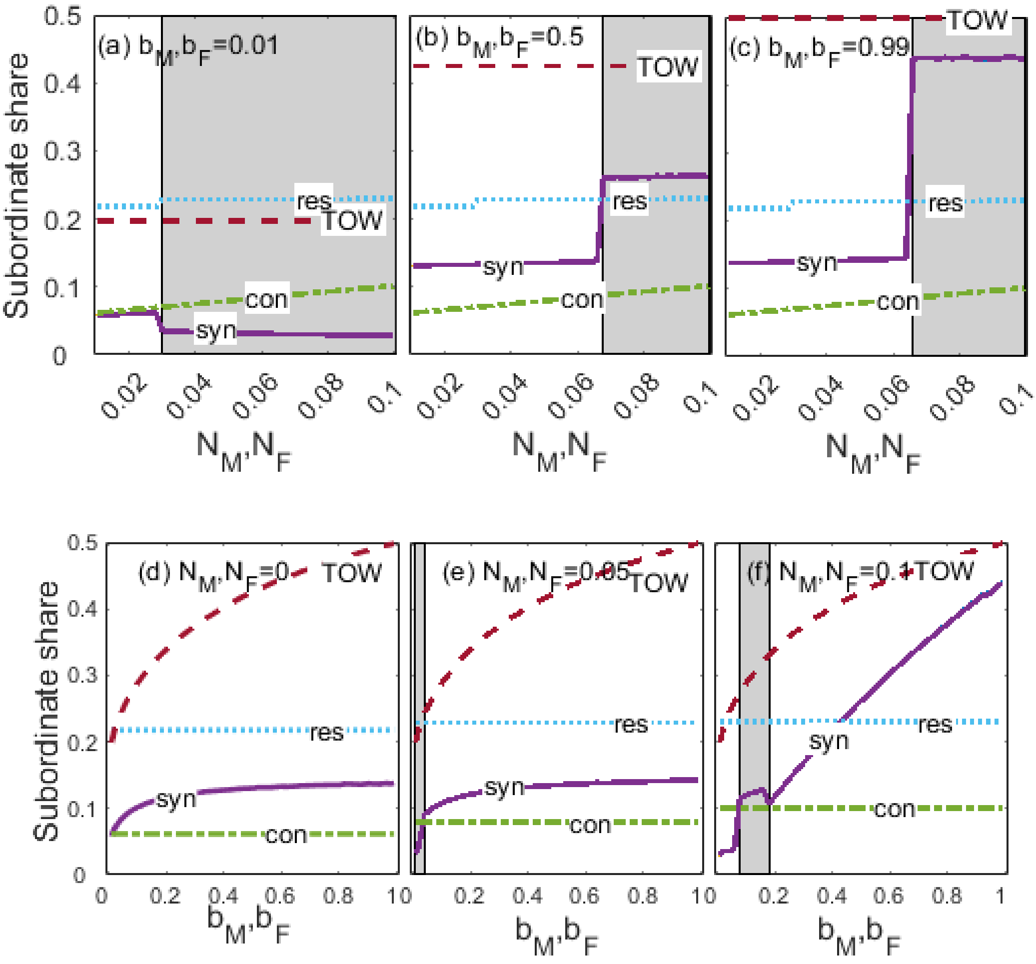

Figure 4.2: Subordinate share as a function of (a,b,c) probability to find a nest *NF, NM* and (d,e,f) subordinate competitive ability *bF, bM*. Synthetic and classic models for (a) low, (b) medium and (c) high subordinate competitive ability, and (d) low, (e) medium and (f) high probability to find a nest. Models: synthetic (violet line), concession (green dash-dot), restraint (blue dot) and tug-of-war (red dash).

Grey boxes show where there is less than 10% probability males form groups (i.e., breed cooperatively), so male subordinate share is not under selection.

Effect of parental effort costs and benefits, and group productivity

Cooperative breeding occurred under all parental effort costs and benefits (Figure 4.3). The synthetic model predicted that parental efforts should not vary with their costs, whereas the parental efforts game predicts a decrease as costs increase (Figure 4.3abc). Subordinate share did not vary with the parental effort costs, but it decreased with the parental effort benefit (Figure 4.3def). The TOW model predicted the highest share, followed by restraint, then concession models (Figure 4.3, 4.4).

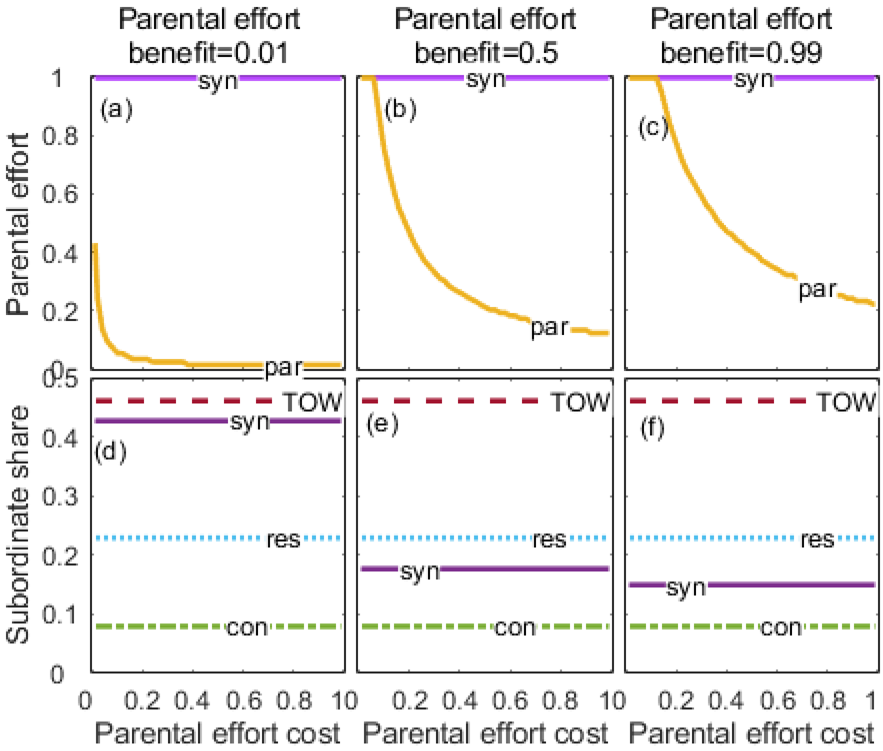

Figure 4.3: (abc) Parental efforts and (def) subordinate share as a function of parental effort costs for (a,d) low, (b,e) medium and (c,f) high parental effort benefit. Models: synthetic numerical (violet line), parental effort (yellow line), concession (green dash-dot), restraint (blue dot) and tug-of- war (red dash). Grey boxes show where groups do not form and subordinate share is not under selection (drift). Constant variables are $b_F = b_M = 0.7$; $N_F = N_M = 0.05$.

The synthetic model predicts higher parental traits than the parental effort model (Figure 4.4abc). Parental traits did not vary with dominant maximal productivity nor with nest availability. The synthetic model predicted a similar slope as the restraint model for subordinate share, but lower values (Figure 4.4def). Indeed, the subordinate share predicted by the synthetic model lies between those of the concession and restraint models.

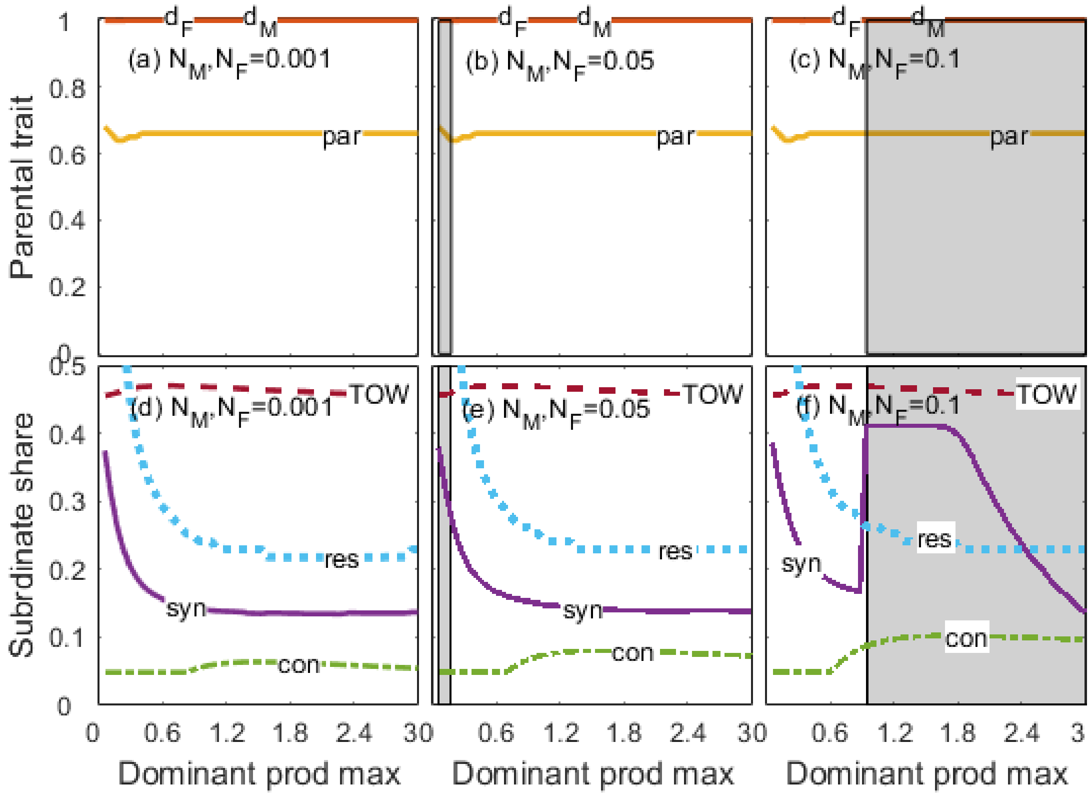

Figure 4.4: (a,b,c) Parental trait and (d,e,f) subordinate share as a function of dominant maximal productivity ϕ for (a,d) low, (b,e) medium and (c,f) high probability to find a nest. Models: (a,b,c): parental (yellow line) and synthetic numerical model (red line); (d,e,f) synthetic numerical (violet line), concession (green dash-dot), restraint (blue dot) and tug-of-war (red dash). Grey boxes show where groups do not form and subordinate share is not under selection (drift). Constant variables are $b_F = b_M = 0.7$; $N_F = N_M = 0.05$.

As for all parameter spaces, female and male dominants evolved maximal parental traits under all circumstances (Figure 4.A4abc). The parental effort game predicted a small drop in parental trait for low dominant maximal productivity and otherwise no change (Figure 4.A4abc). Subordinate share decreased with dominant maximal productivity in the restraint and in the synthetic numerical model, whereas it increased in the concession model (Figure 4.A4def). The synthetic model predicts an intermediate share between the restraint and concession shares.

Effect of sex differences on predictions in synthetic model

Next we varied only the male values, whilst keeping the female values fixed. A sex difference in nest availability or in subordinate competitive abilities selected for a sex difference in the probability to form a group, but females' strategies did not vary with males' subordinate competitive ability and nest availability (Figure 4.5). The probability to find a nest in males influenced their probability to breed cooperatively: groups did not form for high nest availability and medium-high dominant maximal productivity (Figure 4.5abc) and groups did not form for medium nest availability when dominants had very low maximal productivity (Figure 4.5a). Groups always formed for low nest availability (Figure 4.5abc).

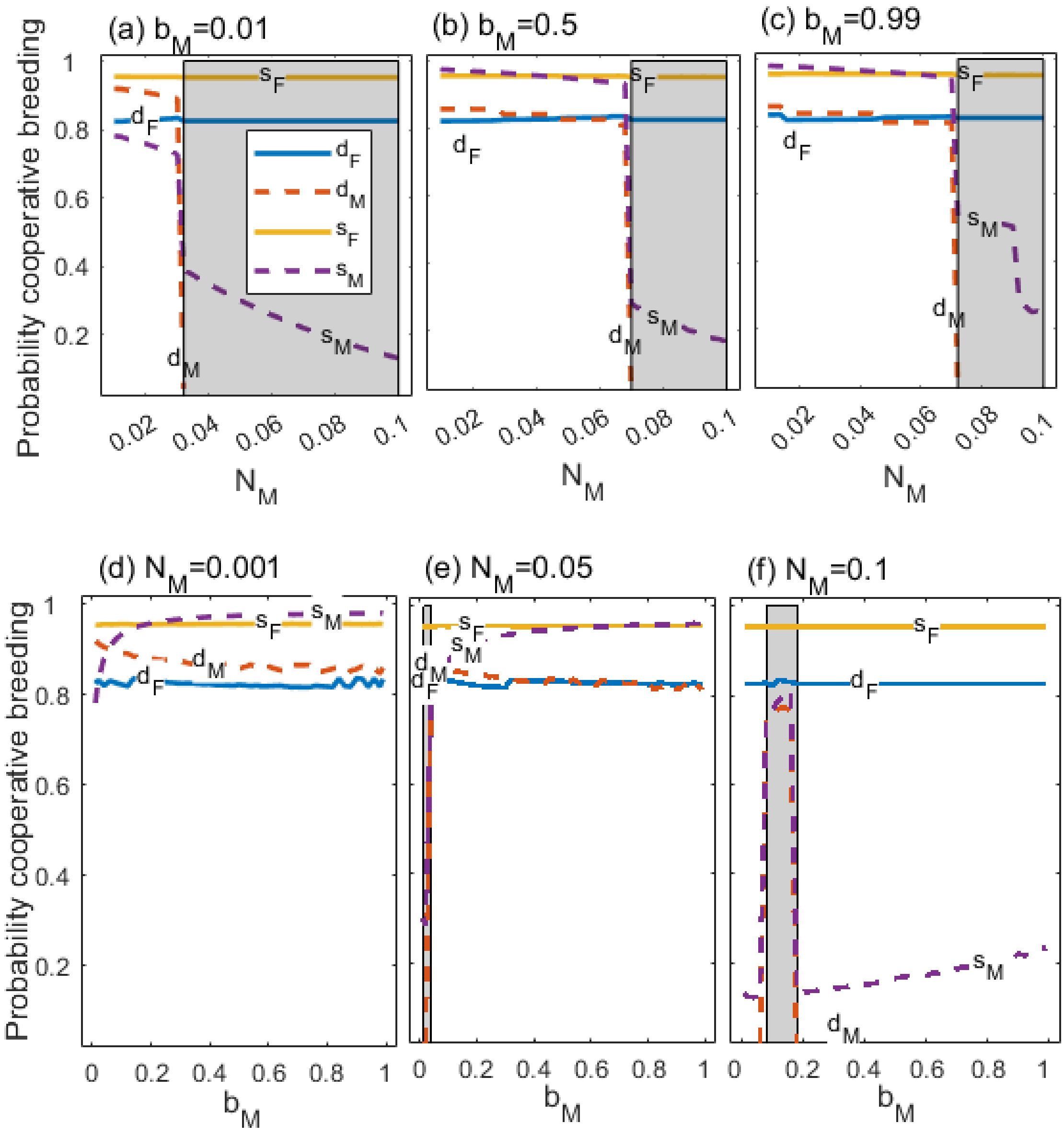

Figure 4.5: Probability to form a group as a function of (a,b,c) probability for males to find a nest N_M and (d,e,f) subordinate male competitive ability b_M. Synthetic and classic models for (a) low, (b) medium and (c) high male subordinate competitive ability, and (d) low, (e) medium and (f) high probability males find a nest. Grey boxes show where probability that males form a group falls below 10%.

Overall female subordinate and dominant conflict traits did not vary with male subordinate competitive ability nor male probability to find a nest (Figure 4.6). Subordinate males with no competitive ability evolved higher conflict traits than subordinate females (Figure 4.6a), whereas males with medium and high competitive ability evolved similar conflict traits as females (Figure 4.6bc). Male dominant conflict trait decreased with male probability to find a nest (Figure 4.6def). Male subordinate and dominant conflict traits were higher than that of females when males have higher nest availability than females (Figure 4.6f) but not when males nest availability was lower or equal to females' (Figure 4.6de). The synthetic model predicts higher subordinate than dominant conflict trait in males for low subordinate competitive ability and no probability to find a nest (Figure 4.6ad).

Subordinate share was higher in dominant females than in subordinates and in dominant males when male subordinate competitive ability was low (Figure 4.7adef). Female share did not vary, whereas male share increased with male subordinate competitive ability (Figure 4.7def), very similarly to how it did when we varied both female and male traits at the same time (Figure 4.2).

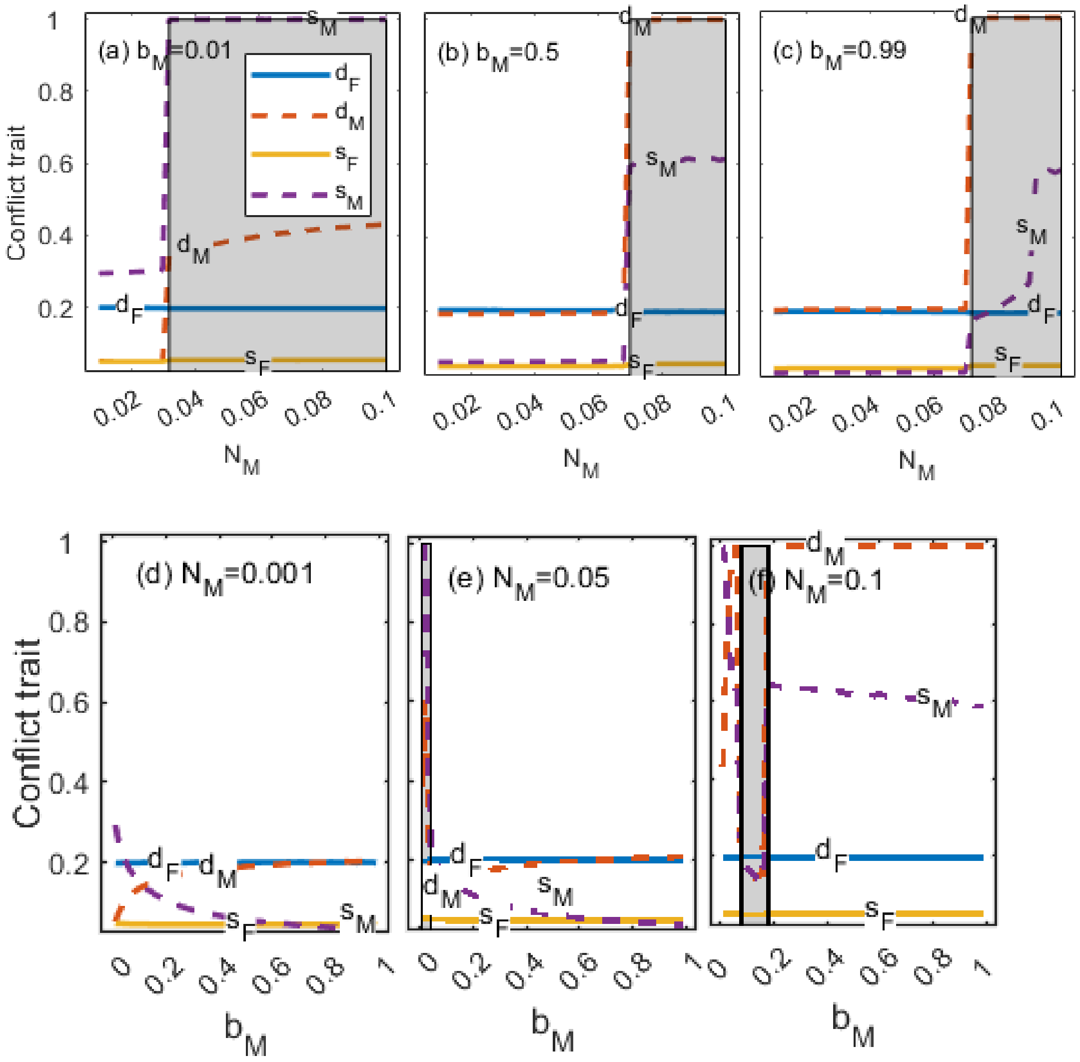

Figure 4.6: Conflict trait as a function of (a,b,c) male probability to find a nest and (d,e,f) male subordinate competitive ability in the synthetic model. Male nest availability is (d) higher, (e) equal to and (f) lower than females' N_F=0.05. Male subordinate competitive ability is (a) higher, (b) equal to and (c) lower than females' b_F=0.5. Grey boxes show where probability that males form a group falls below 10%.

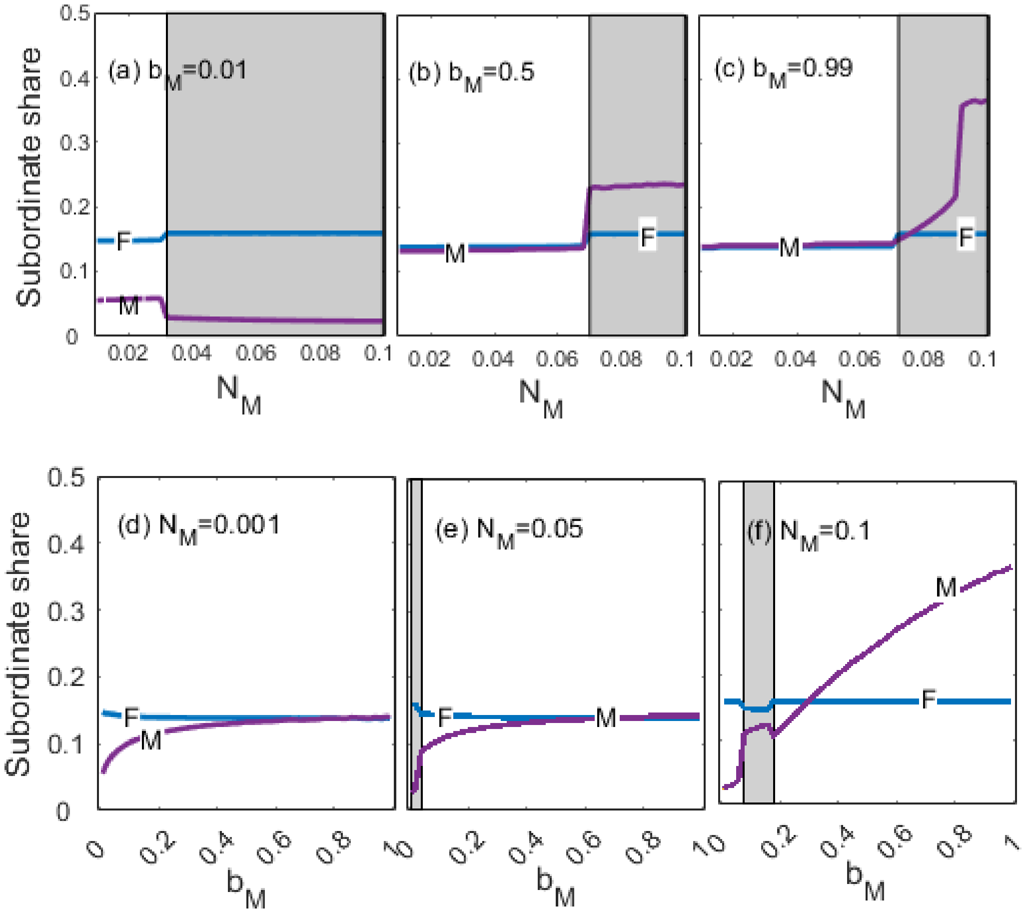

Figure 4.7: Subordinate share as a function of (a,b,c) probability to find a nest N_M and (d,e,f) subordinate competitive ability $b_{M,}$ in the synthetic model for (a) low, (b) medium and (c) high male subordinate competitive ability, and (d) low, (e) medium and (f) high male probability to find a nest. Female: dark blue line and male: green line. Grey boxes show where males do not form a group and their subordinate share is not under selection (drift). Variation in male N_M and b_M; female N_F=0.05, b_F=0.5.

Discussion

Here, we extended the models of skew to examine how combining various models influence skew, group formation and the level of conflict. We compared the classic skew and parental models to the new synthetic model and found that the various games have surprisingly small impact on one another.

Combining skew and parental games

Skew was affected by parental effort benefit but did not vary with parental effort cost, which suggests that where it is possible to breed cooperatively, the costs are not important. Indeed, the presence of helper may buffer against the parental effort costs, as observed in birds where helpers improved the longevity (Crick, 1992; Hammers et al., 2019) and future reproductive success of the dominant parents (Tanaka, Kohda, & Frommen, 2018). Subordinate share decreased with dominant solitary group productivity in the synthetic model, similarly to the restraint model. This prediction suggests that skew increases when dominants have a limited direct fitness, to accommodate a certain level of dominant fitness. Note that if helpers were related to the dominants, the predictions might change due to indirect fitness benefits for both subordinates and dominants.

Cooperative breeding was less frequent with low subordinate competitive ability (no inside option) and medium and high nest availability (high outside options), which is because it is more beneficial for subordinates to breed independently as they have poor inside option but high outside options. With low nest availability, subordinates evolved higher conflict traits as their competitive abilities increased; This prediction is supported in southern pied babbler (*Turdoides bicolor*) where both sexes have low outside options and show higher intrasexual conflict when their competitive ability increases with age (Nelson-Flower, Flower, & Ridley, 2018). Subordinate share increased with subordinate competitive ability in the synthetic model and the TOW model (Reeve et al., 1998) which suggests that incorporating the parental game and the presence of two sexes does not change the predictions of skew.

Subordinate conflict traits are higher than dominants' when dominants have a strong competitive advantage. This finding shows that subordinate, despite evolving high conflict in the reproductive conflict, never reach a high reproductive share (getting a maximum of 10% of group productivity) for a conflict trait of 0.3. Males and females subordinates evolved lower conflict traits than dominants if their subordinate competitive ability was minimal – which meant subordinate were not able to get reproductive share through competition. Otherwise, dominants showed higher conflict traits than subordinates, maybe because a reduction in group productivity is less costly to dominants who get a high share and payoff than to subordinates.

The sum of dominant and subordinate conflict traits is the total level of aggression and it did not vary with subordinate competitive ability in the synthetic model for low and medium nest availability, which is in line with the TOW models for unrelated individuals (Reeve et al., 1998). Indeed, the synthetic model predicts that subordinate conflict decreases while dominant conflict decreases with competitive ability (or vice versa). However, for high nest availability, the total level of aggression increased with subordinate competitive ability in the synthetic model. This mismatch with TOW model predictions occurs because individuals cannot leave the group in the TOW and therefore their nest availability is nil.

The synthetic model predicts maximal parental traits in all situations, contrary to the parental effort game (Houston & Davies 1985). In the synthetic model, subordinates can boost the group productivity, so the effect of future costs is reduced. This finding suggests that dominants in cooperative breeders do not decrease their parental efforts, but invest the maximum efforts when they have subordinates, when subordinates cannot adjust their caring efforts. Dominants reduce their parental efforts in the presence of helpers (Downing, Griffin, & Cornwallis, 2021; Josi, Freudiger, Taborsky, & Frommen, 2020; Kingma, Hall, Arriero, & Peters, 2010). Indeed, Dominants' parental traits may also increase in the synthetic model to maintain dominant payoff, as the TOW conflict decreases group productivity in the synthetic model, but is absent from the parental game.

Effect of a sex difference

We expected when making the model that changes in one sex would select for changes in the strategies of the other sex, whereas the model predicts that variation in one sex did not influence the ESS strategies of the other sex. However, sex differences in nest availability and subordinate competitive ability did create sex differences in reproductive strategies, suggesting that sex differences in life history traits can select for sex differences in skew.

A sex difference in nest availability and the subordinate competitive ability created a sex difference in skew. However, the skew, parental traits and conflict traits of one sex were largely insensitive to these traits in the other sex. Hence the ESS strategies of one sex does not vary with those of the other sex, even when group productivity depends on the behaviour of the subordinate and dominant of the other sex. This surprising prediction suggests that incorporating more complexity into games does not always alter the predictions (McNamara, 2013), and that the single sex model makes the same predictions as making predictions for the sexes in isolation.

As subordinate competitive ability increases, the difference between subordinate and dominant conflict traits decreases in the TOW model (Johnstone, 2000). As male subordinate share increases with male subordinate competitive ability while female's stays constant, females evolved higher subordinate share than males for low male subordinate competitive ability and lower share than males for medium-high male subordinate competitive ability. This finding suggests that a sex difference in skew and in lifetime reproduction can occur (Oring, Colwell, & Reed, 2004) if there is more variation in subordinate competitive ability within one sex than the other (e.g. harems (Kappeler & Schäffler, 2007)).

Future research

Empirical tests of the predictions of this model would entail getting accurate probabilities to find a nest and subordinate competitive ability. Within-species tests may be effective in species showing a variation of nest availability (but overall constant ecology) such as the sociable weaver *(Philetairus socius)* (Monteiro, 2002). Besides, meta-analysis could provide between-species tests by focusing on both parental effort, the occurrence of cooperative breeding and skew.

A natural progression of this work is to add the possibility for subordinates to vary their alloparental care (English et al., 2010). Indeed the optimal level of skew and the probability to form a group might change when all group members can care for the offspring, compared to when only dominants contribute to group productivity. Subordinate's reproductive conflict might increase if their help leads to higher group productivity than in the current model and therefore subordinates can afford higher competition (and reduction group productivity). Alternatively, subordinate conflict trait might decrease if the dominant specialises in breeding and the subordinate specialises in offspring care.

In social insects, workers can eat the eggs of other workers to suppress their reproduction and favour the offspring of the queen - this is worker policing (Beekman & Oldroyd, 2005). A concession model of skew investigated the effect of worker policing by removing the status from the model and focusing on a large group; when the summed decisions of all group members determine the decision of each individuals, the individual that is most related to all group members becomes the dominant with a high skew (Reeve and Jeanne, 2003). Working policing could be introduced in an extension of the synthetic model, as combining the three models might change the predictions.

This study suggests that the reproductive strategies of the philopatric sex will not vary with changes in the nest availability of the dispersing sex (e.g. addition of nest boxes or environmental disruptions) in cooperative breeders with one philopatric sex. Further research on the effect of variation in the cost of caring would be of great help to understand better how climate change, which can increase caring costs, might affect animals' reproductive strategies.

Costs, benefits and caveats

Subordinate share decreased with the parental effort benefit. Increase in parental effort benefit increases the overall group productivity produced for a given parental effort, so subordinates may need a lower reproductive share to get the same direct fitness for a higher parental effort benefit. Subordinate share did not vary with parental effort costs, which may imply that the models of skew are applicable to cooperative breeders where parental effort costs vary. The synthetic and the restraint models predict subordinate share decreases with dominant maximal productivity, whereas the concession model predicts it increases, for low values of dominant group productivity. This finding suggests subordinate self-restraint when dominants have low solitary reproductive success and get higher relative benefits from the help of a subordinate (Johnstone, 2000a). Taken together these predictions suggest that dominant direct fitness (which is influenced by their parental effort benefit and their group productivity alone) determines subordinate share. A caveat, though, is that our synthetic model did not incorporate subordinate alloparental effort costs, which may have changed the costs and benefits of the strategies and therefore subordinate share.

Dominant payoff increased with parental effort benefit. In the synthetic model payoffs did not vary with parental effort costs whereas they decreased with parental effort costs in the parental game. This suggests that the skew game enables individuals to compensate for rise in parental costs with cooperative breeding.

This study has demonstrated that integrating animal decisions which are often considered separate can change the predictions and might explain observed variation, since combining the skew and parental games modified the optimal strategies. However, it also shows that some life history traits and reproductive strategies can vary in one sex and influence its reproductive strategies without altering the reproductive strategies of the other sex. These findings highlight the importance of making complex models that combine several games, to determine whether this added complexity improve the biological realism and shed new light on the evolution of cooperation (McNamara, 2013).

Chapter 5 – Sex and period interact to influence sentinel contribution around dominance acquisition

Dwarf mongoose (*Helogale parvula*) by Glavo via Pixabay

Abstract

Individuals of different sex and dominance status may experience different costs and benefits to cooperative behaviour. Whilst female breeders bear the nutritional costs of pregnancy and lactation, males may show lower intra-sexual conflict. When dominants monopolise reproduction, status and sex may thus interact in influencing cooperative investment; however few empirical studies have investigated these influences *within* individuals: before and after becoming dominant. In dwarf mongooses, sentinel behaviour is more nutritionally costly than grooming behaviour, so comparing investment in these may illuminate the effect of costs and benefits on cooperation. We analysed detailed field data from the four weeks before and four weeks after dominance acquisition. We predicted that females would decrease contributions to sentinel behaviour once dominant and that this effect would be stronger under food scarcity, due to pregnancy costs. By contrast, we predicted that both sexes would increase grooming after becoming dominant to reinforce their new status. In our findings, while status itself did not predict sentinel behaviour, period interacted with sex. Male sentinel contributions were higher than females' in the second fortnight after becoming dominant, possibly due to sex differences in costs over time. The analysis of group-grooming and grooming duration did not support our predictions and environmental quality did not influence the cooperative behaviours. Overall these results suggest that sex differences in costs may modulate sentinel behaviour.

Introduction

In cooperative breeders, dominant individuals typically produce most of the offspring while subordinates help them raise the young (Jeon & Choe, 2003; Sharp & Clutton-Brock, 2011; Woxvold, Mulder, & Magrath, 2006). Helpers assist in tasks such as territory defence (Heg & Taborsky, 2010), food provisioning and grooming of the young (König, 1997; Woxvold et al., 2006), and coordinated vigilance for predators (i.e., sentinel behaviour) (Santema & Clutton-Brock, 2013). Such cooperative behaviour is costly (Heinsohn & Legge, 1999; van de Crommenacker et al., 2011). Hamilton's rule predicts that an individual should cooperate if the benefit to the recipient times the relatedness to the recipient exceeds the cost of cooperating (Hamilton, 1964), and that all these factors may vary within and between individuals. Within-species variation in cooperative behaviour is ubiquitous (e.g., in mammals: English et al., (2010), birds: Canestrari, Marcos, & Baglione, (2005), insects: Jeanson & Weidenmüller, (2014a) and fish: Schürch & Heg, (2010)). Yet, the effects of individual traits on cooperative behaviour are not fully understood.

Cooperative investment may be influenced by the sex of individuals. When costs of helping are higher for subordinates of one sex, then subordinates of the other sex may help more (if they reap similar benefits) (Downing et al., 2018). The sex-asymmetry in the cost of breeding, where mothers face higher costs than fathers (Scantlebury et al., 2002), may lead dominant females to provide less energetically-demanding cooperative behaviour than dominant males, especially if their body condition is poor. If only the dominant pair reproduces, then status should influence the cooperative contribution of female, but not male, dominants because only dominant females bear offspring. Besides, evidence suggests females may be more socially flexible than males. Female meerkat (*Suricata suricatta*) helpers and breeders, but not males, adjust offspring provisioning in response to signals of hunger in young (English et al., 2008). Similarly, female house sparrows (*Passer domesticus*) vary their provisioning more than do males (Nakagawa, Gillespie, Hatchwell, & Burke, 2007). By contrast, dominant male sociable weavers (*Philetairus socius*), but not male helpers nor females, responded to the number of begging calls (Fortuna et al., 2022a), which suggests status may interact with sex difference to influence cooperative contributions.

If costs and benefits are different for dominants and subordinates, then cooperative behaviour may change when individuals change dominance or breeding status, and such changes may be sex-dependent. For dominant females, but not for subordinate females who do not breed (Cant et al., 2014; Creel & Rabenold, 1994), cooperative behaviour is costly to their ability to produce offspring in the next breeding attempt. Indeed, females meerkats become less cooperative after acquiring dominance (Carter, English, & Clutton-Brock, 2014). In birds, the sex that is more likely to reproduce as a subordinate shows higher cooperative efforts as a helper, which suggests that the potential direct fitness of helpers influences their helping decisions (Downing et al., 2018). Damaraland mole-rats (*Fukomys damarensis*) exhibited a sex-difference with females breeders carrying the offspring more than helper females, whilst helper males carried less than male breeders (Zöttl et al., 2018). Sex and status may interact in carrion crows (*Corvus corone corone*) where male helpers provision more than female helpers, and dominants provision more than helpers (Canestrari et al., 2005). This interaction may due to sex-specific costs and shape the extent to which an individual engages in cooperative behaviour.

Environmental variation can affect the costs and benefits of cooperative behaviour, potentially creating between-individual variation in cooperative contributions. Harsh, bad environments, characterised by extreme temperatures and rainfall, reduce food availability and so increase the necessary foraging time (Litzow, Piatt, Litzow, And Piatt, & Piatt, 2003). Longer foraging times increase the cost of cooperative behaviours that are dependent on body condition (e.g., acting as a sentinel (Rauber, Clutton-Brock, & Manser, 2019)), causing some individuals to stop cooperating (Lindstedt et al., 2018). However, as environmental constraints influence cooperative breeding (e.g., Sheehan et al., 2015), cooperative behaviours can be more beneficial in harsh than in favourable environments (Emlen, 1982; Koenig, Walters, & Haydock, 2011). Recent evidence that only females increase their investment into beak coloration – a costly ornament – in favourable conditions (Freitas, Marques, Cardoso, & Trigo, 2021) suggests that females adjust the allocation to costly traits with environmental conditions, potentially to preserve energy for reproduction. Similarly, breeding females may reduce costly cooperative behaviours in low quality environments. In a cichlid fish, juvenile and small helpers, but not breeders or large helpers, decrease cooperative behaviour as it becomes more costly when food is scarce due to a trade-off between foraging and cooperation (Bruintjes, Hekman, & Taborsky, 2010b). Under food scarcity, breeding females defended the eggs more than breeding males (Bruintjes et al., 2010b). The proportion of female helpers increased linearly with rainfall in Seychelles warblers (*Acrocephalus sechellensis*), whereas males were most likely to help in favourable medium rainfall (Borger et al., 2023). By increasing the costs of cooperation, bad environments may reveal subtle interactions between sex and status.

Within-subject studies may be the best way to understand the effects of sex and status on cooperative behaviour. Between-individual differences, such as the effect of generation and the rearing environment, can influence cooperative behaviour (Kuijper & Johnstone, 2018). Observing individuals before and after they become dominant provides fewer factors of variation than comparison of dominants and subordinates at a given time. Indeed, while between-subject studies can capture the differences at a given date, they overlook between-individual differences. Although extensive research has been carried out on the association between sex, status and environmental quality, no study to our knowledge has tracked cooperative contribution *within-individuals* for different status (English et al., 2010; Forssman, Marneweck, O'Riain, Davies-Mostert, & Mills, 2018; MacGregor & Cockburn, 2002; Marshall et al., 2016).

In this within-individual study, we investigate a costly and a less costly cooperative behaviour around the time of dominance acquisition, which may allow determination of how sex, status and environmental quality interact as predictor variables. Sentinel behaviour involves an individual adopting a raised position to scan the environment for danger, providing protection to the whole group at the expense of their own foraging (Hollén, Bell, & Radford, 2008). Sentinels are therefore trading-off energy gain for the survival of group members (Radford & Fawcett, 2012; Rasa, 1989b). Cooperatively breeding Arabian babblers (*Turdoides squamicep*) increased their sentinel contribution after supplementary feeding, which suggests that sentinel effort is state-dependent (Wright, Maklakov, & Khazin, 2001). Pied babblers (*Turdoides bicolor*) communicate their energetic states which indicate their future sentinel contribution and adjust their sentinel behaviour to changes in the energetic states of others, to negotiate and ensure group protection (Bell, Radford, Smith, Thompson, & Ridley, 2010). Grooming is a cooperative behaviour since it gives social and stress-reducing benefits and a reduction in parasitic load to the recipients (Bray & Gilby, 2020; Hillegass et al., 2010; Kutsukake & Clutton-Brock, 2010; Radford, 2012; Sonnweber et al., 2015). Grooming helps to develop a bond with the recipient (Fedurek & Dunbar, 2009; Kutsukake & Clutton-Brock, 2006; Mishra et al., 2020). Compared to sentinel behaviour, grooming has a low energetic cost, especially in species where it is performed at the burrow during resting periods ((Kern & Radford, 2018), AR personal observation).

Dwarf mongoose cooperation

To study whether variation in cooperative behaviour can be explained by individual sex, dominance status and their interaction, we looked at sentinel and grooming behaviours in dwarf mongooses (*Helogale parvula).* This cooperatively breeding species shows high skew with a clear distinction between dominants and subordinates (Creel & Creel, 1991; Creel & Rabenold, 1994; Keane et al., 1994). Dwarf mongoose groups consist in a dominant breeding pair and subordinate helpers of both sexes (Keane et al., 1994a). Dwarf mongooses live in groups of 3-30 individuals. Dominants are identifiable from the outcome of aggressive interactions such as foraging displacements (Radford and Kern, 2013, 2016). In our study, the subordinates became dominants in their natal group after the previous dominant died (except one disperser); typically in this case the oldest same-sex subordinate acquires dominance (Rood, 1990). Since the benefits and relatedness to group members are equal between females and males, and cooperative behaviours may be more costly for females, we predict that males would produce more cooperative efforts than females.

Dwarf mongoose group members act as a sentinel to detect predators while the rest of the group mostly digs for preys (Kern & Radford, 2013; Rasa, 1989a). As dwarf mongoose sentinel behaviour is state-dependent – individuals do more when satiated (Arbon, Kern, Morris-Drake, & Radford, 2020a) – dominant females may incur a stronger trade-off between foraging and sentinel behaviour than males and subordinate females because of pregnancy costs. All individuals engage in grooming, predominantly whilst at the sleeping burrow. Subordinates may favour grooming the dominant over other subordinates as they are more valuable social partners, so that recent dominants would receive more grooming. Dwarf mongooses trade-off foraging and sentinel behaviour, but not grooming, which makes sentinel behaviour more costly than grooming. Dwarf mongooses are thus ideally suited for the investigation of the consequences of the costs of cooperation, as they use year-round a relatively costly (sentinel) and non-costly (grooming) cooperative behaviours.

Dwarf mongooses live in dry woodland savanna where rainfall determines environmental quality, so we can investigate how cooperative efforts vary with environmental quality. In harsher periods of time (hereafter: ‘bad environments’), sentinel behaviour is more costly than in good environments because food scarcity requires animals to spend more time and energy foraging to meet energetic needs (Houston, Clark, McNamara, & Mangel, 1988). Building strong social relationships may be even more important when the environment is harsh (Cimarelli, Marshall-Pescini, Range, Berghänel, & Virányi, 2021; Henzi, Lusseau, Weingrill, Van Schaik, & Barrett, 2009), which would increase grooming as it has a low cost. Hence, bad environments may reveal sex and status differences more strikingly (by increasing such effects); for example, females may decrease their costly cooperative behaviour after becoming a dominant breeder more when conditions are harsher (Shen, Emlen, Koenig, & Rubenstein, 2017).

In harsh environmental periods, dwarf mongooses may need to adjust their time budgets to their most pressing needs for their fitness: surviving and reproducing. Animals that recently became dominant may strengthen their bonds with helpers to encourage them to do more alloparental care, via reciprocation (Finkenwirth & Burkart, 2018), which would ultimately increase their future direct fitness. At the proximate level, all other group members may increase their grooming to reduce their own and subordinates’ stress, hence improving their body condition (Blumstein, Keeley, & Smith, 2016; van de Crommenacker et al., 2011).

A long-term study of wild, habituated dwarf mongooses makes them an excellent model system to disentangle the effects of sex differences in costs on cooperative behaviours. Here we investigate whether a sex difference in costs might have selected for a sex difference in status-dependent changes in cooperative investment. We analysed longitudinal field data on sentinel and grooming behaviour conducted by individual dwarf mongooses before and after acquisition of a dominant breeding position. We tested three prediction. *Prediction 1a*: females, but not males, will reduce their sentinel contributions after becoming dominant due to costs of gestation. Prediction 1b: that sentinel contribution will change with time differently for females and males, due to sex differences in costs, resulting in an interaction between period and sex. *Prediction 2*: becoming dominant will increase the proportion of the group's grooming received by that individual and the duration of grooming bouts in which it is involved. *Prediction 3*: sex- and status-differences will be stronger in bad than in good environments.

Methods

Field site and population

The data were collected on the Dwarf Mongoose Research Project, Sorabi Rock Lodge Reserve in South Africa (Kern & Radford, 2013, 2014). The climate is hot and dry, with precipitation primarily from December to February (Appendix Figure 5.A1). The study population between 2014 and 2020 comprised 4–10 habituated social groups of 3–17 individuals (mean=8) (Morris-Drake, unpublished data). The number of study groups varied between years, as some groups died off and others were added to the study population.

Environmental and individual state data

Daily rainfall (mm) was collected from June 2011 to November 2019 (Appendix Table 5.A1, Figure 5.A1). Seasons refer to wet (September to February) and dry (March to August) seasons. Diurnal variation in temperature (i.e., maximal – minimal temperature per 24-hour day), does not vary over the year (Appendix Figure 5.A1). Rainfall is associated with high abundance of invertebrate prey, so dwarf mongooses mainly breed in the wet season (Rood, 1990); as rainfall is an important factor we operationalised rainfall (present/absent) as environmental quality. Vegetation grows faster in the wet season (JMK, personal observation). We classified environmental quality as good if it rained and bad in the absence of rain in the period of dominance acquisition, and the 5 weeks and 1 week before in the wet and dry season, respectively.

We have trained dwarf mongooses to sit on a scale for up to three daily recordings of body mass. To study the variation in energetic state across periods, the same hour of the day must be compared due to daily fluctuation of body mass with foraging (daily) patterns. To calculate the body mass values, we focused on the weighing which had the highest number of individuals: the evening weighing. Evening body mass was recorded in all four two-week periods for three females and two males, and in at least one period for seven females and four males (Appendix Figure 5.A.7-5.A8). This gives a total of 35 body-mass days collected for 11 focal individuals (4 males) with at least one body mass per day.

Data collection

We used a long-term year-round dataset of two cooperative behaviours: sentinel behaviour and grooming. Each day of data collection started at the sleeping burrow, after which the dwarf mongoose group was followed during foraging before returning to the sleeping burrow in the evening. This study focuses on the four weeks before and four weeks after a change in the identity of one or both of the dominant breeders (Table 5.). Each period (labelled A, B, C, D) was two weeks; Period C started on the day of dominance acquisition. Each period corresponds to a different context: The period just before and just after becoming dominant likely reflect the social changes and disturbances that accompany a dominance change. By contrast the other two periods describe individual decisions in the preparation to dominance change (period A) and possibly to the preparation of reproduction (if in the breeding season) (period D). Each period likely corresponds to a suite of behavioural traits that develop over time. In this study, we were not interested in the direction of the link between time and a behaviour but on the time at which an individual changes its behaviour. We were interested in the time necessary for an individual who became dominant to adopt a “typical dominant behaviour”, such a higher sentinel contributions than subordinates (Kern et al., 2016). Variation in the number of observations recorded per individual did not allow us to compare sentinel and grooming rates; instead, we compared sentinel contribution, grooming proportion of the observed grooming in the group and grooming bout duration.

S*entinel behaviour*

Instantaneous scan sampling (ISS) (Altmann, 1974) were conducted every 30 minutes during foraging sessions, on all visible individuals of the group. Each scan sampling, they recorded whether one or more sentinels were active and their identity, which gives for every group member a binary response at each scan: sentinel or not. Following (Kern & Radford, 2013), sentinels were defined as individuals actively scanning the environment while perched on their feet at least 10 cm above the ground. We analysed a total of 1610 observations where at least one individual was sentinel for the 20 focal individuals (i.e., binary scan: sentinel or not) (Table 5.1). Eight females and 11 males inherited dominance in their group after the same-sex dominant left or died, whereas one female immigrated to become dominant.

Table 5.1: Number of observations for sentinel scans, grooming proportion of the observed grooming in the group and full grooming bouts per status and sex in the four two-week periods around dominance acquisition. The analysis focused on individuals with data on sentinel contribution, and/or grooming proportion, in each period. However, due to the small sample size, all complete grooming bouts from incoming/recent dominants were included. N: number of individuals. One group grooming proportion was calculated per period and per individual.

			Subordinate		**Dominant**		**Total**
Cooperative behaviour	**Sex**	**N**	Period A -4-3 weeks	Period B -2-1 weeks	Period C 1-2 weeks	Period D 3-4 weeks	All 4 periods
Sentinel scan	Female	9	223	199	140	161	723
	Male	11	173	252	254	208	887
Group grooming proportion	Female	3	1	1	1	1	4
	Male	8	1	1	1	1	4
Full grooming bouts	Female	15	26	9	40	59	134
	Male	12	34	65	215	102	416

Grooming behaviour

Following Kern & Radford (2018), we collected grooming data opportunistically (Altmann, 1974). The direction of grooming (donor vs recipient) was not considered since dwarf mongooses reciprocate grooming 95% of the time, often grooming simultaneously (Kern & Radford, 2018). A grooming bout was considered to have started when one individual begins grooming. Grooming bout duration (seconds) was measured for all bouts that were recorded from the beginning to end. Group grooming proportion refers to the proportion of total number of grooming interactions in which the focal individual was involved of the group and observation day; it includes incomplete grooming bouts i.e. bouts that are not observed from the start to the end (Table 5.1, Appendix Table 5.A1).

Statistical analysis

We analysed the relative frequency of sentinel contribution, group-grooming proportion and grooming bout duration with separate models. Generalised Linear Mixed Models (GLMMs) were constructed in R Version 1.3.1093 (The R Core Team, 2020) and used the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). The script used is accessible on Zenodo https://zenodo.org/doi/10.5281/zenodo.10009613.

Grooming bout duration and group-grooming proportion were divided by their standard deviation (the mean was not substracted since the response variable must be non-negative for the distributions we used). Bolker et al. (2009) recommend at least 5–6 observations per level of a random factor (i.e., n>5 scans per individual), which was not the case for the group identity, so we did not include group identity as a random factor but individual identity (‘ID’) instead. As data were pooled from individuals who were not necessarily observed grooming during all of the four periods, we included date as a random factor.

To test the predictions, we started with full models containing the interaction under study and the fixed factors that are likely to influence the cooperative behaviour (Season (e.g. Sharpe et al., 2016), Group size (Kern et al., 2016)). We used a multi-model comparison approach to test each of the predictions, by including only the fixed factors and interactions explicitly stated in the predictions. The fixed factors and the results of the tests are shown in Table 5.2. We performed multi-model inference with the MuMIn package to determine the best model: the best average model was obtained using the dredge function and the explanatory power of the fixed and random factors was assessed with

R.squaredglmm (Package “MuMIn” Title Multi-Model Inference, 2020). It was impossible to have Period and Status in the same model since these two fixed factors overlap: subordinate corresponds to period A and B, dominant corresponds to period C and D. The two-week periods enabled an investigation of sentinel contribution at a finer temporal scale than status.

Sentinel behaviour

During each recorded occurrence of sentinel behaviour for a given group on a given day, the focal adult mongoose was either the sentinel or not. As sentinel behaviour is a binary response variable, we used the family “binomial logit”. As the mixed model of the binary variable sentinel (yes/no) included less than three random effects (i.e., ID and date), we used the Laplace method to estimate the parameters of the models (lme4, glmer) (Bolker et al., 2009).

Grooming behaviour

In the grooming model, we weighted each group-grooming proportion by the number of days where grooming was observed in that group during that period (adding constant 0.001) to decrease sampling bias. After visual inspection of the histogram of data distribution, we confirmed that the transformed data followed the gamma distribution using the package fitdistrplus (Delignette-Muller, 2014).

Grooming duration was the mean duration (in seconds) of all full grooming bouts for each period that were observed from the start till the end for each period and individual. The response variable was the grooming duration, centred by dividing it by its standard deviation. We tested the link between grooming duration and status with the fixed factor status (See Results).

Body mass

To assess the role of body condition on cooperative behaviour, we compared the body mass of males and females.

Results

Sentinel contribution

There was no support for *prediction 1a* because dominants did not do more sentinel duty than subordinates overall. Indeed, the best model included only the fixed factor of group size (Table 5.2, 5.3, Figure 5.A2). There was no support for *prediction 3a* because environmental quality did not influence sentinel contribution. Indeed, once we added environmental quality to the model with status, the best model for sentinel contribution still only included group size as a fixed factor (Table 5.2, 5.3).

There was support for *prediction 1b*, because sentinel contribution varied with period and sex (Table 5.2, 5.4, Figure 5.1). Indeed, the best model included sex, period and their interaction, which suggests that sex differences occur during the dominance acquisition process. The model with period, sex and their interaction was better than that with group size due to a higher explanatory power of the model and a lower AICc (Table 5.2). Sentinel contribution was lower in period D for females than for males (Figure 5.1, Table 5.3). Females showed higher sentinel contributions in period C than in period B and D.

Table 5.2 Summary of the best mixed models for each prediction with effect sizes and AICc

Test	Response variable	Fixed factors	R^2m	R^2c	AICc
1a	Sentinel contribution	Group size (not significant)	0.0125	0.1261	1114.5
1b	Sentinel contribution	Sex*Period	0.0394	0.1312	1111.1
2a	Grooming duration	Status (not significant)	0.0149	0.1128	1507.8
2b	Group-grooming proportion	None	0	0	70.9
3a	Sentinel contribution	Group size (not significant)	0.0125	0.1261	1114.5
3b	Grooming duration	Status (not significant)	0.0149	0.1128	1507.8
3c	Group-grooming proportion	None	0	0	70.9

Table 5.3 Summary of the best model for sentinel contribution with status (Predictions 1a and 3a)

Fixed factors	**Estimate**	**Std. error**	**Z value**	**P value**
Intercept	1.60	0.387	4.125	3.71×10^{-5}
Group size	0.073	0.048	1.50	0.133
Random factors	*Variance*	*Std. deviation*		
Day	0.131	0.362		
ID	0.296	0.544		

Table 5.4 Summary of the best model for sentinel contribution with period instead of status (Prediction 1b). The reference levels are period C and females

Fixed factors	**Estimate**	**Std. error**	**Z value**	**P value**
Intercept	3.032	0.432	7.018	0
Period B	**-1.079**	**0.444**	**-2.43**	**0.015**
Period D	**-1.553**	**0.0453**	**-3.43**	**0.0006**
Period A	-0.876	0.449	-1.95	0.051
Sex M	**-1.208**	**0.502**	**-2.40**	**0.016**
Period B: Sex M	**1.325**	**0.524**	**2.52**	**0.011**
Period D: Sex M	**2.171**	**0.562**	**3.87**	**0.0001**
Period A: Sex M	**1.378**	**0.557**	**2.47**	**0.013**
Random factors	**Variance**	**Std. deviation**		
Day	1.16 x10-7	0.0004		
ID	0.348	0.590		

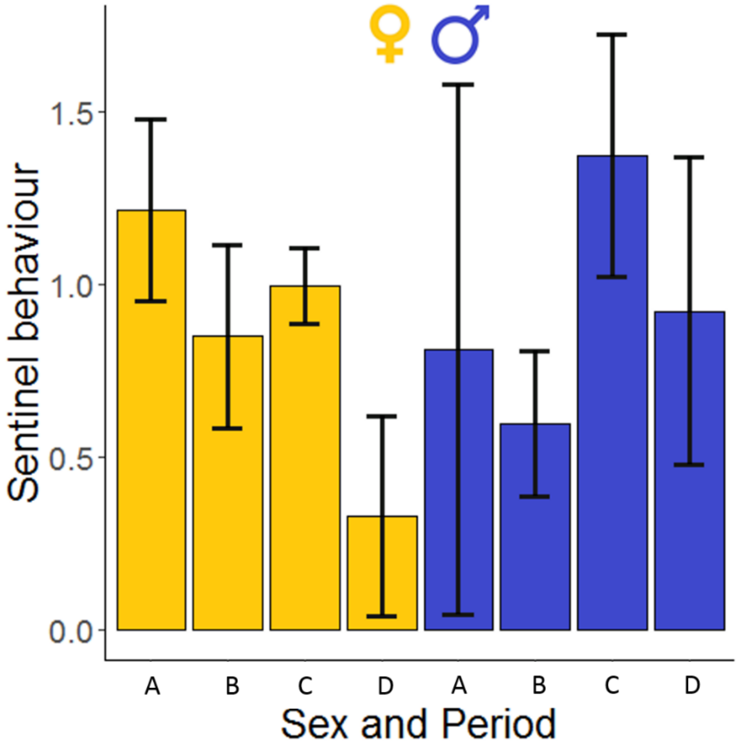

Figure 5.1 Sentinel contribution (Mean ± 1 SD) as a function of sex and period. Females in yellow and males in dark blue in the four periods. Period A: 4-3 weeks before, B: 2-1 weeks before, and C: 1-2 weeks and D: 3-4 weeks after becoming dominant. N=9 females, 11 males

Grooming duration

Prediction 2a was not supported since grooming duration was not higher in dominants than in subordinates (Figure 5.2, Table 5.5). While the best model for grooming duration included Status, it did not significantly predict grooming duration. This result suggests that status is more important than sex, season and group size in predicting grooming bout length.

There was no support for *prediction 3b* because environmental quality did not influence grooming duration. Indeed, once we added environmental quality to the model testing the effect of status, the best model still only included Status (Figure 5.2, Table 5.2, 5.5).

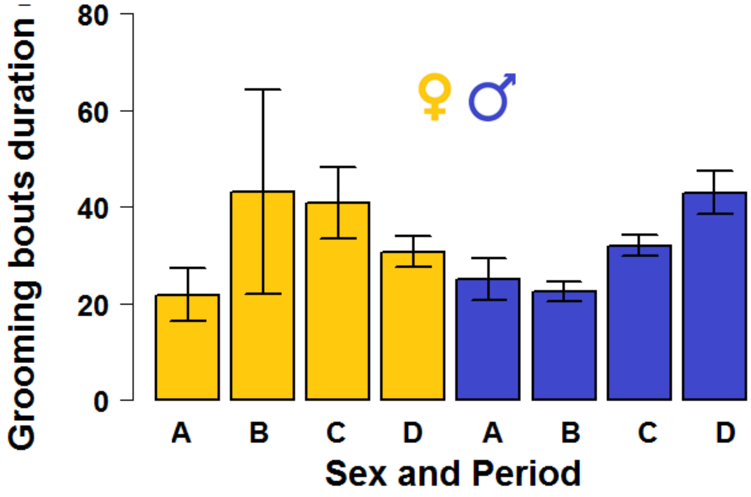

Figure 5.2 Duration of full grooming bouts as a function of sex and period (divided by Standard Deviation) (Mean ± SD). Females (left) are shown in yellow and males (right) in blue. Males did shorter grooming bouts period B, compared to period A and to females. Period A: 4-3 weeks before; B: 2-1 weeks before becoming dominant; C: 1-2 weeks and 3-4 weeks; D: after dominance change

Table 5.5 Summary of the best model for grooming duration (Predictions 2a and 3b)

Fixed factors	**Estimate**	**Std. error**	**Z value**
Intercept	0.718	0.094	7.604
Status Dominant	0.284	0.108	2.64
Random factors	**Variance**	**Std. deviation**	
Day	0.097	0.312	
ID	0	0	
Residuals	0.882	0.939	

Group-grooming proportion

We were not able to make any meaningful conclusions about group-grooming proportion as none of the fixed factors explained this behaviour (Table 5.2, 5.6, Figure 5.3).

Overall, the results show that the interaction between environmental quality and status is not significant and does not support the *predictions 3a, 3b* and *3c* (Table 5.2, 5.3, 5.5, 5.6).

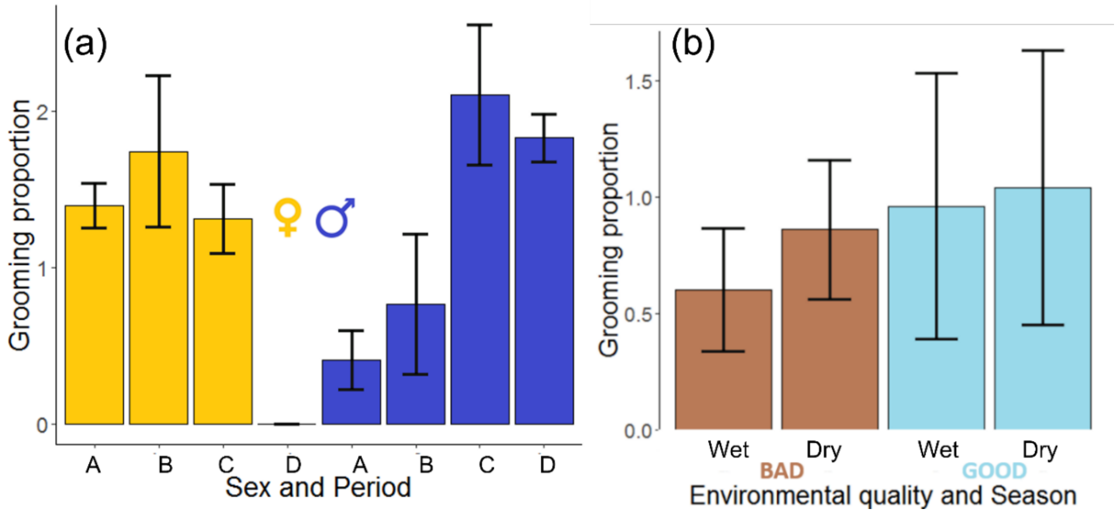

Figure 5.3 (a) Grooming proportion per sex and period in good environments (Mean ± SD, non-weighted). Females in yellow (n=3) and males in blue (n=8). Periods: 4-3 weeks before (A), 2-1 weeks before (B), and 1-2 weeks (C) and 3-4 weeks (D) after dominance acquisition. (b) Grooming proportion as a function of season and environmental quality (Mean ± SD). Bad environments (brown), good environments (light blue)

Table 5.6 Summary of the best model for group-grooming proportion (Predictions 2b and 3c)

Fixed factors	**Estimate**	**Std. error**	**Z value**	**P value**
Intercept	0.855	0.211	4.05	5x10^{-5}
Random factors	**Variance**	**Std. deviation**		
Day	0	0		
ID	0	0		
Residuals	0.713	0.844		

Body mass

Overall, whilst there was a tendency for males to be heavier than females (Figure 5.4, 5.A5), this difference was not statistically significant when all periods were pooled (Student's two-tailed test: t = -2.20, df = 12.8, *p* = 0.08, N=7 females, 4 males). No such sex difference was detected in the fortnight preceding dominance change, for which the most data were collected (t = -1.82, df = 5.17, p = 0.127, N=6 female, 2 males). Body mass positively correlated with group size (ANOVA: $F_{1,33}$=16.4, p=0.0003, N=11).

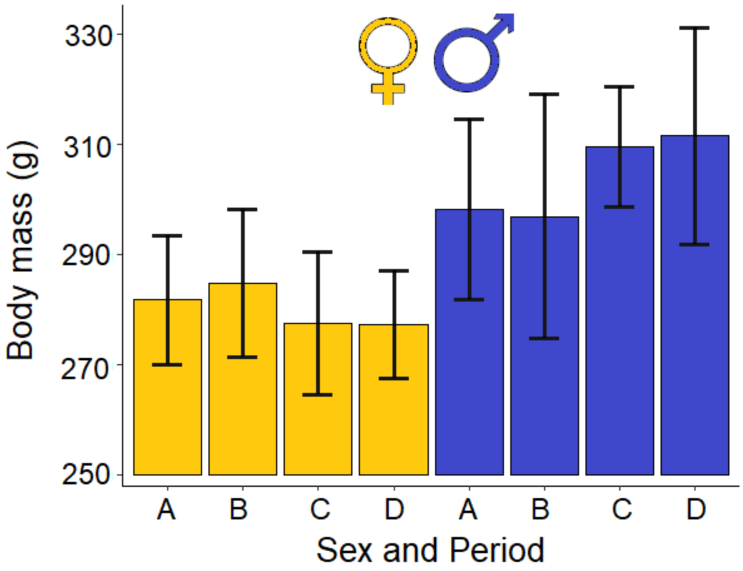

Figure 5.4 Body mass (in grams, +/- SD) as a function of sex, in the four periods around focal dominance acquisition. Females (yellow) showed lower body mass than males (dark blue). Individuals were weighted in the evening. N=7 females, 4 males

Discussion

We investigated how sex, dominance status and environmental quality affect cooperative behaviours in wild dwarf mongooses, focusing on within-individual changes from before to after attainment of a dominant breeding position. There was no evidence that individuals engaged in longer grooming bouts, higher sentinel contribution, nor were involved in a greater proportion of group-grooming once they became dominant compared to the preceding period as a subordinate. Investigating the timescale (rather than the status) in sentinel behaviour revealed that individuals varied their contributions as a function of their sex and the period. The effects of sex and status were not more visible in bad environments than in good environments.

Sentinel contribution may be linked to sex differences in costs

Contrary to *prediction 1a*, females did not reduce their sentinel contributions after becoming dominant because status did not influence this behaviour. Sentinel contribution changed with period differently for females and males, which supports *prediction 1b*. Contrary to earlier studies, sentinel contributions were not the highest in subordinate males (Rasa, 1989a), probably because this previous study had between subject design in a different population. We note that males' sentinel contribution was not consistently higher than females', which contradicts our hypothesis based on a simple application of Hamilton's rule (Hamilton, 1964) and highlights the complexity of cooperative decisions. All individuals except one female became dominants in their natal group, which indicates they lived with close kin and did not suffer any immigration costs in addition to the costs of dominance change. So, it is likely that other social and ecological factors influence the costs and benefits of a phenotypic expression as fleeting as a costly cooperative behaviour, and thus explain the documented sex difference.

I uncovered an interaction between sex and period in contributions to costly sentinel activity, with males contributing more than females in the second fortnight after individuals acquire dominance. The interaction between sex and period may be caused by several factors, with two ultimate and one proximate mechanism. First, females face higher reproductive costs than males (Clutton-Brock, Albon, & Guinness, 1989; Scantlebury et al., 2002), so that, for a similar energetic loss at status change, females need to recover more. Due to the energetic demands of gestation (Wasser et al., 2017), females would be selected to compensate by decreasing their sentinel contribution to carry out reproduction as quickly as possible and incur no fitness loss. A monogamous seabird shows parental coordination, as females forage more to restore nutritionally after egg laying, whilst males forage more before egg laying and do the longest first incubation shift (Pinet, Jaquemet, Phillips, & Le Corre, 2012). Dwarf mongooses may coordinate similarly, with the dominant male carrying out more sentinel behaviour to enable the dominant female to restore body condition just before breeding. Second, females may face higher absolute or relative costs to becoming dominant due to high intra-sex competition. Harsh female-female conflict is well-documented in dwarf mongooses and the closely related meerkats (Creel & Rabenold, 1994; Dantzer et al., 2019; Dimac-Stohl et al., 2018; Sharp & Clutton-

Brock, 2011; Sharpe et al., 2016). Besides, female reproduction may require reproductive activation and necessitate greater physiological changes than that in males (Clutton-Brock et al., 2010; Rood, 1980; Sharpe, Rubow, & Cherry, 2016). The hypothesis that individuals who have higher energetic needs or costs reduce their sentinel contribution temporarily to (re)gain body condition by foraging is supported by evidence that recent dwarf mongoose immigrants contribute less than before their dispersion, potentially due to energetic costs (Kern & Radford, 2017).

A third reason for male's higher sentinel contribution immediately after becoming dominant is that females may have evolved to respond to a different rule than males to decide their sentinel contribution, due to the sex-specific energetic needs (Scantlebury et al., 2002; Clutton-Brock, 1989). Overall, there is a trend for males to be heavier than females, which suggests that females may have a lower basal energetic state than males, for instance lower fat reserves. Consequently, males, but not females, may increase temporarily their sentinel contribution after becoming dominant, at the cost of their body mass (Appendix Figure 5A.7). A similar energetic loss could be perceived as more negative by females than by males. Females, due to their lower body mass and higher energetic needs for reproduction, may be more sensitive to body mass loss; they may have evolved a flexible rule to be sensitive to low food availability, to adjust their sentinel behaviour to environmental variation (Higginson, Fawcett, & Houston, 2015). A caveat is that males may have higher energetic demands due to a higher body mass (Hudson, Isaac, & Reuman, 2013). The current body mass data did not allow determination of whether females re-gain quickly the energy they needed and/or lose more energy at dominance acquisition. These preliminary data do not contradict the hypothesis that females need to forage more than males due to lower body mass, which may have selected for a temporary increase in sentinel contribution by recent dominant males to allow potential mates to build fat reserves.

This sex difference in sentinel contributions may be equivalent to the variation in provisioning rules by bird parents. For example, in Manx shearwaters (*Puffinus puffinus*), males carry out the bulk of chick-provisioning but are not as sensitive to offspring needs as females, which suggests a sex-specific optima where males reduce their provisioning for a higher chick satiety/quality than females (Hamer, Quillfeldt, Masello, & Fletcher, 2006). Our findings regarding sentinel contribution contrast those on parental care, where females have been shown to be less predictable – thus more flexible – than males (Nakagawa et al., 2007). Dwarf mongoose females may have been selected to be responsive to the needs of the offspring. By contrast, males' lower reproductive costs may have allowed the evolution of sensitivity to the needs of the group (including the survival of potential mates and future offspring). Theoretical models predict variation in behavioural rules/strategies as a function of personality (Favreau et al., 2014; McNamara et al., 2009; Michelena, Jeanson, Deneubourg, & Sibbald, 2010) and hints in empirical data supports this possibility (Michelena, Sibbald, Erhard, & McLeod, 2009).

Grooming behaviours are not explained

Our results did not provide any evidence that individuals show higher grooming as dominants than as subordinate and therefore do not support *prediction 2*. Overall, contrary to *prediction 3* stating that the interaction between sex and status should be more visible in bad environments, we did not detect more significant effects in harsh periods ('bad') than in favourable periods ('good environments'). The best model for group-grooming proportion did not contain any fixed factor, and overall the models explained a <1.5% of the variance of the data; this may suggest that we did not capture the most relevant factors for this behaviour and/or that the sample size is too small to get sufficient power. Caution must be taken in the interpretation. Further research is needed to clarify which factors influence grooming behaviour in individuals who become dominants.

Implications and future studies

To my knowledge, this is the first study to explore the continuous change over time in cooperative behaviours in a cooperative breeder, before and after becoming dominant, as a function of sex, dominance status and environmental quality. Taken together, the results suggest that dwarf mongooses do not show an immediate "switch" in grooming and sentinel contribution at dominance acquisition. Since the interaction between period and sex was significant, sentinel contribution may stem from a sex difference in behavioural rules and in the reproductive costs.

These results suggest costs may modulate sentinel contribution. This study contributes to the growing understanding that animals change their cooperative behaviour flexibly as a function of variations in costs and benefits. This chapter also sheds light on the potential interaction between sex and environmental quality in the temporal changes in behaviours with dominance. However, with the limited sample size, caution must be taken, so that further investigation is required to confirm and validate how cooperative behaviour varies with the interaction between sex, status and environmental quality.

A limitation to the comparability of the relatively costly and non-costly behaviours is that individuals studied for grooming were not all the same as the individuals studied for sentinel behaviour. To develop a full picture of dwarf mongooses' costs and benefits of cooperative behaviour, additional studies will be needed that assess the reproductive skew in this population as it gives the direct fitness benefits to dominants and subordinates. Measuring the costs of these cooperative behaviours is crucial; for instance linking the body mass gain or loss with morning and evening weighing, to the sentinel contribution that day, would provide information on the real cost of sentinel behaviour and whether it varies with status or sex. Further test of the causes of the short-term sex difference in sentinel contribution in recent dominant may be conducted by weighing the individuals at all times. Indeed, assessing body condition is required to determine whether dominance acquisition is more costly for females and if they need higher body conditions to breed than males.

This study focused on two behaviours that benefit either the whole group or the dyad involved. Further research is required to investigate the influence of sex, status and environmental quality on parental and alloparental care, to better understand the factors that shape variation in cooperative behaviours. Exploring these factors and behaviours in other cooperative breeders is likely to be fruitful too. In summary, our results suggest that dominance acquisition does not lead to quick stable changes in contribution to vigilance, but that females and males may adjust their coordinated vigilance to sex-specific and temporal variation in the costs of status acquisition and reproduction.

Chapter 6 – General Discussion

Rock hyrax (*Procavia capensis*)

1. Summary of thesis findings

The aim of this PhD was to investigate how individual differences, such as quality and sex, influence the reproductive strategies of cooperative breeders and understand the influences on reproductive skew and the decision to breed cooperatively. I have addressed gaps in the knowledge of cooperative breeders' reproductive strategies by focusing on the causes and consequences of individual differences. The main hypothesis was that subordinate quality and relatedness (Chapter 2, 3), and sex differences in life history traits (Chapter 4, 5), will influence reproductive strategies and underlie the diversity among the strategies of cooperative breeders.

I found that subordinate outside options and its link to helping effects were key predictors of social behaviour (Chapter 2, 3), more so than sex differences (Chapter 4,5). This research revealed an overall positive association between relatedness and reproductive skew (Chapter 2). Variation in subordinate quality and the quantity of information about subordinate quality could strongly influence reproductive strategies (Chapter 3). Introducing a sex difference in subordinate competitive ability and probability to find a nest of one sex did not influence skew and cooperative breeding in the other sex, suggesting the skew of males and females may be effectively studied in isolation (Chapter 4). Sex differences changed over time in cooperative breeding mongooses, as males showed higher contributions to a costly cooperative behaviour than females in the second fortnight after becoming dominants (Chapter 5).

2. Implications of individual differences

Differences in subordinate outside options and helping effect

One theme that emerges in this thesis is the importance of subordinates' outside option and inside option (fitness inside the group). For unrelated subordinates, the inside option is the subordinate share of the group productivity. The subordinate independent breeding success outside the group determines whether subordinate will stay, as it weighs its option inside and outside the group. I investigated the effect of a factor that links the outside option and the contribution to group productivity by the subordinate, since good helpers may have high or low outside options. Our extended concession model predicts that, when the link between helping and outside option is positive and strong, skew should decrease with subordinate outside options; otherwise skew should increase with it (Chapter 2). By contrast, the classic concession model predicts that skew always correlates negatively with subordinate's outside options (Johnstone, 2000). Despite decades of research, empirical tests of models of skew had not provided a consensus, making our more precise predictions potentially useful.

Chapter 2 also made new predictions for the restraint and tug-of-war models: Indeed, skew increases with relatedness in the restraint with negative quality-productivity coefficient (QPC) and high subordinate quality. Furthermore, the tug-of-war model predicted a positive correlation between skew and relatedness with low quality subordinates, but none with high quality subordinates. The meta-analysis of observational data found a positive link between skew and relatedness that overall supports the restraint and tug-of-war models. The exception is that when subordinate have high outside options but low helping effect (i.e., negative QPC), the concession model applies. The review of skew only systematically examined the link between relatedness and skew. Future meta-analysis should determine how skew changes with subordinate competitive ability, subordinate outside option and quality-productivity coefficient, since empirical tests are needed to determine whether our other predictions hold true.

Subordinate quality is an ill-defined concept as it has been used by different modellers to mean different things: either competitive ability (Reeve et al., 1998) or outside options (Verhencamp, 1983). Clarifying which facet of individual quality the model focuses on is critical to make testable and comparable predictions. Indeed, definition is crucial for scientific advances (Kristensen et al., 2012), to compare models and link models to empirical studies. My findings highlight the relevance of being explicit about what it is that model parameter actually refer to (Chapter 2, 3).

Incorporating complexity into models of skew led to different consequences

Our findings have shown that the strength and sign of the association between helping effect and outside option can change the predictions of the concession and restraint model of skew (Chapter 2). This finding highlights the importance of incorporating more complexity into models to understand what causes the diversity in cooperative breeders. However, the reproductive strategies of one sex did not vary when the nest availability and subordinate competitive ability of the other sex (and their reproductive strategies) were altered (Chapter 4), which suggests that males and females could have reproductive strategies that are insensitive to the conflict over skew between dominants and subordinates of the other sex, despite contributing to a common good. This prediction suggests that the parental and the skew games can be studied in isolation, and skew games do not need to include both sexes. More broadly, our analysis suggests that adding complexity to models does not always change the predictions, which may be explained by differences in how the factors influence fitness. Indeed, in Chapter 4 subordinate outside options are a combination of nest availability and solitary breeding success, which depends on dominant ‘solitary’ productivity; this means that subordinate outside options are not directly affected by changes in nest availability. Similarly, subordinate competitive ability is not directly tied to subordinate inside or outside option. By contrast, the quality-productivity coefficient affects directly the outside options and the group productivity, and indirectly the inside option of the subordinate. The conflict over parental efforts seems to disappear once cooperative breeding is possible, since all breeders performed the highest efforts, whereas the reproductive conflict remained (Chapter 4).

Implications of sex differences

Another key facet of individual differences is sex differences in life histories, which might select for different response to conflict. My study of wild dwarf mongooses (Chapter 5) revealed no consistent sex difference in a relatively costly cooperative behaviour. However, males showed higher contributions than females after becoming dominant, which suggests a sex difference in the costs of cooperation occur at this moment of their lives. Indeed, individuals may adjust their cooperative behaviours to changes in their short-term costs and benefits (Arbon, Kern, Morris-Drake, & Radford, 2020b; Kern & Radford, 2017, 2018). Further longitudinal studies would enable to clarify the ontogenic trajectories of sentinel contributions (or other costly cooperative behaviours) in males and females.

Our model of skew with females and males predicts that individuals should not vary their own strategies, including investment in the reproductive conflict, with changes in the other's nest availability or subordinate competitive ability. This findings suggests that the two sex may evolve their reproductive strategies quite independently. It contradicts my expectation that the presence or absence of helper in one sex would influence skew and cooperative breeding in the other sex due to a change in group productivity.

Taken together, my findings may suggest that sex differences in reproductive costs, subordinate outside option and subordinate competitive ability can be associated with subtle sex differences in cooperative behaviour and skew. Indeed, cooperative breeders seem to consider more the inside and outside options in their own sex, when making reproductive decisions. Sex differences in reproductive conflict may not be the main drivers of skew in most cooperative breeders. Future research may explore how incorporating sex differences in subordinate quality and helping effect influences the reproductive strategies.

3. Effect of uncertainty

A growing trend in behavioural ecology is the study of the effects of information, its costs and benefits (Budaev, Jørgensen, Mangel, Eliassen, & Giske, 2019; Champagne, 2008; Dechaume-Moncharmont et al., 2005; Sinead English, Fawcett, Higginson, Trimmer, & Uller, 2016; Mariette, 2019; McNamara & Dall, 2010b; McNamara et al., 2009; Mesterton-Gibbons & Heap, 2015; Trimmer, Higginson, Fawcett, McNamara, & Houston, 2015). Uncertainty, coming from imperfect information has increasingly been studied (Dantzer et al., 2019; Fawcett & Frankenhuis, 2015; Kennedy et al., 2018; Matsumura et al., 2010).

A concession model of skew predicted that if subordinates do not have perfect information about of their benefits of staying in the group, cooperative breeding is not evolutionary stable (Kokko, 2003). This earlier model showed that subordinate's uncertainty about their inside option influenced the strategies. A model of cooperation that uses mechanism design investigated the effect of having imperfect information about partners' outside option and predicted that evolution does not evolve, unless individuals are closely related (Akcay et al., 2012). To clarify what animals should do under various levels of uncertainty about partners' outside options, I introduced variation in the amount of dominant information about the subordinate's quality (Chapter 3). Taken together, these findings suggest that in concession models of skew, cooperative breeding can evolve if only dominants have uncertainty about subordinate quality.

Chapter 3 investigated the optimal level of uncertainty about subordinate outside option and predicted that dominants should evolve to seek information about it. The subordinate's outside option may reflect environmental quality in at least three ways. First, the availability of (suitable) breeding site strongly influences the possibility for independent breeding (Eikenaar, Richardson, Brouwer, Bristol, & Komdeur, 2009). Second, high predation risk increases dispersal mortality and/or the possibility to breed successfully without helper, therefore reducing the outside option (Groenewoud et al., 2016). Third, subordinates are often the older offspring of the dominant (pair) and their quality as a breeder is affected by food provisioning and other factors influenced by early-life environment (Sinead English et al., 2016; Groothuis, Müller, von Engelhardt, Carere, & Eising, 2005; Tibbetts, Vernier, & Jinn, 2013; Vitikainen, Thompson, Marshall, & Cant, 2019) or parents' prenatal environment (Shah & Rubenstein, 2022). Environmental quality can therefore directly influence subordinate outside options, but also other factors such as dominant solitary breeding success (Lin et al., 2019) and helping benefit (Van de Ven, Fuller, & Clutton-Brock, 2020a). Future research should investigate how uncertainty about these factors affect social behaviours.

My study demonstrates the influence of incorporating variation and uncertainty on model predictions, which supports the argument to add complexity to models to get better theoretical insights (McNamara, 2013). To better understand how cooperative breeders use each socio-ecological factor to make decisions, it may be useful to further investigate the optimal level of information of other factors that have been found to influence the reproductive strategies, such as subordinate information about dominant outside option, dominant's information about subordinate QPC. To determine which factors shape the strategies of animals in behavioural ecology more broadly, it may be fruitful to predict the optimal quantity of information and the effect of uncertainty in other contexts than cooperative breeding.

4. Limitations and future research

The models developed in this thesis are based on static equilibrium. Models where animals can respond to each other, dynamic games (Houston & McNamara, 1999), advanced for instance the fields of parental effort games (Ewald et al., 2007) and Hawk-Dove competitive games (Fawcett & Johnstone, 2010). However, at an evolutionary scale the short-term changes in parental efforts in Chapter 4 may be less important than the baseline level as parents adjust their efforts in response to their own energetic state and offspring needs. The helpers may adjust their efforts too as a function of the potential costs and benefits, making the predictions potentially valid. Besides, focusing on QPC may be more powerful than incorporating small-scale behavioural adjustments in efforts as this factor is novel, this model explored the ultimate mechanisms, and it is useful to build simple models before adding in complexity (McNamara 2013).

It was beyond the scope of this thesis to explore the influence of variation in dominant quality on skew and group formation. However, variation in subordinate quality is arguably more important than variation in dominant quality, for three reasons. Firstly, since subordinates may or may be able to breed (e.g. sterile helpers in eusocial societies (English, Browning, & Raihani, 2015), vs banded mongooses (*M. mungo*) who can physiologically breed (de Luca & Ginsberg, 2001)). Secondly dominants can all breed so variation in quality only creates variation in the quantity of direct fitness (not the presence/absence of offspring production). Thirdly, subordinate quality determines their outside options, which is a crucial factor to understand which strategy would be most optimal in each given situation (Chapter 2, 3). Variation in dominant outside option (quality) would enable to compare the obligatory cooperative breeders who get no reproductive success without helper(s), to facultative cooperative breeders (e.g. tropical grey-throated babbler *Stachyris nigriceps* (Kaiser et al., 2018)).

In this thesis, we tackled each factor of individual difference in a chapter and model instead of incorporating all the factors and uncertainty at once. A limitation is the lack of integration of the different types of models created in the Chapters 2, 3 and 4. The model in Chapter 4 combines the three models of skew but it does not consider the link between subordinate quality and helping effect and does not vary information about any factor. Perhaps adding this link might reveal that the predictions of the parental and skew games change for both sexes for low or negative QPC.

5. Cooperative breeders and behavioural plasticity

Chapter 5 used a within-subject design and did not find any evidence of the role of environmental quality on grooming and sentinel behaviours. Further work on all individuals, a longer time span and alloparental care behaviours may shed light on how dwarf mongooses change their cooperative behaviours in bad environments. This may help predict how individuals of different sex and status will be affected by climate change, and how populations may cope with it.

Although dominants can often adjust their parental care to offspring need (Fortuna et al., 2022b) and their own energetic levels (Baldan, Hinde, & Lessells, 2019), Chapter 4 concentrated on identical dominants with fixed parental care. If the individuals are not sure about the quality of their partner, then it is not possible for them to perfectly know their partner's effort, and response rules will evolve rather than fixed levels of efforts (Houston & McNamara, 1999). In nature, animals can perceive and respond to each other's behaviour (to a certain extent). For instance, a dominant may increase its reproductive control (e.g. eviction, aggression) when it observes that the subordinate decreases its caring effort (i.e.

uncooperativeness is reciprocated) (Fischer, Zottl, Groenewoud, & Taborsky, 2014b). Using response rules in a parental effort game altered the predictions: the parental effort chosen at the end of the negotiation gives lower fitness than that of the original parental effort game (McNamara, Gasson, et al., 1999). This means that I neglected plasticity in parental effort in Chapter 4, which may have changed the predictions (McNamara, Gasson, et al., 1999). Consequently, fixed strategies might not be sufficient to predict cooperative breeders' reproductive strategies and future models where dominants are plastic in their parental care may clarify whether subordinate and dominant care co-evolve.

Dominant breeders are typically bigger than subordinates. In cooperatively breeding insects, early life conditions determine the developmental trajectory into a breeder or a helper (Schwander et al., 2008; Tibbetts & Izzo, 2009). In mammalian cooperative breeders, however, growth trajectories remain plastic and animals can adjust their body size to the environmental conditions (Heg & Hamilton, 2008; Huchard et al., 2014).

Theoretical studies have started to explore how animal may adapt their behaviours to changes in their environments. A recent simulation investigated how plastic behaviour evolved in response to changing environments, when individuals living in one of two environments could switch between two behaviours (Gomes & Cardoso, 2020). For each behaviour, the animal started with performance zero and increased its performance as it used it (e.g. learn skills and improve efficacy in a foraging technique). The performance of the behaviour also decreased when the animals did not use it. Only when the ratio between the rates of increase and decrease in behavioural performance was sufficiently high (Gomes &Cardoso, 2020). Besides, the psychological mechanisms animals have evolved may prevent them from behaving optimally if the rate of environmental change is too fast for natural selection to evolve compensatory mechanisms (Fawcett et al., 2012). Many cooperative breeders may thus fail to adapt to global environmental change, consequently using sub-optimal strategies.

6. Cooperative breeders and environmental change

Human induced rapid environmental changes (HIREC) such as land use modification, temperature or noise pollution are ubiquitous and cause alterations in animals' habitats (Sih, 2013). HIREC lead animals to have more uncertainty about their expected fitness (Sih, 2013), and may disrupt the reliability of the early life cues they use to choose optimal strategies (Kuijper & Johnstone, 2018). While the rate of environmental change is too high for genetic adaptations to emerge, little is known about potential behavioural responses to HIREC in cooperative breeders (Robertson, Rehage, & Sih, 2013; Sih, 2013). If the information processing systems of the animals perceive HIREC, and if cooperative breeders' behavioural flexibility is sufficiently high, behavioural adaptation may emerge as a response to HIREC (Sih, 2013). However, constraints may limit behavioural flexibility, leading cooperative breeders to not adjust to HIREC (Van de Ven, Fuller, & Clutton-Brock, 2020b).

Little is known of the extent of behavioural plasticity in helping and reproductive sharing, since the factors affecting animals' decisions and the response rules are not clear. HIREC may increase the stress levels of all individuals, who may respond by changing their reproductive decisions (Wingfield & Sapolsky, 2003) and helping (Starcke & Brand, 2012). On the one hand, helper contribution may decrease with a challenging environment, as individuals may favour investing in their survival rather than in the offspring of the group. For instance, meerkat helpers (*S. suricatta*) (Dantzer et al., 2017; MacLeod, Nielsen, & Clutton-Brock, 2013; Van de Ven et al., 2020b) and chestnut-crowned babbler helpers and males (*Pomatostomus ruficeps*) (Nomano, Savage, Browning, Griffith, & Russell, 2019) reduce their offspring care under harsh conditions, leading to lower group reproductive output (Rood, 1990). On the other hand, higher environmental uncertainty may reduce the probability of breeding successfully alone (Hatchwell & Komdeur, 2000), which would thus decrease the subordinates' outside options and the expected fitness of a solitary breeder, therefore increasing in helping behaviour (Hammerstein & Noë, 2016). Further research would shed some lights on the short-term and medium-term evolutionary trajectories of cooperative breeders' behaviours, and inform conservation efforts.

Conclusion

Cooperative breeders are a very diverse group, which makes it ideally suited to study the evolution and function of cooperation because they differ in the costs and benefits of cooperative behaviours. Yet, it remains a challenge to develop a theory that fully encompasses the cooperative behaviour since animals differ in the relatedness between the subordinate and the dominant, outside options, helping effects, group size, skew, and other environmental drivers. This thesis is an attempt to further our understanding on these questions by using evolutionary models and empirical studies. I hope that the theoretical predictions will be taken to the field and that empirical tests of their assumptions and predictions will be conducted.

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ANNEXES

ANNEXE 2.A: Supplementary figures and tables for Chapter 2

Table 2.A1: Empirical data on the direction of the link between reproductive skew and socio-ecological factors in insects and vertebrates. The links test the association between skew and subordinate quality, the quality-productivity coefficient, relatedness and dominant's competitive advantage. N=73

Links tested	**0**	**-**	**+**	**Grand Total**
Subordinate quality & skew	4	3	2	9
Insect	1			1
Vertebrate	3	3	2	8
Quality-productivity coefficient & skew			2	2
Insect			1	1
Vertebrate			1	1
Relatedness & skew	31	6	8	45
Insect	14	4	4	22
Vertebrate	17	2	4	23
Dominant's competitive advantage & skew	9	2	6	17
Insect	7	1	0	8
Vertebrate	2	1	6	9
Grand Total	44	11	18	73

Table 2.A2: Numbers and proportion of empirical tests supporting TOW model of skew, concession model and restraint model in insects and vertebrates. The total number of studies testing each association predicted by the model is indicated in the last row. N=62

Model supported	**Proportions**	***r&y***	***x&y***	***b&y***	***QPC&y***	**N support**	**N overall**	**% support**
TOW	Insects	0.81	0	0	1	27	41	*65.0%*
	Vertebrates	0.833	0.2	0.5	1	26	37	*70.3%*
	Total	0.822	0.167	0.111	1	52	62	*67.5%*
Concession	Insects	0.381	0	0	0	10	41	*25.0%*
	Vertebrates	0.25	0.2	0.5	0	10	37	*27.0%*
	Total	0.222	0.167	0.111	0	20	62	*26.0%*
Restraint	Insects	0.19	0	0.143	0	5	41	*12.5%*
	Vertebrates	0.167	0.8	0.5	0	9	37	*24.3%*
	Total	0.178	0.667	0.222	0	14	62	*18.2%*
	N total	45	6	9	2			

Table 2.A3: Co-occurrence of empirical tests of the link between skew and relatedness (vertically); and skew and (a) subordinate quality x and (b) group productivity k. Each model that predicts the combination is indicated in parentheses (Figure 2.1).

Co-occurrence		**$y \sim x$** -	**0**	**+**
	-	1 (concession)	0	0 (concession)
$y \sim r$	0	0	1 (restraint)	1 (tug-of-war)
	+	0	0 (restraint)	1 (restraint)

Co-occurrence		**$y \sim k$** -	**0**	**+**
	-	0	7	2
$y \sim r$	0	0	2	0
	+	0	0	1

Table 2.A4: Average effect size g (±Standard Deviation) for insects and vertebrates as a function of the direction of the link between relatedness and skew recorded in the study. N=16

Direction of *r&y*	**Insect**	**Vertebrate**	**Average**
negative	-1.32	-0.24	-0.600 ±SD 1.018
nil	0.304 ±SD 0.358	0.516 ±SD 0.531	0.410 ±SD 0.441
positive	1.27 ±SD 0.611	1.82	1.407 ±SD 0.570
Average	0.396 ±SD 0.907	0.733 ±SD 0.713	0.533 ±SD 0.798

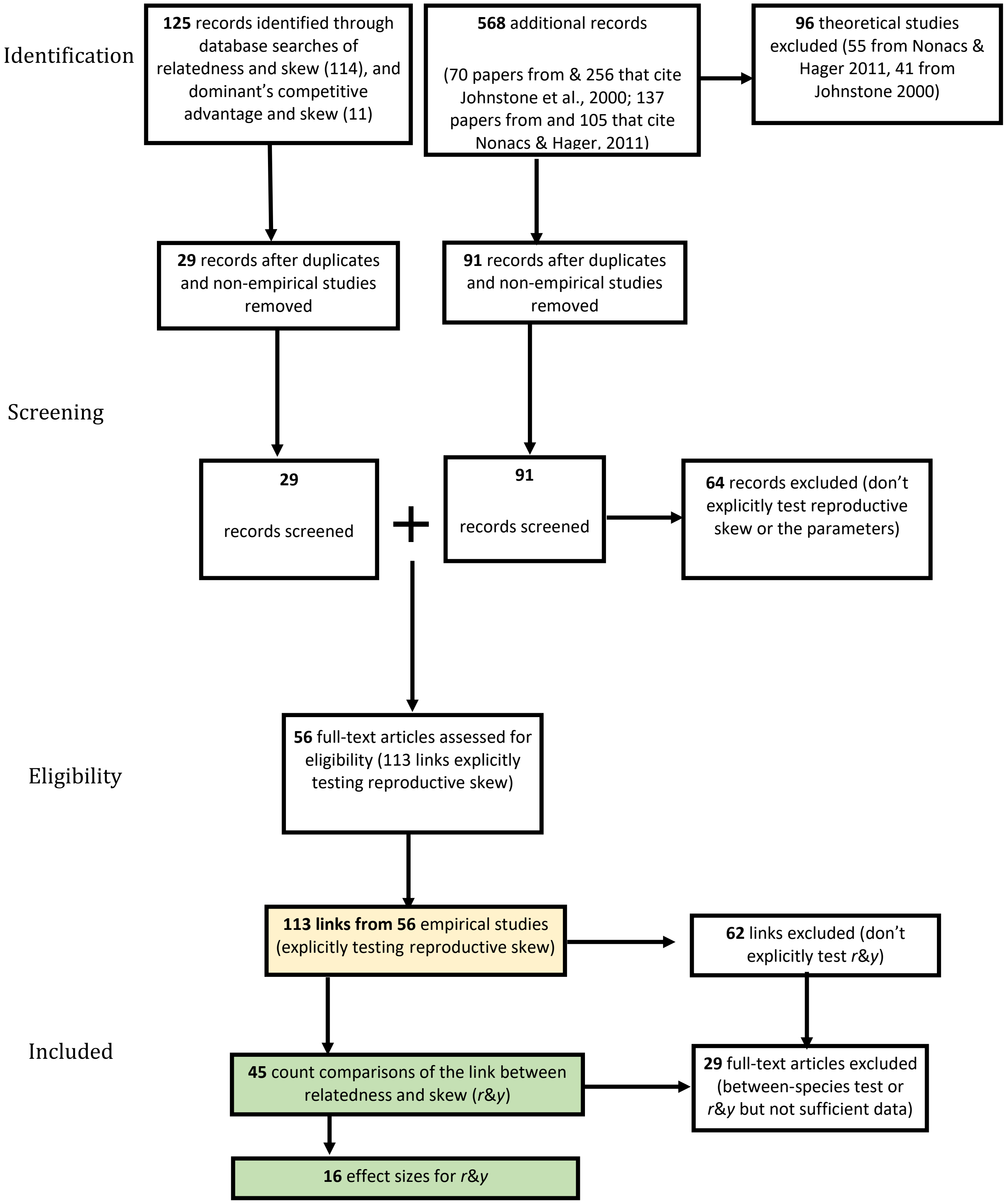

Figure 2.A1: Schematic PRIMSA flow diagram outlining the systematic literature review process. All links are tested (count comparison, orange, n=113) but only some *r&y* studies are included for effect size calculation (green, n=16)

Table 2.A5: Empirical tests of several parameters of the observed effect of the link between skew and other parameters. The link tested was either negative (-), positive (+), nil (0) or unclear. Unavailable data is blank (empty). Only species tested for several links are shown here. Most studies cited or were cited in (Nonacs & Hager, 2011). Reference: studies whose data was extracted; Taxa: phylogenetic group; NbTest: number of empirical tests of the link *r&y* for this species; Species: scientific name of the species studied; *r&y*: link between relatedness and skew; *x&y*: link between subordinate quality and skew; *k&y*: link between group productivity and skew;-*r&k*: link between relatedness and group productivity; *b&y*: link between dominant's competitive advantage and skew; *h&k*: link between helping effect and group productivity; *x&k*: link between subordinate quality and group productivity; *h&r*: link between helping effect and relatedness; *a&y*: link between quality-productivity coefficient and skew.

Reference	**Taxa**	**Nb Test**	**Species**	**r&y**	**x&y**	**k&y**	**r&k**	**b&y**	**h&k**	**x&k**	**h&r**	**a&y**
Hannonen 2003	ant	1	*Formica fusca*	0(workers) /-(queens)		0		0				
Hammond et al, 2006; Gill & Hammond, 2011; Gill et al, 2009; Walter 2015	ant	1	*Leptothorax acervorum*	0/+		0	0	-	+			
Fournier et al, 2004	ant	1	*Pheidole pallidula*	0		0						
Hogendoorn & Velthuis 1999	bee	1	*Ceratina spp*	0		0						
Langer et al 2004	bee	1	*Exoneura nigrescens*	-	0	0	+					
Langer et al 2006, 2012	bee	1	*Exoneura robusta*	0/-		0	0					
Heinsohn	bird	1	*Corcorax melanorhamphos*	+	+							

Haydock & Koenig 2003	bird	1	*Melanerpes formicivorus*	0	0				0	
Jamieson 1997	bird	1	*Porphyrio porphyrio*	-	+					
Lu et al 2012	bird	1	*Pseudopodoces humilis*	-		0				
Whittingham et al 1997	bird	1	*Sericornis frontalis*	0		0				
Kaiser et al 2018	bird	1	*Stachyris nigricips*	0	-					
Heg & Hamilton, 2008; Heg et al, 2006; Stiver et al, 2005	fish	1	*Neolamprologus pulcher*		0			+/+		unclear (+/-)
Kappeler & Port (2008)	mammal	1	*Eulemur fulvus rufus*	0		+				
Dudgale et al 2008	mammal	1	*Meles meles*	0		0	0			
Kappeler & Shaffler 2008	mammal	1	*Propithecux verreauxi*		0			0		
Clutton-Brock et al 2001, Cram et al 2001	mammal	1	*Suricata suricatta*	0	+/-	+		+		
Miyazaki et al 2014	termite	1	*Reticulitermes speratus*	+			-			
Sumner et al, 2002	wasp	1	*Liostenogaster flavolineata*	0		0		0		
Fanelli et al, 2005, 2008	wasp	2	*Parischnogaster mellyi*	0/0		0/0		0/0		

Field et al 1998	wasp	1	*Polistes bellicosus*	0		0		
Seppa et al 2002	wasp	1	*Polistes carolina*	0	0	0		
Liebert & Starks, 2006; Monnin et al, 2009; Queller et al, 2000	wasp	3	*Polistes dominula*	0/0/0				
Reeve et al, 2000	wasp	1	*Polistes fuscatus*	+			+	+

ANNEXE 2.B: Methodology for Chapter 2

Literature search and screening

We conducted a review of the peer-reviewed literature; We searched on Google Scholar among the 207 papers cited by the most comprehensive reviews (Johnstone, 2000a; Nonacs & Hager, 2011) and papers that have cited them (n=361). We used the keywords: reproductive skew AND relatedness (PubMed, 19/07/21). To further explore the association between skew and group productivity (i.e. total fecundity of the group), we used the following keywords (Web of Science, 15/10/21): reproductive skew group productivity fecundity; reproductive skew test productivity; "reproductive skew" fecundity AND "reproductive skew" "group productivity" AND skew "group productivity". Our criteria for reproductive skew were that studies had measured reproductive skew by genotyping the offspring/eggs and the potential breeders. We excluded theoretical studies since we aimed to test the predictions. We also excluded experimental studies with a sample size of less than 3 and observational studies where variation in skew and relatedness/group productivity/outside options were suggested but not measured. Overall, the screening phase retained 56 studies. From these, we identified 113 observational and experimental tests of the link between skew and another of our parameters of interest (Table 2.A1 and A2). See Figure 2.A2 for a schematic of our methodology.

To investigate potential drivers of reproductive strategies, we extracted data on reproductive skew, relatedness, subordinate outside option/quality, dominant's competitive advantage, group productivity and quality-productivity coefficient (Table 1). The reproductive skew is dominant's proportion of offspring in the group (i.e. complete skew is reproductive monopolisation). Relatedness is the genetic kinship between same-sex breeders (i.e. who could potentially compete over reproduction) measured via genotyping. Subordinate outside option (i.e. quality) is the payoff they would get if they leave the group to breed on their own. Dominant's competitive advantage is the relative abilities of the dominant to monopolise reproduction, and is measured through an array of traits: body size, relative body size, weight, canine length, female:male sex ratio or low female synchrony (i.e. dominant males are less able to prevent subordinate male reproduction). Group fecundity is the number of young, eggs, fledglings produced by the group (i.e. not necessarily dominant's offspring). To operationalise the quality-productivity coefficient *a*, we assumed that sneaker males, who do not help the group, have low *a*, whereas satellite males who help have high *a* (only 1 study). When the data was not explicitly provided in a table or the text, we extracted it from the plots with WebPlotDigitizer after validating for 30% of the data that this software gave similar results as the manual extraction (https://automeris.io/WebPlotDigitizer/). In total we identified 113 links of interest from 56 papers. We conducted a meta-analysis of the association between skew and relatedness, and argue meta-analyses of *b&y*, *k&y, x&y* and *a&y* would help advance the field.

Meta-analysis of r&y: effect size calculation

We follow Harding et al (2019) to compute this effect size. To quantify the link between relatedness and reproductive skew, we calculated standardized effect sizes (*Hedges' g*) using the compute.es package in R (R Core Team, 2016; www.R-project.org), correcting for small sample size bias. Effect sizes were calculated using a within-subjects design if either a correlation test between skew and relatedness, a t-test comparing the means, or the raw means (± standard error or SD and sample size) of the reproductive skew under high and low relatedness. Effect sizes were calculated for 16 studies, comprising 11 insects and 6 vertebrates.

Count comparisons

To test the new predictions of the tug-of-war (TOW), concession and restraint models, we focused on the links *r&y, x&y, b&y, k&y* and *a&y* within a species (Table 2.A2). To test the effect of sex and taxa, we considered each study which found evidence for both males and females as two data points and removed reviews (between-species comparisons).

ANNEXE 2.C: Predictions of the new models for Chapter 2

Concession

Relatedness *r* (derived over *x*)

Numerator of slope $= \frac{-k^2(x-k+1)}{k}$

$$\Leftrightarrow -k(x-k+1) > 0$$
$$\Leftrightarrow -kx+k^2+k > 0$$
$$\Leftrightarrow -kx > -k^2-k$$
$$\Leftrightarrow x < k-1$$

Substituting *k* by its components gives

$$x < 1+m+ax-1$$
$$\Leftrightarrow -ax+x < m \Leftrightarrow x(1-a) < m$$
$$\Leftrightarrow x < \frac{m}{1-a} \Leftrightarrow x > \frac{-m}{a-1}$$

The concession model predicts skew correlates positively with relatedness when QPC is a>-1, which is expected to be the case unless individuals have strong differentiation into helper or breeder strategies.

Outside option *x* (derived over *r)*

Numerator of slope $= \frac{-((r-1)(k)^2)}{k}$

$$\Leftrightarrow \frac{(r-1)k^2}{-k} > 0$$
$$\Leftrightarrow -(r-1)k > 0$$
$$\Leftrightarrow -rk+k > 0$$
$$\Leftrightarrow k > rk$$
$$\Leftrightarrow r < 1$$

Consequently, the concession model predicts *x* and skew should always correlate positively.

Group bonus *m* (over *r*) (synergy effect)

Numerator of slope = $\frac{r+x}{r-1}$

$$\Leftrightarrow \frac{r}{r-1}+\frac{x}{r-1}>0$$
$$\Leftrightarrow \frac{r}{r-1}>\frac{-x}{r-1}$$
$$\Leftrightarrow r>-x$$

Thus, skew significantly correlates with *m* when *x*>0.

Quality-productivity coefficient (over *r*)

Numerator of the slope = $2x(r+x)(r-1)$

$$\Leftrightarrow (2xr+2x^2)(r-1)$$
$$\Leftrightarrow 2xr^2+2x^2r-2xr-2x^2>0$$
$$\Leftrightarrow x^2<xr^2+x^2r-xr$$
$$\Leftrightarrow x<r^2+xr-r$$
$$\Leftrightarrow x-xr<r^2-r$$
$$\Leftrightarrow x(1-r)<(r-1)r$$
$$x<r$$
$$r>x$$

The critical value is *r* = *x*, which predicts that closely related, low quality subordinates show a positive association between reproductive share and QPC.

Restraint model

The optimal maximal reproductive share of the subordinate is $\frac{(rx-k+1)}{k(r-1)}$

Relatedness *r* (over *x*)

Numerator of slope = $\frac{-k^2(x-k+1)}{k}$

$$\Leftrightarrow -k(x-k+1)>0$$
$$\Leftrightarrow -kx+k^2+k>0$$
$$\Leftrightarrow -kx>-k^2-k$$
$$\Leftrightarrow x<k-1$$

Substituting *k* by its components gives

$$x<1+m+ax-1 \Leftrightarrow -ax+x<m$$
$$\Leftrightarrow x(1-a)<m$$
$$\Leftrightarrow x<\frac{m}{1-a} \Leftrightarrow x>\frac{-m}{a-1}$$

Therefore, the critical value is either *r*=0 or *r*=1. Consequently, the reproductive share increases with *x* between those two values i.e. for all biologically realistic values.

Outside option *x* (over *r*)

Numerator of slope = $\frac{r(r-1)(m+ax+1)^2}{k}=\frac{r(r-1)k^2}{k}$

$$\Leftrightarrow r(r-1)k>0$$
$$\Leftrightarrow kr^2-rk>0 \Leftrightarrow r^2k>rk$$
$$r=0$$
$$r=1$$

The critical values for outside option are $r>0$ and $r<1$, so that skew always correlate significantly (negatively) with subordinate outside options (Figure 2.A3).

Group benefit *m*

Numerator of slope = $-(rx+1)(r-1)$

$$\Leftrightarrow -r^2x+rx-r+1>0$$
$$\Leftrightarrow -r^2x+rx-r>-1$$
$$\Leftrightarrow -r^2x>-1-rx+r$$
$$\Leftrightarrow -rx>1-x-\frac{1}{r}$$

Simplifying, the critical value of *r* for *m* should be $\frac{-1}{x}$.

Quality-productivity coefficient *a* (over *r*)

Numerator of slope=
$$\begin{aligned}&-2x\left(rx+1\right)(r-1)\\&\Leftrightarrow -2x^2r-2x-2xr+2x>0\\&\Leftrightarrow -2xr>2x^2r>0\\&\Leftrightarrow r>-xr\end{aligned}$$

Since $0<r\leq 1,\ -x>1\Leftrightarrow x<-1$

Therefore the critical value of *r* is $-\frac{1}{x}$.

Table 2.A6: Factors included in the model, their symbol and baseline value. Based on Johnstone (2000)

Description	Symbol	Baseline value
Group productivity	*k*	1.8
Group benefit (synergy effect)	*m*	0.3
Quality-productivity coefficient	*a*	1
Outside option	*x*	0.5
Relatedness	*r*	0.5
Subordinate strength	*b*	0.5

Assume $k=1+m+ax$ throughout

Table 2.A7: Effects (slopes) of each parameter on the subordinate share of reproduction under the 3 models with subordinate quality effects. Condition for each parameter to be positive.

Parameter	**Concession**	**Restraint**	**Tug-of-war**
Inequality	$k(p+r(1-p)) > x+r$	$k(rp+(1-p)) > 1+xr$	-
Subordinate share	$p_{\min} = \frac{x-r(m+ax)}{(1+m+ax)(1-r)}$.	$p_{\max} = \frac{k-rx-1}{k(1-r)}$	$p_{tow} = \frac{c_s x}{c_d + c_s x}$
Relatedness	$\frac{dp_{\min}}{dr} = \frac{(1-k)k(1-r)+k(r-kr+x)}{(1+m+ax)^2(1-r)^2}$ Since the denominator is positive, concession increases as group productivity increases if $x > r$ Subordinate share decreases as relatedness increases if $\frac{-m}{a-1} < x < \frac{-m-1}{2a}$	$\frac{dp_{\max}}{dr} = \frac{(1-k)k(1-r)+k(r-kr+x)}{(1+m+ax)^2(1-r)^2}$ Since the denominator is positive, subordinate share increases as relatedness increases if $x < k-1 \Leftrightarrow x > \frac{-m}{2a-1}$ $\frac{-m}{2a-1} < x < \frac{-m-1}{2a}$	Always negative
x	$\frac{dp_{\min}}{dx} = \frac{-r+x}{(1+m+ax)^2(1-r)}$ Subordinate share decreases as subordinate quality increases if $1 < r < \frac{m+1}{2a}$	$\frac{dp_{\max}}{dx} = \frac{r-2a+mr}{(r-1)(m+2ax+1)^2}$ Subordinate share decreases as subordinate quality increases if $\frac{2a}{m+1} < r < 1$	Always positive

m	$\frac{dp_{\min}}{dm}=\frac{1}{k(1-r)}$, which is always positive, so subordinate share increases as the synergy effect increases if $-x<r<1$ For all reasonable values of r and above -*x*, the effect of *m* on subordinate share is negative.	$\frac{dp_{\max}}{dm}=\frac{-(rx+1)}{(r-1)(m+2ax+1)^2}$ Subordinate share decreases as the synergy effect *m* increases if $\frac{-1}{x}<r<1$ Since *x*≥0, for all reasonable values of *r* subordinate share decreases with synergy effect.	No effect (Synergy effect does not influence skew)
a	$\frac{dp_{\min}}{da}=\frac{-r+x}{(1+m+ax)^2(1-r)}$ Since by definition *r* ≤ 1 the denominator cannot be negative, the effect of relatedness on concession is positive if $m+ax<x$ i.e. if the group is less productive than the separate individuals, which implies it will be negative in most cases where group living evolves. For all reasonable values of *r* and above -*x*, the effect of *a* on subordinate share is negative: $-x<r<1$	$\frac{dp_{\max}}{da}=\frac{-(2x(rx+1)}{(r-1)(m+2ax+1)^2}$ Subordinate share decreases as the quality-productivity coefficient increases if $\frac{-1}{x}<r<1$ Lower concession with higher *x*.	No effect: Quality-productivity coefficient does not influence subordinate share.

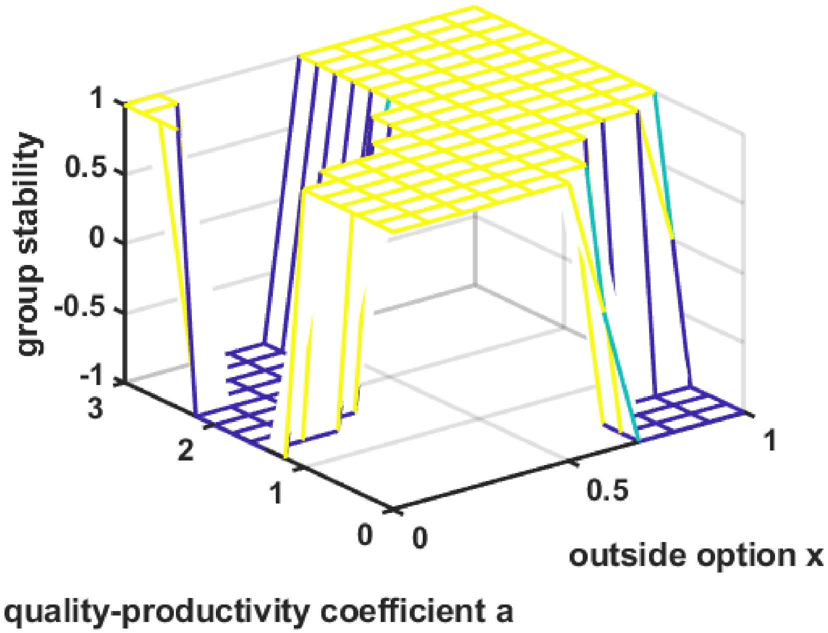

Figure 2.A2: Group stability as a function of outside option *x* and quality-productivity coefficient *a.* Calculated by subtracting the minimal reproductive share (restraint model) to the maximal reproductive share (concession model) in Johnstone (2000)

Groups are stable in most of the parameter space, entailing that most combinations of outside options and quality-productivity coefficient favour group formation (Figure 2.A2). Individuals should breed solitarily when the outside option is high, but the quality-productivity coefficient low, or the quality-productivity coefficient is high but the outside options low (vice-versa).

ANNEXE 3.A: Analyses of the effect of information about subordinate quality for Chapter 3

1. General description

a. Extensions of the concession model of skew

The dominants' level of information about subordinate's outside option payoff may select for various levels of skew and group formation, which may make more realistic predictions and help to explain the between-species variation in skew. To assess the effect of uncertainty about subordinate quality, we built a numerical and an analytical model. An analytical model solves the optimal concession and the conditions where individuals should form groups, by finding mathematically closed form solutions (see Table 3.A1 for variables). We numerically investigated the effect of dominants' intermediate levels of information about subordinate's quality by systematically varying the quantity of information and other key parameters. Implementing a numerical and an analytical model of the effect of information also make cross-validation (of the predictions) possible.

We based our approach on the concession model (Johnstone, 2000; Verhencamp, 1983) in which the dominant must concede sufficient share of the reproduction to get the subordinate to stay, and has perfect information about the subordinate's outside option x¸ which we assume to be determined by their individual quality (Appendix 3.A algebraic model). In this model, the dominant offers a share of the reproduction to a subordinate (i.e. helper) to incentivise it to stay and help. In this concessional model, the dominant is assumed to be in complete control of the reproductive share, but the subordinate may choose to leave in response. Subordinates vary in the direct fitness payoff associated with their outside options x (hereafter *quality*), which affects how much direct fitness they require to stay in the group (Table 3.A1). Dominants have access to either perfect information, no information or imperfect information about subordinates' direct fitness payoff associated with their outside options x.

Table 3.A1: Description of the variables in the analytical model and their baseline values.

Symbol	Definition	Values
x	Quality of the subordinate (i.e. direct fitness if breeding independently) $0>x>b$	
y	Reproductive share offered to subordinate by dominant (i.e. proportion of group fecundity)	
b	Direct fitness of a solitary dominant breeder	1
a	Quality-productivity coefficient (QPC): effect of subordinate's quality group fecundity	1
r	Symmetric relatedness between the dominant and the subordinate	0.5
h	Effect of helping on group reproductive output, $h= kx + m$	x+0.1
m	Minimal effect of helping on group reproductive output (i.e. synergy effect, intercept)	0.1
x_i	Quality of this individual subordinate	
x^*_0	Critical subordinate quality if dominant adopts strategy y=0	
x^*_y	Critical subordinate quality if dominant adopts strategy y^*	
x_{crit}	Critical quality x at which subordinate's options have equal fitness consequences for the dominant (i.e. below/above which subordinate will leave the group, as a function of y)	
y_{crit}	Critical share above which subordinate will help	
y^*	Optimal reproductive share	
Ω	Dominant's sampling about subordinate's quality: information uncertainty $0> \Omega>+\infty$	
d	Reproductive value of the dominant (i.e. inclusive fitness per breeding season)	
d_A	Dominant's inclusive fitness when alone (i.e. solitary breeding)	

d_C	Dominant’s inclusive fitness with a subordinate (i.e. cooperative breeding)
$d_{D,i}$	Dominant’s inclusive fitness when cooperatively breeding with reproductive share y_i
d_p	Dominant’s inclusive fitness when they have perfect information about x
s	Subordinate inclusive fitness (i.e. its reproductive value)
s_A	Subordinate’s inclusive fitness when alone (i.e. solitary breeding)
$s_{D,i}$	Subordinate’s inclusive fitness when cooperatively breeding with reproductive share y_i
θ	Beta-weighted distribution of what dominant infers from its observation Ω about x

b. Model specifications

We are interested in the case where *x* varies among subordinates and the dominant payoff is the expected value over the range of possible subordinates. Here, we assume that subordinate quality *x* follows a uniform distribution, and compare the fitness and reproductive strategies with perfect and with no information about subordinate quality, for which we can get analytical results.

The direct fitness required by the subordinate to help depends on its outside options *x* (Table 3.1, 3.3, 3.A1). We assume that the dominant's quality is *b*. So the value of the dominant and subordinate that are symmetrically related with proportion *r* if they don't stay together are respectively

$$d_A = b + rx\,, \tag{3.A1}$$

$$s_A = rb + x\,, \tag{3.A2}$$

Since *b* scales the group productivity and dominant quality, without loss of generality we assume the maximum value of *x* is unity. Because *x* is uniformly distributed between 0 and 1, the expected dominant fitness for all *x* is

$$D_A = b + \frac{r}{2} \tag{3.A3}$$

We denote the direct fitness when cooperatively breeding of the dominant and subordinate by d_D and s_D, respectively. The cooperatively breeding group is assumed to have greater success than the sum of the solitary values even when *x*=0 by a value *m* so that

$$d_D + s_D = b(1 + m + ax) \tag{3.A4}$$

where *a* controls the association between the subordinate's outside option and their contribution to group productivity. Hence, with a subordinate *i* with quality *x*, the fecundity of a dominant who gives reproductive share y_i is

$$d_{D,i} = b(1 + m + ax)(1 - y_i) \tag{3.A5}$$

and the subordinate is

$$s_{D,i} = b(1 + m + ax)y_i \tag{3.A6}$$

Therefore, the dominant's inclusive fitness when cooperatively breeding, and when they are related to the subordinate by *r* is

$$d_C = d_{D,i} + rs_C = (1-y_i)b(1+m+ax_i) + ry_i b(1+m+ax_i) \qquad (3.A7)$$

$$= [(1-y_i)+ry_i]b(1+m+ax)$$

$$= [1+(r-1)y_i]b(1+m+ax)$$

Clearly, for $r<1$ the dominant fitness decreases as y_i increases, so they should give the smallest share possible to the subordinate to get them to stay, $s_C>s_A$, provided that $d_C>d_A$.

The critical value of *x* at which the subordinate would stay depends on the concession given to all subordinates *y* and is the solution for *x* (3.A8). We determine if the subordinate will stay for each *x* and each *y*, from their inclusive fitness if they breed cooperatively (left-hand-side) or breed alone (right-hand-side):

$$b(1+1+m+ax)[y+r(1-y)] > x+br \qquad (3.A8)$$

2. Perfect information about subordinate quality
    a. Analytical solution

The critical concession share required to get the subordinate to stay can be found by setting the subordinate's within group inclusive fitness equal to the inclusive fitness if breeding alone,

$$s_C = s_A \Leftrightarrow b(1+m+ax)(y+r[1-y]) = br+x\,, \qquad (3.A9)$$

Solving for *y* gives

$$y_P{*} = \frac{x-br(m+ax)}{b(1-r)(m+ax+1)} \qquad (3.A10)$$

Note that if b=1 and a=0 then the group productivity does not depend on the subordinate's quality and 3.A10 reduces to the original concession model (Reeve and

Ratnieks, 1993), though note that they assume group productivity is *k* and we assume *k=m+1* here.

$$y_P*(a=0,b=1)=\frac{x-rm}{(1-r)(m+1)} \tag{3.A11}$$

The concession (proportion of reproduction) cannot be negative, and the value of *x* at which *y** is zero or less is

$$x_{y_P*=0}=\frac{bmr}{1-bar}, \tag{3.A12}$$

so any subordinates with lower quality get a greater fitness than they would alone.

For some *a* and *m* at very high *x* the necessary concession is so great that the dominant would be better off alone, so should offer nothing. The dominant would have higher fitness if alone if subordinate quality is above

$$x_{D_P*=D_A}=\frac{bm}{1-ba} \tag{3.A13}$$

Otherwise, the concession will increase with *x*. This results in either a negative or positive change in dominant fitness as *x* increases (Figure 3.1e-h, 3.7e-h). This suggests that given a choice between potential subordinates, in some cases dominants would prefer weaker subordinates. The dominant’s fitness between these limits is

$$d_P=b(1+m+ax)\left[ry*+1-y*\right] \tag{3.A14}$$

i.e.

$$d_P=b(1+m+ax)\left[\frac{x-br(m+ax)}{b(1-r)(1+m+ax)}(r-1)+1\right] \tag{3.A15}$$

which simplifies to

$$d_P=b(1+r)(m+ax)+b-x \tag{3.A16}$$

By solving $\frac{dd_P}{dx}>0$, we find that dominant fitness increases with *x* if

$$a > \frac{1}{b(1+r)} \tag{3.A17}$$

That is, increasing the quality-productivity coefficient (*a*), the dominant quality (*b*) and the relatedness (*r*) all increase the chance that dominants prefer high quality subordinates. For the values of *b* and *r* used in Figure 3A.1 this is 2/3 (cf. solid lines in Figure 3.A1g,h where slope changes from negative to positive).

For m<0 it would be better for the dominant to be alone than paired with a very weak subordinate (x=0), but if *a* is sufficiently large they would pair with higher quality subordinates (Figure 3.A1j). Hence, for m<0 the concession may decrease with *x* (Figure 3.A1j), when

$$a > \frac{m+1}{br} \tag{3.A18}$$

The expected inclusive fitness of dominants when subordinate quality is uniformly distributed between 0 and 1 is

$$\overline{v_P} = \int_{0}^{x_{y_P*=0}} v_P(x,0)\,dx + \int_{x_{y_P*=0}}^{x_{D_P*=D_A}} v_P(x, y_P*(x))\,dx + \int_{x_{D_P*=D_A}}^{1} v_A\,dx \tag{3.A19}$$

where the first term is when the concession is zero, the second term is where the concession is the critical concession necessary and the third term is where the dominant gets higher fitness when alone. This is

$$\overline{v_P} = r + 2b + \frac{m^2}{2a^2}\left[\frac{1}{bar-1} - r - ab - \frac{r+1}{ba-1}\right] \tag{3.A20}$$

$$\overline{v_P} = r + 2b - \frac{a^3 m^2 (ab^3 + rb^2 - arb + r)}{2b(ab-1)}$$

b. Numerical solution

Effect of perfect information on group formation for each quality

We investigate the effect of perfect information about subordinate quality on inclusive fitness and group formation, as a function of subordinate quality and the quality-productivity coefficient.

The dominants' and subordinates' inclusive fitness as a function of x when y=y^* and dominants have perfect information are respectively

$$d_P = (r+1)b(1+m+ax) - br - x \qquad (3.A26)$$

from equation (3.A12), and

$$s_P = b(1+m+ax)\left[y^* + r(1-y^*)\right] \qquad (3.A27)$$

i.e.

$$s_P = b(1+m+ax)\left[\frac{br + x - br(m+ax+1)}{b(1-r)(m+ax+1)}(1-r) + r\right] \qquad (3.A28)$$

which simplifies to

$$s_P = br + x = s_A \qquad (3.A29)$$

due to the optimisation by the dominant $d_P \geq d_N$ for all x. The group is stable under perfect information only if $d_P > d_A$ and under no information only if $s_N > s_A$ (Figure 3.A1e-l). If $d_P < d_A$ then the dominant does not allow the subordinate to stay in the group. If $s_P < s_A$ (when $y_N^* < y_P^*$) then the subordinate does not stay in the group.

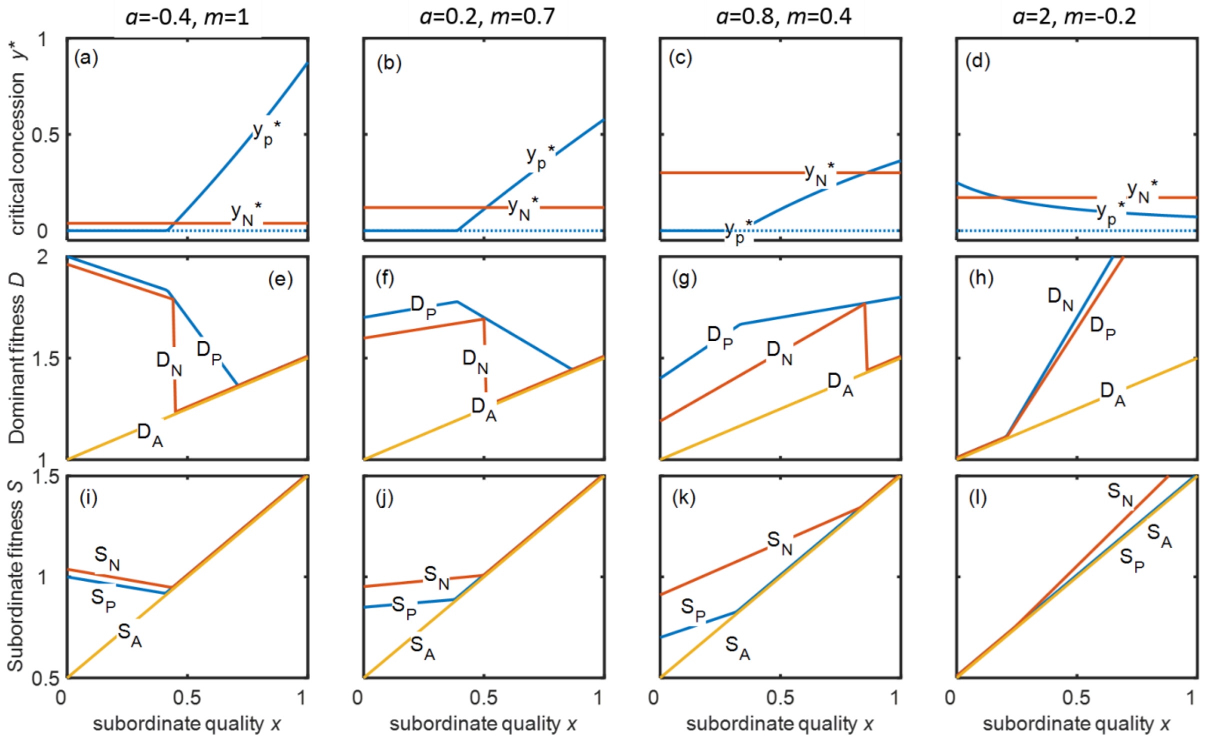

Figure 3.A1 Concession (top row), dominant inclusive fitness (middle row), and subordinate inclusive fitness (bottom row) as a function of *x,* for some representative values of *a* and *m* under perfect information P, no information N, and when alone A. The dotted lines indicate *y*=0. The dominant fitness depends on whether the dominant is better with the subordinate than alone ($d_P > d_A$) and whether the subordinate chooses to stay ($s_N > s_A$). The dominant always does at least as well as no information when they have perfect information, whereas the opposite is true of the subordinate.

The total value of information when group productivity does not depend on subordinate quality.

The equations become much simpler if the group productivity does not depend on the subordinate quality (*a*=0). Here, we show how the value of information is affected by individual quality and group productivity, and relatedness

The optimal concession simplifies to

$$y_P* = \frac{x - brm}{b(1-r)(m+1)}, \qquad (3.A30)$$

and the *x* at which concession is zero is

$$x_{y_P*=0} = bmr \tag{3.A31}$$

The payoff to dominants simplifies to

$$d_C = b[(1+r)m+1]-x \tag{3.A32}$$

And the *x* at which the dominant is better off alone is

$$x_{D_P*=D_A} = bm \tag{3.A33}$$

The expected fitness of the dominant is

$$\overline{v_P} = \int_0^{x_{y_P*=0}} d_P(x,0)\ dx + \int_{x_{y_P*=0}}^{x_{D_P*=D_A}} d_P(x,y_P*(x))\ dx + \int_{x_{D_P*=D_A}}^{1} d_A\ dx \tag{3.A34}$$

$$\overline{v_P} = \int_0^{bmr} m+1\ dx + \int_{bmr}^{bm} (1+r)m+1-x\ dx + \int_{bm}^{1} 1+rx\ dx$$

$$\overline{v_P} = \left[mx+x\right]_0^{bmr} + \left[mx+rmx+x-x^2\right]_{bmr}^{bm} + \left[x+rx^2\right]_{bm}^{1}$$

$$\overline{v_P} = b+\frac{r}{2}+\frac{b^2m^2}{2}\left[1+r-r^2\right] \tag{3.A35}$$

3. No information about subordinate quality
    a. Analytical solution

We compare the situation above (i.e. perfect information) to one where dominants have no information about the quality of their potential subordinate. The subordinate quality is known to be uniformly distributed between 0 and 1. The dominant receives help for subordinates with quality $0<x<x_c$ and breeds alone for those with $x_c>x>b$. To solve the optimal reproductive share which maximizes the payoff of the dominant, we integrated it with respect to *x* and then differentiated the integral over the different parts of the reproductive output function of the subordinate (i.e. above and below the threshold of reproductive share), as follows.

The critical value of *x* at which the subordinate would stay depends on the concession given to all subordinates *y* and is the solution for *x* to

$$b(1+h)(y+r[1-y]) = x+br \qquad (3.A21)$$

which is

$$x_c(y) = \frac{b(m+1)(y+r[1-y])-br}{1-ab(y+r[1-y])} \qquad (3.A22)$$

We seek the extreme point of the derivative of the fecundity of the dominant with respect to *y* and to *x*, in order to find the maximal and minimal points of the reproductive share function: what is the subordinate quality $x_{\min}$ to get the minimal reproductive share $y_{\min}$; likewise what is $x_{\max}$ where dominant gives maximal $y_{\max}$.

Thus the general inclusive fitness of uninformed dominants can be integrated as

$$\overline{v_N} = \int_0^{x_c(y)} D_P(x,y)\;dx + \int_{x_c(y)}^{1} D_A(x)\;dx \qquad (3.A23)$$

If the dominant should prefer higher quality subordinates (i.e. $a > \frac{m+1}{br}$), then this should be reversed.

$$\overline{v_N} = \int_0^{x^*(y)} v_A(x)\;dx + \int_{x^*(y)}^{1} v_P(x,y)\;dx \qquad (3.A24)$$

$$\overline{v_N} = \int_0^{x^*(y)} b(1+m+ax)\left[ry+1-y\right]\;dx + \int_{x^*(y)}^{1} b+rx\;dx$$

$$\overline{v_N} = \left[\frac{bx(2+2m+ax)\left[ry+1-y\right]}{2}\right]_0^{x^*(y)} + \left[\frac{2bx+rx^2}{2}\right]_{x^*(y)}^{1}$$

$$\overline{v_N} = \frac{bx^*(2+2m+ax^*)\left[ry+1-y\right]}{2} + \frac{2b+r}{2} - \frac{2bx^*+r(x^*)^2}{2}$$

$$\overline{v_N} = \frac{bx^*(2+2m+ax^*)\left[ry+1-y\right]}{2} + \frac{2b+r}{2} - \frac{2bx^*+r(x^*)^2}{2} \qquad (3.A25)$$

By solving $\frac{d\overline{v_N}}{dy}=0$ we find the optimal *y* under no information is y_N*, but this is too complex to display. We explore this numerically in the main text and in Figure 3.1a-d, 3.2 and 3.A2.

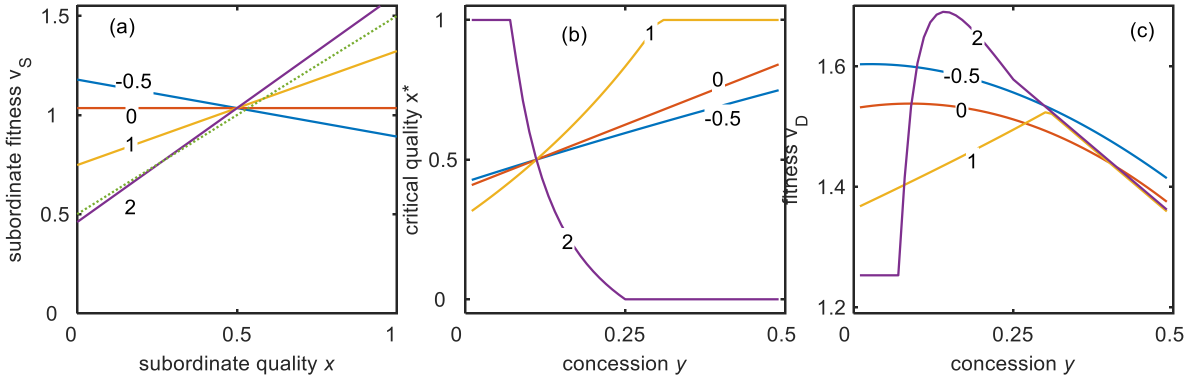

Figure 3.A2: Fitness and critical quality under no information about subordinate quality *x* for representative values of *k* and *m* (*k* shown on lines; *m*=0.8 – *a*/2), as a function of (a) subordinate quality *x* and (b, c) concession *y*. (a) Subordinate fitness if *y*=0.2, (b) Critical quality as a function of concession *y*, (c) Total dominant fitness for all *x* as a function of concession

b. Numerical solution

We can make the same simplifications for the no information case

$$x^*(y)=b(m+1)(y+r[1-y])-br$$

(3.A36)

$$\overline{v_N}=\frac{x^*b(2+2m)\left[ry+1-y\right]}{2}+\frac{2b+r}{2}-\frac{2bx^*+r(x^*)^2}{2} \qquad (3.A37)$$

$$\overline{v_N}=\frac{1}{2}\left[x^*(2+2m)\left[ry+1-y\right]+2+r-2x^*-r(x^*)^2\right] \qquad (3.A38)$$

We then differentiate the payoff of the dominant over the reproductive share *y*. We determine the extreme maximum point of this derivative (i.e. maximal fecundity; where the derivative is equal to 0) to find the optimal strategy *y**:

$$y_N{*} = \frac{m(r^2+r-1)}{r-2m+mr+mr^2+r^2-2} \qquad (3.A34)$$

Thus, after substituting *y** and simplifying, for the optimal reproductive share *y** the optimal fitness of dominant *V** is

$$\overline{v_N}{*} = b+\frac{1}{2}\left[\frac{b^2m^2}{r+2}+r(b^2m^2+1)\right] \qquad (3.A35)$$

We can now compare the fitness of the dominant under perfect and no information. The value of knowing quality is

$$\overline{v_P}{*}-\overline{v_N}{*} = b+\frac{r}{2}+\frac{b^2m^2}{2}\left[1+r-r^2\right]-b-\frac{1}{2}\left[\frac{b^2m^2}{r+2}+r(b^2m^2+1)\right]$$

$$\overline{v_P}{*}-\overline{v_N}{*} = \frac{1}{2}\left[r+b^2m^2\left[1+r-r^2\right]-\frac{b^2m^2}{r+2}-r(b^2m^2+1)\right]$$

$$\overline{v_P}{*}-\overline{v_N}{*} = \frac{b^2m^2}{2}\left[1-r^2-\frac{1}{r+2}\right] \qquad (3.A36)$$

which is positive unless *r*>0.8. The value of information always increases as *b* and *m* increase, and by differentiating with respect to *r* we find that the value decreases as *r* increases if *r* > 0.112.

The subordinates' payoff under perfect information is

$$s_P = b(1+m)(y{*}+r[1-y{*}]) \qquad (3.A37)$$

$$s_P = b(1+m)\left(\frac{x-brm}{b(1-r)(m+1)}(1-r)+r\right) \qquad (3.A38)$$

$$s_P = x+br\,; \qquad (3.A39)$$

i.e. the solitary payoff since the dominant matches it and if $bmr < x < bm$. Since the higher quality dominants also get this (solitary breeding) we do not need to calculate it.

For low quality individuals for which *y**=0, *x*<*bmr*, the payoff is

$$s_P = b(1+m)(0+r[1-0])$$

$$s_P = b(1+m)r \tag{3.A40}$$

The subordinate payoff under no information if they stay does not depend on *x*

$$s_N = b(1+m)\left(\frac{m(r^2+r-1)}{r-2m+mr+mr^2+r^2-2}(1-r)+r\right)$$

$$s_N = b(m+r)-\frac{bm}{r+2} \tag{3.A41}$$

To high *x* the benefit of the dominant having perfect information is

$$s_P*-s_N* = x+br-b(m+r)+\frac{bm}{r+2} \tag{3.A42}$$

$$w_P*-w_N* = x-bm\left(1-\frac{1}{r+2}\right)$$

Which is positive if

$$x > bm\left(1-\frac{1}{r+2}\right) \tag{3.A43}$$

The critical value of *x* below which the subordinate stays is

$$x*(y*) = b(m+1)(y*+r[1-y*])-br$$

$$x*(y*) = \frac{bm(r+1)}{r+2} \tag{3.A44}$$

The benefit of information occurs for a region where the subordinate would stay if

$$bm\left(1-\frac{1}{r+2}\right) < \frac{bm(r+1)}{r+2} \tag{3.A45}$$

$$bm-\frac{bm}{r+2} < \frac{bm(r+1)}{r+2}$$

$$1-\frac{1}{r+2}<\frac{r+1}{r+2}$$

$$r+2-1<r+1$$

$$1<1$$

i.e. never.

Low quality individuals (*x*<*bmr*) benefit from no information if

$$s_P*<s_N*=b(1+m)r-b(m+r)+\frac{bm}{r+2} \quad (3.A46)$$

$$s_P*<s_N*=r(r+1)<1,$$

Which is when *r*<0.618.

In summary, high quality individuals do not benefit from the dominant having information about their quality, whereas low quality individuals benefit from the dominant not knowing their quality.

4. Effect of imperfect information about subordinate quality
    a. Numerical model

The aim is to calculate dominant and subordinate inclusive fitness and optimal reproductive share as a function of information and subordinate quality *x.* The dominant has a prior belief about the probability distribution of the outside options of a potential subordinate *x*. It chooses a sampling strategy Ω to acquire more information about *x*. With this information, it updates its subjective knowledge about *x*: its prior belief becomes a posterior belief. This way of updating information is Bayesian learning (Trimmer et al., 2011). The model systematically tests how the quantity of information about *x* influences the inclusive fitness and the optimal reproductive decision of the dominant by simulating 12 sampling strategies (0 ≤ Ω ≤+∞). We systematically explore group formation for different values of relatedness *r*, QPC *a* and synergy effect *m* (Figures 3.10, 3.11).

Bayesian learning occurs when the dominant has imperfect information: the dominant only infers the quality of the subordinate it meets by observing a number Ω of times (McNamara, Green, & Olsson, 2006). Dominants who perform the maximal sampling Ω are assumed to have perfect information (i.e. know *x* without error). In this sequential model, the dominant uses a sampling strategy Ω and forms a belief about the probability distribution of *x* before deciding which proportion of the total group reproduction *y* to offer to a potential helper. This probability distribution (3.A48) is weighted by what the dominant knows with the parameters α and β.

$$\alpha = 1 + x_{val} + \Omega$$
$$\beta = 1 + (1 - x_{val})\Omega$$

(3.A47)

These alpha and beta parameters control the shape of the probability beta-weighted distribution function of the belief of the dominant about the quality of the subordinate. Subordinate's quality *x* is a probability of successful helping per attempt, where the subordinate can either help or leave. Since each subordinate-dominant interaction only has one outcome, all subordinates' outside options are independent of each other and each interaction has the same probability of success, *x,* which is a binomial distribution.

We calculate the beta-weighted distribution *θ(x)* of the probability that the dominant perceives each subordinate quality *x* given the real quality *x*

$$\theta(x) = x^{\alpha-1}(1-x)^{\beta-1} = P(perceived \mid actual) \qquad (3.A48)$$

The probability of the perceived subordinate quality, as a function of the quantity of information sampling and the parameters α and β, is

$$P(\Omega \mid \alpha, \beta) = \frac{1}{\theta(\alpha, \beta)} \Omega^{\alpha-1}(1-\Omega)^{\beta-1} I_{[0,1]}(p) \qquad (3.A49)$$

To normalise the weighted beta distribution, we divide each beta-weighted distribution by the sum of the beta-weighted distribution so it sums to unity. As sampling Ω gets very large the distribution gets increasingly narrow; i.e. perfect information.

Given the probability of each perceived *x*, we can calculate the probability of each actual *x* given the perception

$$P(actual \mid perceived) = P(perceived \mid actual)\frac{P(actual)}{P(perceived)} \qquad (3.A50)$$

We store the perceived and actual inclusive fitness, since dominants with limited information cannot know exactly what payoff they will get.

We create a weighted payoff to the dominant for each share *y*, because the probability to meet a subordinate of a given quality is a function of the position of the quality on the distribution function. Dominants base their decision on all subordinates weighted by the probability on the probability of each actual given their perceived distribution *θ* (perceived fitness), although their actual payoff is from this particular subordinate. We calculate dominants' perceived inclusive fitness for each *x* and *y*, as a function of the expected decision of the subordinate, as was done in the No Information case.

We calculate actual inclusive fitness by determining if subordinates of the possible qualities stay with $y^*_{Imperfect}$ or leave weighted by their probabilities. Note that if the payoff from solitary breeding is higher than that of breeding cooperatively, then the dominant gets the same payoff if it has perfect information as if it makes errors, which suggests that information about a potential subordinate is not valuable when the dominant prefers solitary breeding.

b. Predictions for imperfect information about subordinate quality

When group productivity strongly depends on subordinate quality and weak subordinates reduce productivity (Figure 3.A1), dominants avoid accepting low-quality subordinates. They therefore have a threshold of perceived quality below which they would evict the subordinate. For less than perfect information (Figure 3.A1a,b,c) the threshold of maximal quality for which subordinate will stay, and the threshold of quality below which dominant will evict them, divide the (*x,z*) space into quadrants where both, neither or one of the individuals want to form a group. With more information *y** decreases as *z* increases (above a minimum) which results in an increasing subordinate's threshold: when $z<x$ subordinates do not join the group as the concession is insufficient.

When subordinate quality negatively affects group productivity – perhaps by increasing conflict or if strong subordinates require more food but don't work harder – then dominants should evict strong subordinates. For no or some information the subordinate's and dominant's thresholds divide the (*x,z*) space into quadrants where both, neither or one of the individuals want to form a group (Figure 3.A1). For high information there is a band in the *z* dimension where the dominant does not want the subordinate to join, but has a high concession so that lower-quality subordinates will try to join.

ANNEXE 3.B: Numerical model investigating unknown relatedness for Chapter 3

We systematically explored how dominants' uncertainty about their relatedness to the subordinate influences the optimal concession (Figure 3.B1, Table 3.B1). This numerical model is based on the concession model of skew.

Table 3.B1 Description of the variables specific to the numerical model of unknown relatedness and their baseline values. For other variables see Table 3.A1

Symbol	Definition	Values
r	Symmetric relatedness between the dominant and the subordinate	[0-1]
r^*	Critical value of relatedness	
$r_{y_{P^*=0}}$	Relatedness above which the concession is zero	
$r^*(y)$	Critical relatedness below which subordinates would not stay, for a given concession *y*	
y^*_N	Optimal concession to all possible subordinates	
y'	Change in concession given information about r	

Asocial

The expected fitness when alone for the dominant is

$$\overline{v_A} = \int_0^{r*} b + rx \, dr \tag{3.B1}$$

$$\overline{v_A} = \left[br + r^2 x \right]_0^{r*}$$

$$\overline{v_A} = br * + \frac{r *^2 x}{2}$$

Perfect information

What is the effect of information when relatedness is uncertain? Since *x* is a constant we don't need to show *x, a,* or *m*.

$$s_C > s_A \Leftrightarrow b(1+h)(y + r[1-y]) > br + x \text{ ,} \tag{3.B2}$$

The optimal concession is

$$y* = \frac{x - bhr}{b(1-r)(1+h)}$$

The optimal concession declines as *r* increases, so the relatedness above which the concession is zero is

$$r_{y_P*=0} < \frac{x}{bm} \text{ ,} \tag{3.B3}$$

The fitness of the dominant is

$$d_C = b[(1+r)m+1] - x \tag{3.B4}$$

When cooperating better than alone for the dominant

$$d_C > d_A \Leftrightarrow b[(1+r)m+1] - x > b + xr \tag{3.B5}$$

$$r* > -1$$

which is always the case. The change in the difference between cooperative and asocial fitness for the subordinate with respect to *r* is

$$\frac{d}{dr} = b(1+m)[1-y]-b \tag{3.B6}$$

which is positive provided

$$y < \frac{m}{m+1} \tag{3.B7}$$

Since $y<0.5$, the dominant won’t concede more than half the reproduction; this will always occur if $m>1$. Therefore, under most situations the more related the subordinate is, the more they are inclined to stay. This is why y^* decreases as r increases.

Dominant fitness over a range of subordinate relatedness is

$$\overline{v_P} = \int_{0}^{r_{y_P*=0}} d_P(r, y_P*(r))\ dr + \int_{r_{y_P*=0}}^{r*} d_P(r,0)\ dr \tag{3.B8}$$

$$\overline{v_P} = br*(m+1) - \frac{x^2}{2bm} \tag{3.B9}$$

No information

The critical relatedness below which they would not stay is

$$r*(y) < 1 + \frac{x-bm}{b[m-y(m+1)]} \tag{3.B10}$$

So the total dominant fitness is

$$\overline{v_N} = \int_{0}^{r*} s_A(r)\ dr + \int_{r*}^{R} s_P(r,y)\ dr \tag{3.B11}$$

$$\overline{w_N} = \left[\frac{r^2x+2br}{2}\right]_0^{r*(y)} + \left[\frac{b(m+1)[r^2y+2r(1-y)]}{2}\right]_{r*(y)}^{R} \tag{3.B12}$$

The optimal concession to all possible subordinates is

$$y_N * = \frac{1}{3} - \frac{b-2x}{3b(1+h)} \tag{3.B13}$$

The change in concession given information is

$$y' = y_N * - y_P * = \frac{x-bhr}{b(1-r)(1+h)} - \frac{1}{3} + \frac{b-2x}{3b(1+h)} \tag{3.B14}$$

$$y' = \frac{(bh-x)(2r+1)}{3b(1-r)(1+h)}$$

The value of knowing relatedness for the dominant is

$$d_P * - d_N * = bR(m+1) - \frac{x^2}{2bm} - br*(m+1) + \frac{x}{2} - \frac{bm(1+r*^2)}{2} + xr* \tag{3.B15}$$

$$d_P * - d_N * = x\left(r* + \frac{1}{2}\right) - \frac{x^2}{2bm} - \frac{bm(1+r*^2)}{2}$$

The change in subordinate fitness when dominant knows relatedness (Figure 3.6) is

$$\begin{aligned}
& b(1+h)[y' + r(1-y')] + br + x \\
&= (b+bh)[\frac{(bh-x)(2r+1)}{3b(1-r)(1+h)} + r(1 - \frac{(bh-x)(2r+1)}{3b(1-r)(1+h)})] \\
&= \frac{bm}{3} - \frac{x}{3} + br - \frac{2rx}{3} + \frac{abx}{3} + \frac{5bmr}{3} + \frac{5abrx}{3} \\
&= \frac{1}{3}(bm - x + 3br - 2rx + abx + 5bmr + 5abrx)
\end{aligned} \tag{3.B16}$$

The value of information to the subordinate is never positive the dominants, consequently subordinates should not signal their relatedness (Figure 3.6b,c). Hiding strategies might evolve. The information is most harmful to a related subordinate with very high quality and QPC=2 (Figure 3.6c).

The value of information to the dominant is maximal for low-medium subordinate quality when the quality-productivity coefficient is low, but increases with subordinate quality when QPC is high (Figure 3.6a).

Dominant information about relatedness does not change subordinate fitness when *x* is

$$x = \frac{bm + 3br + 5bmr}{2r - ab - 5abr + 1} \tag{3.B17}$$

When *b*=1, which is the baseline value in our models, this simplifies to

$$x = \frac{m + 3r + 5mr}{2r - a(5r + 1) + 1} \tag{3.B18}$$

Or when *a* is

$$a = \frac{-bm + x - 3br + 2rx - 5bmr}{bx + 5brx} \tag{3.B19}$$

When *b*=1 and *r*=0.5 as in diploid families, a simplifies to

$$a = \frac{-7m - 4x + 3}{7x} \tag{3.B20}$$

When *m*=0.1, dominant's level of information about relatedness does not change subordinate fitness if *a*~=0.0857. So subordinate quality's influence on helping effect is negligible when subordinate fitness is not influenced by information about relatedness. The change in subordinate fitness when dominant knows relatedness increases as *a* increases. The value for subordinate of signalling or not their relatedness depends on how their help translates into helping, *a*.

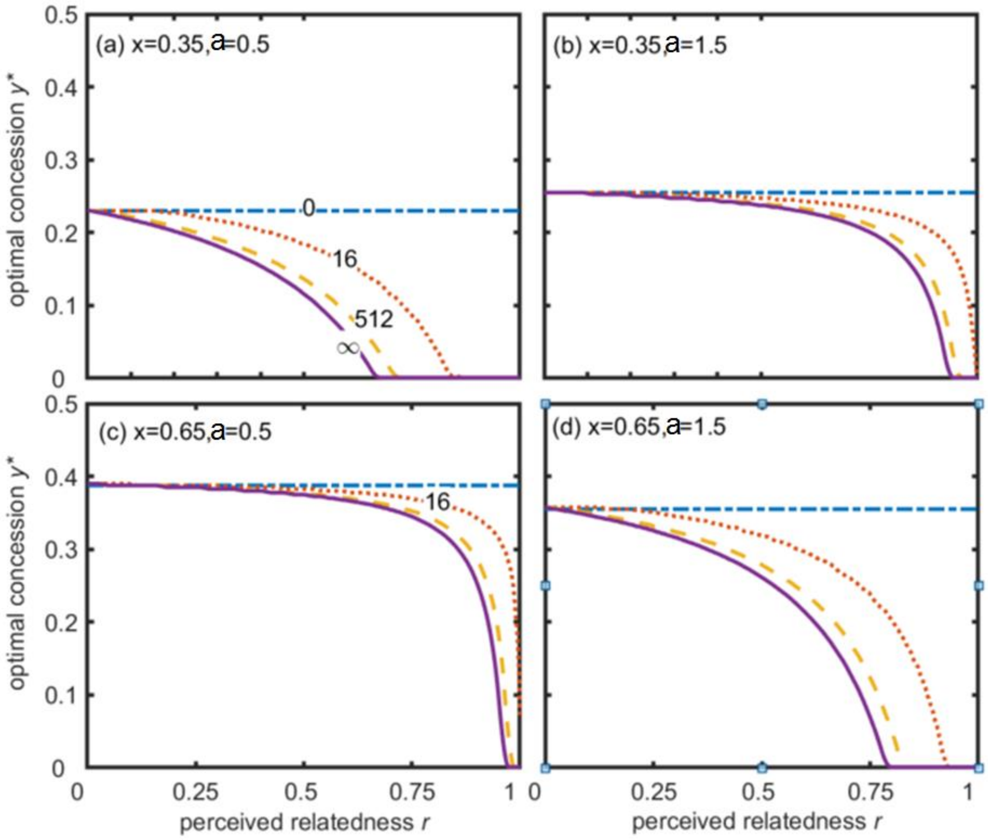

Figure 3.B1 Effect of perceived relatedness on the optimal concession y^* for 4 values of information (lines): no information about relatedness Ω =0 (dot-dash line), some information Ω =16 (dotted line), high information Ω =512 (dashed line), perfect information $\Omega = \infty$ (solid line). Panels show (a, b) low and (c, d) high quality subordinate and (a, c) weak and (a, b, d) strong dependence of group productivity on subordinate quality. In all cases and for all relatedness values, the concession declines as relatedness and information increase.

ANNEXE 3.C: Supplementary figures for Chapter 3

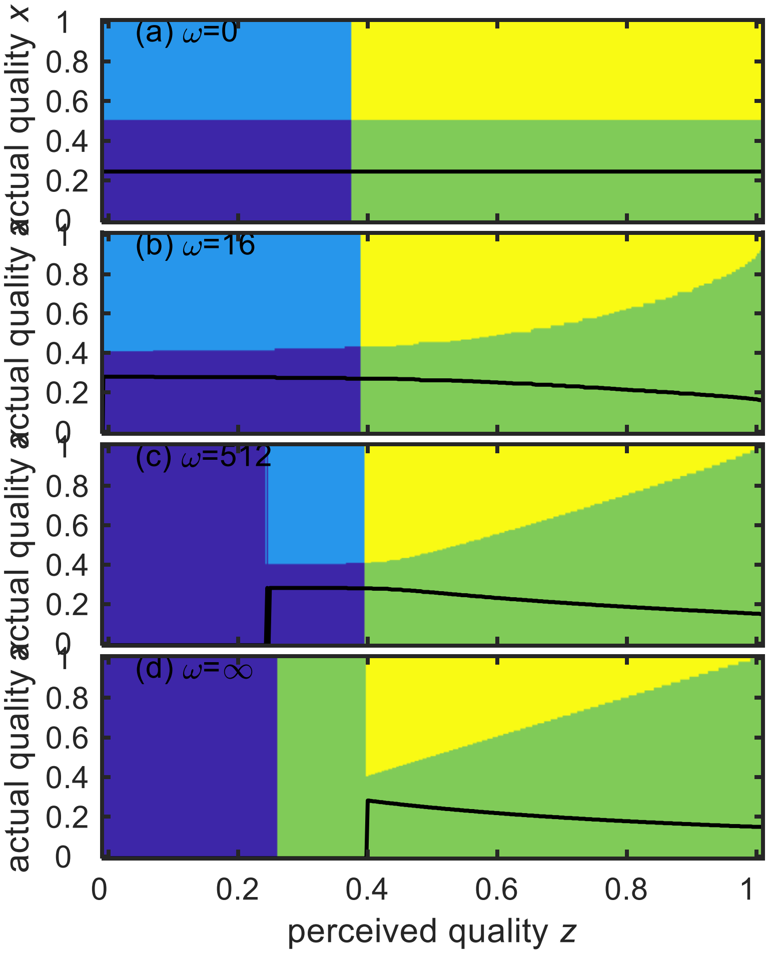

Figure 3.C1 As Figure 3.2 but where group productivity strongly increases with subordinate quality and subordinates are more highly related (*a*=2, *m*=-0.4, *r*=0.5). The colours show the areas of perceived quality by dominant (horizontal axis) and actual quality of subordinate (vertical axis) where for the optimal *y* (green) both dominant and subordinate would do better in a group*;* (yellow) only the dominant would do better in a group; (cyan) only the subordinate would do better in a group; (blue) neither would do better in a group. Parameter values: *a*=0.5, *m*=0.35, *r*=0.25. Note that *m*<0 so that dominants avoid accepting poor quality subordinates. They therefore have a threshold along the *z* axis.

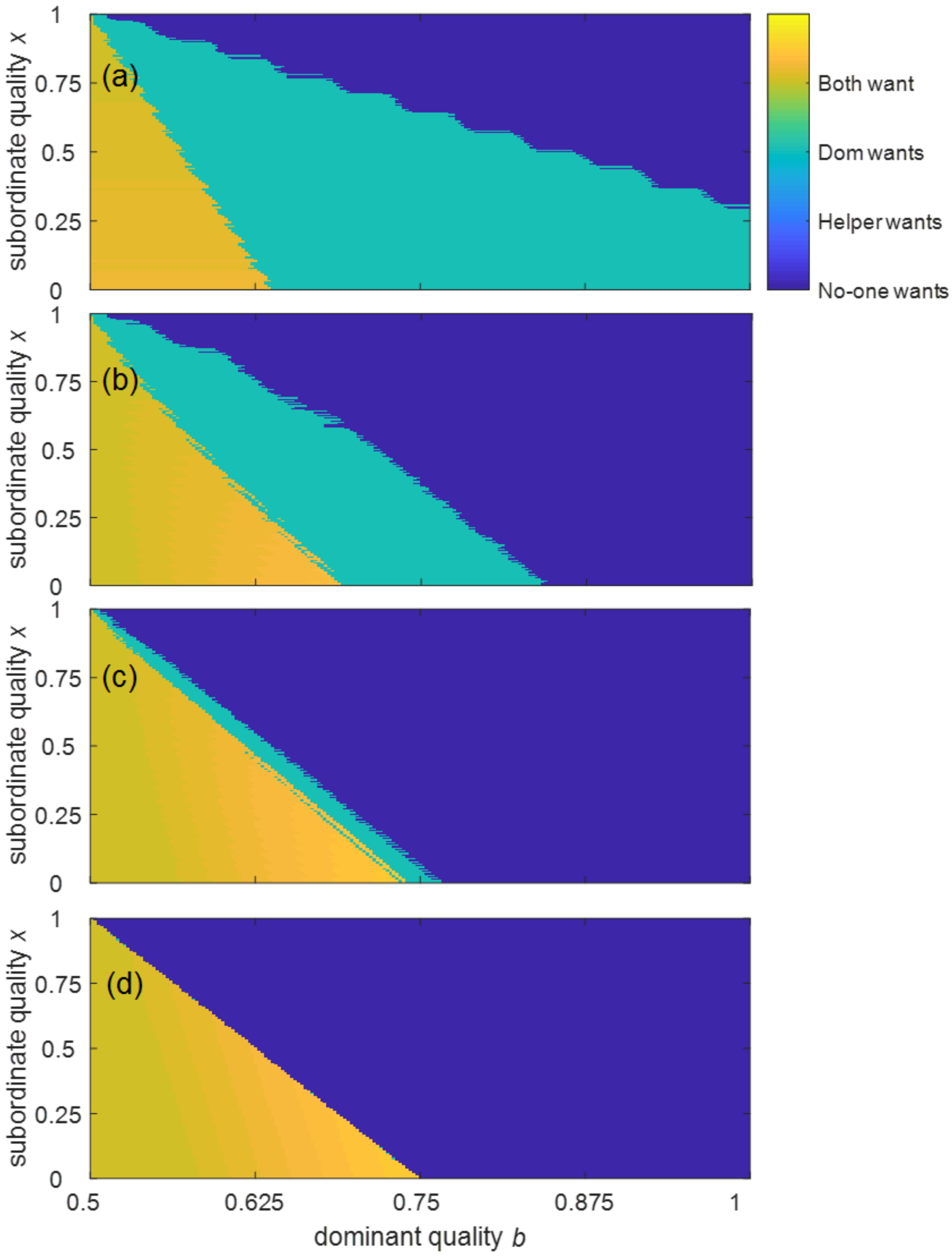

Figure 3.C2 Group formation as function of outside option *x* and benefit of cooperation *m*. Comparison of the numerical model where dominants have no information to a previous model that assumed symmetrical lack of information (Akcay et al. 2012). In order to compare directly we varied dominant quality *b* (0.5≤*b*≤1) and subordinate quality *x* (0≤*x*≤1), set *a*=0 and fixed the group productivity $b(1+m+ax)=1$ by and fixing $m=\frac{1}{b}-1$ Optimal decisions regarding cooperative breeding as a function of subordinate and dominant qualities, for increasing quality-productivity coefficient.

ANNEXE 4: Supplementary figures for Chapter 4

Overall, the numerical versions of the concession, restraint and tug-of-war skew models predict similar optimal share to the classic analytical versions. Groups always form when subordinates cannot leave (i.e. no probability to find a nest = no outside option) (Figure 4.A4a-d). Dominants get higher payoff than subordinates (Figure 4.A5). Dominant payoff decreases slightly with subordinate probability to find a nest (Figure 4.A5abc), whereas it increases slightly with subordinate competitive ability (Figure 4.A5def).

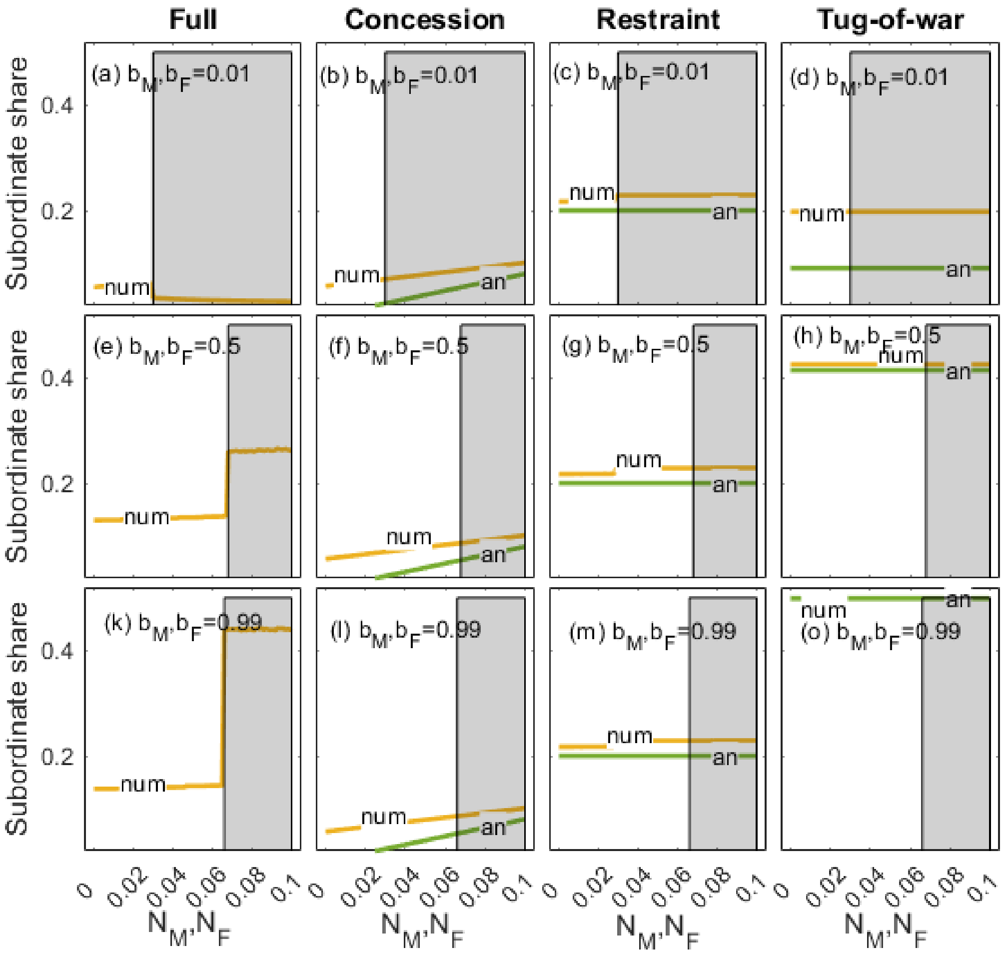

Figure 4.A1: Subordinate share as a function of probability to find a nest, for the synthetic model and the classical models. Subordinate competitive ability increases from top to bottom panels. Grey boxes show where groups do not form and subordinate share is not under selection (drift). Variation in both female and male probability to find a nest.

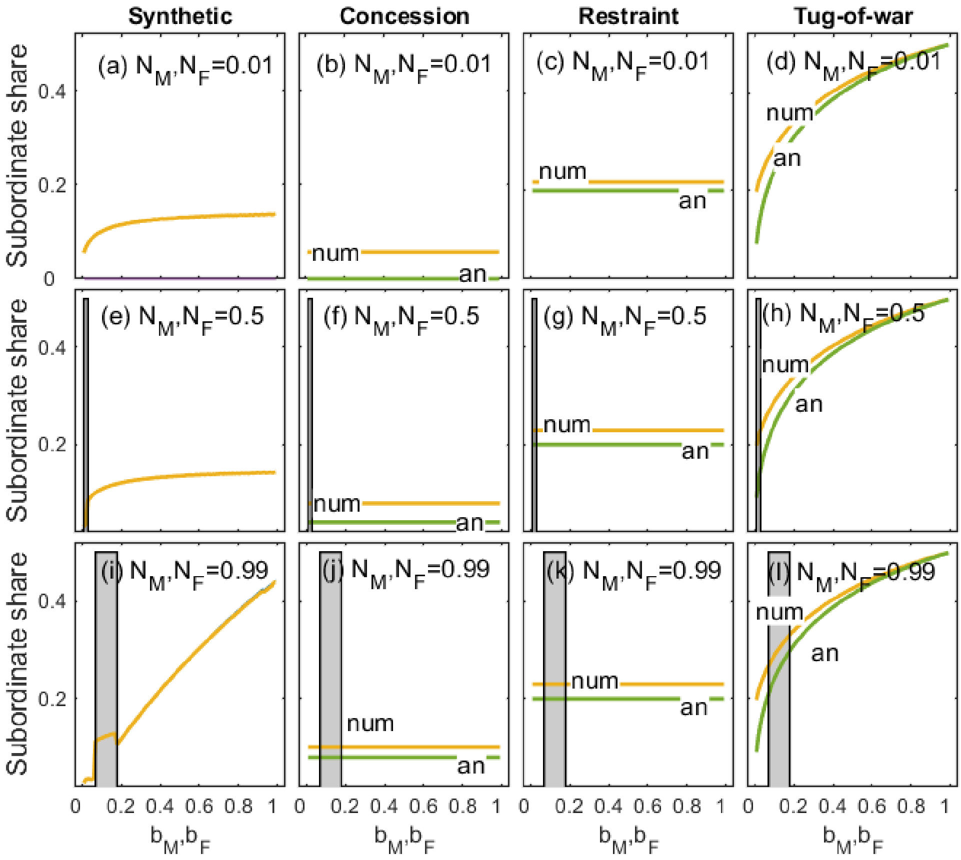

Figure 4.A2: Subordinate share as a function of subordinate competitive ability, for the synthetic model and the classical models. Subordinate competitive ability increases from top to bottom panels. Grey boxes show where groups do not form and subordinate share is not under selection (drift). Variation in both female and male subordinate probability to find a nest.

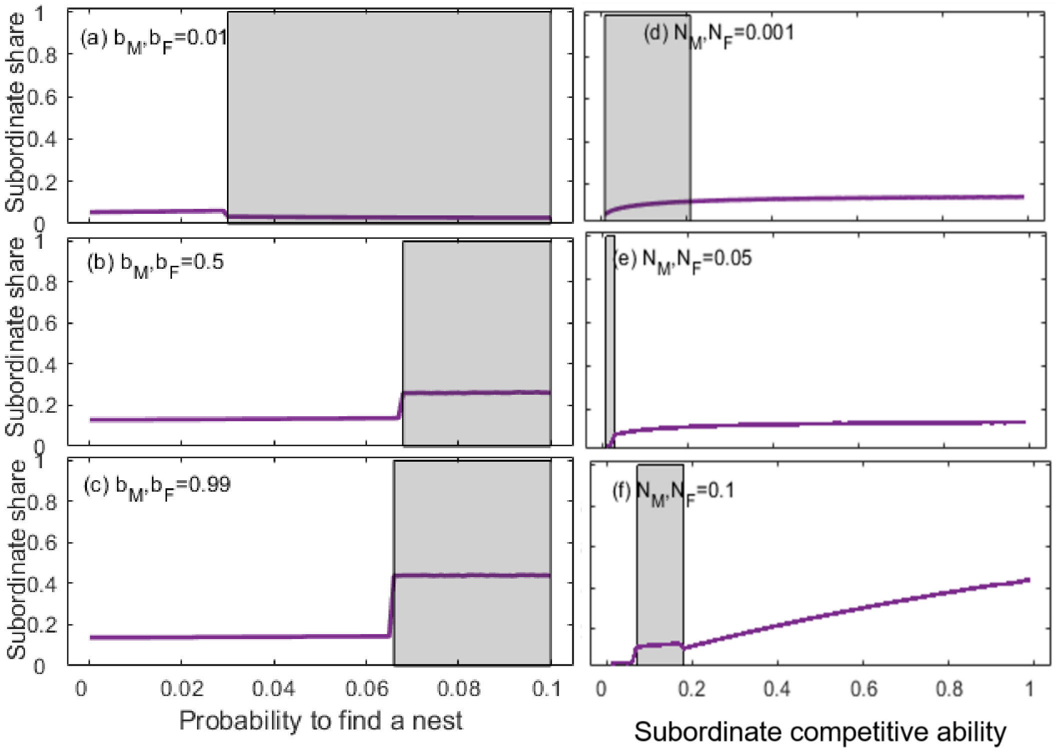

Figure 4.A3: Subordinate share as a function of (a,b,c) probability to find a nest and (d,e,f) subordinate competitive ability in the synthetic model. b_F=b_M; N_F=N_M.

Subordinate share did not vary with the probability to find a nest but did increase with subordinate competitive ability (for a medium probability to find a nest) (Figure 4.A3abc). Besides subordinate share increased with subordinate competitive ability when it was likely to find a nest (Figure 4.A3f).

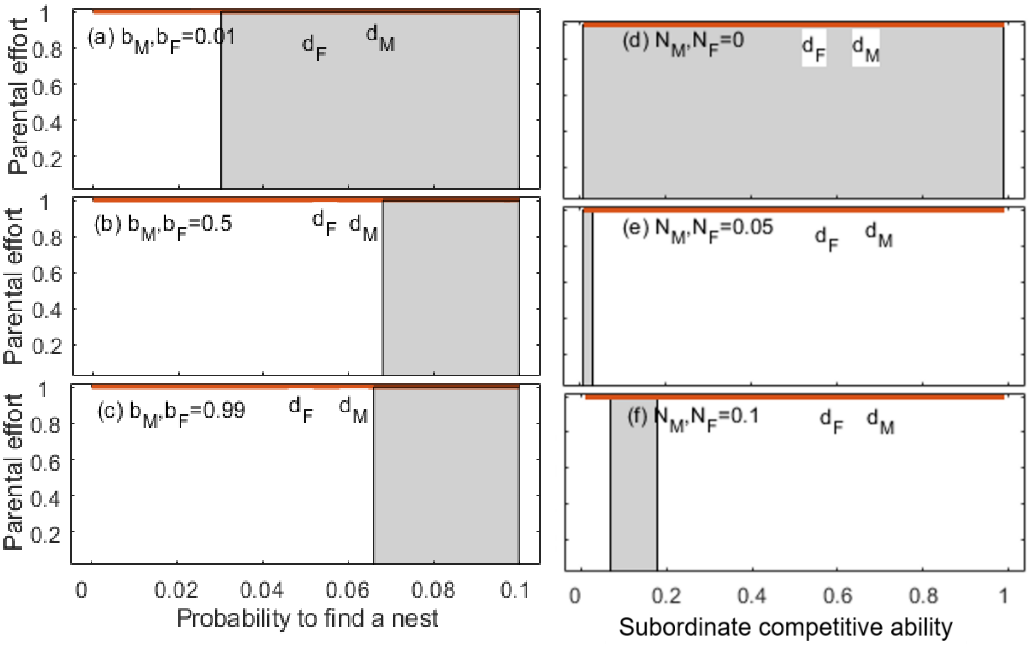

Figure 4.A4: Parental effort as a function of (a,b,c) probability to find nest and (d,e,f) subordinate competitive ability. Subordinate competitive ability is (a) low, (bedf) medium and (c) high. Probability to find nest is (d) low, (abce) medium and (f) high.

Parental efforts was maximal and did not vary with subordinate competitive ability or subordinate probability to find a nest (Figure 4.A4).

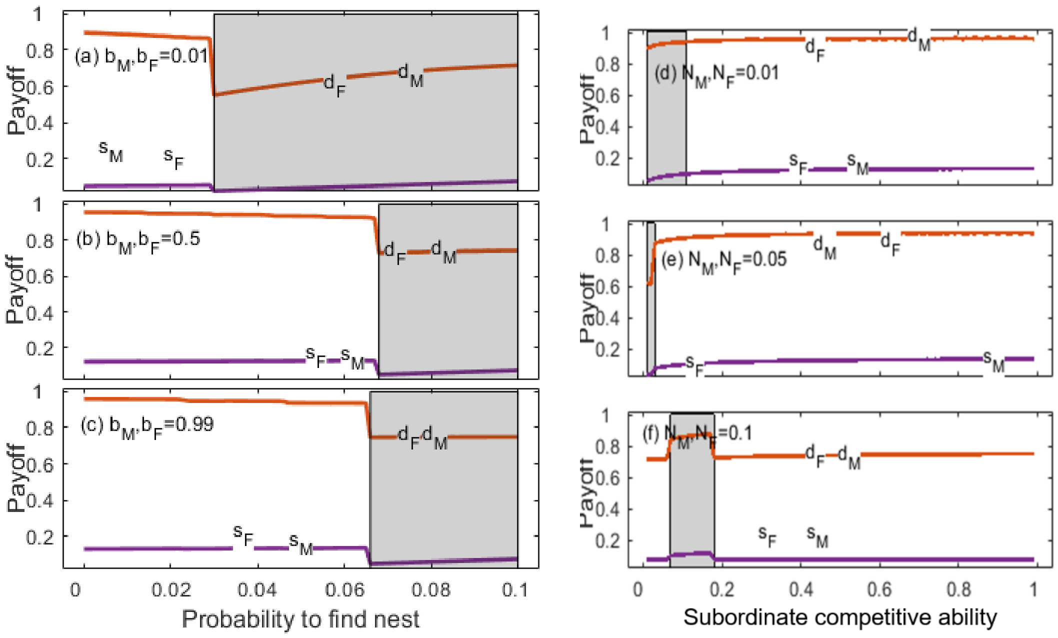

Figure 4.A5: Payoff to dominant (red) and subordinate (violet) as a function of the (a,b,c) probability to find nest and (d,e,f) subordinate competitive ability.

ANNEXE 5: Supplementary tables and figures for Chapter 5

The presence of rainfall was used as the proxy for environmental quality.

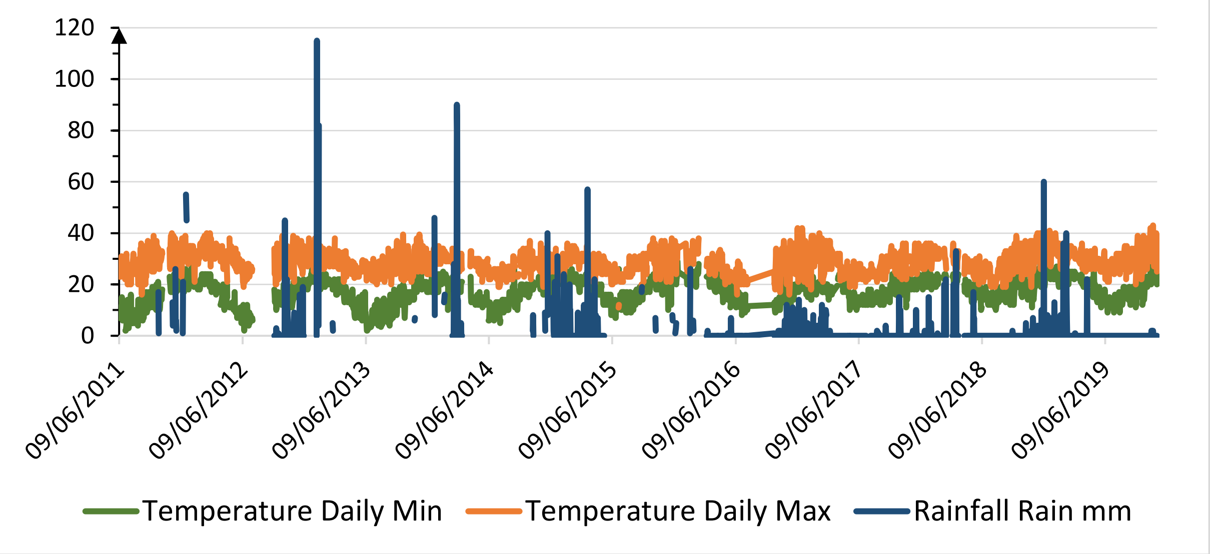

Figure 5.A1: Daily rainfall (mm, blue), minimal (green) and maximal (orange) temperatures (degree Celcius) as a function of time. 2011-2020. Note that most rainfalls occur in the wet season from September to February

Table 5.A1: List of studied variables and associated hypotheses

Variable	**Operationalised measure**	**Variation in the dataset**	**Hypothesis: environment quality**
Less costly cooperative behaviour	Allo-grooming (individual frequency with Instantaneous Scan Sampling (ISS) every 30 min, and duration *ad libitum*) from 2014 to June 2020.	Significant between-individual variation in grooming received: Coefficient of variation per group=[0.58-1.19] (Kern & Radford, 2018)	Decrease once dominant for females but not males.
Costly cooperative behaviour	Individual sentinel behaviour (30 min ISS and ad libitum) in function of habitat, wind, post height. From 2014 to June 2020.	Average duration 147.5 sec, Standard Deviation=238sec	Decrease once dominant for females but not males.
Environmental variation	Daily rainfall (mm) from June 2011 to November 2019.	0 to 290; average=2.20; median=0.	Rainfall decreases the cost of breeding, so helpers decrease and dominant female increase cooperativeness.

SENTINEL CONTRIBUTION

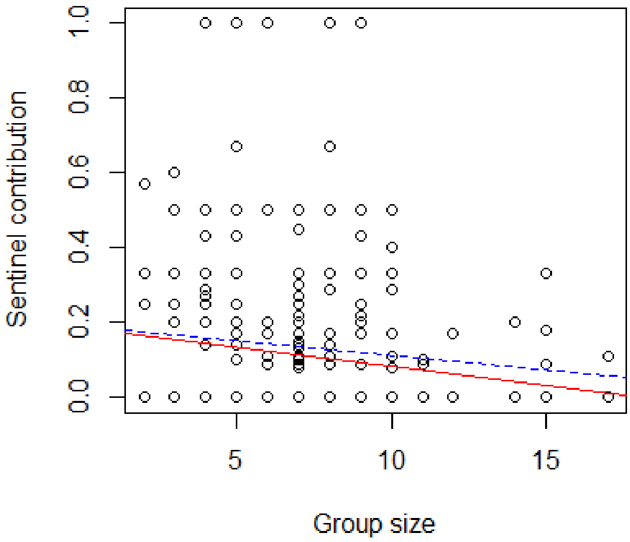

Figure 5.A2: Sentinel contribution as a function of group size, with the regressions for females (red line, -0.157) and males (blue dotted line, -0.130). Sentinel contribution is the (raw) proportion of bouts done by focal individual, in the group). Each dot is a proportion for one individual. N=9 females, 11 males

GROOMING

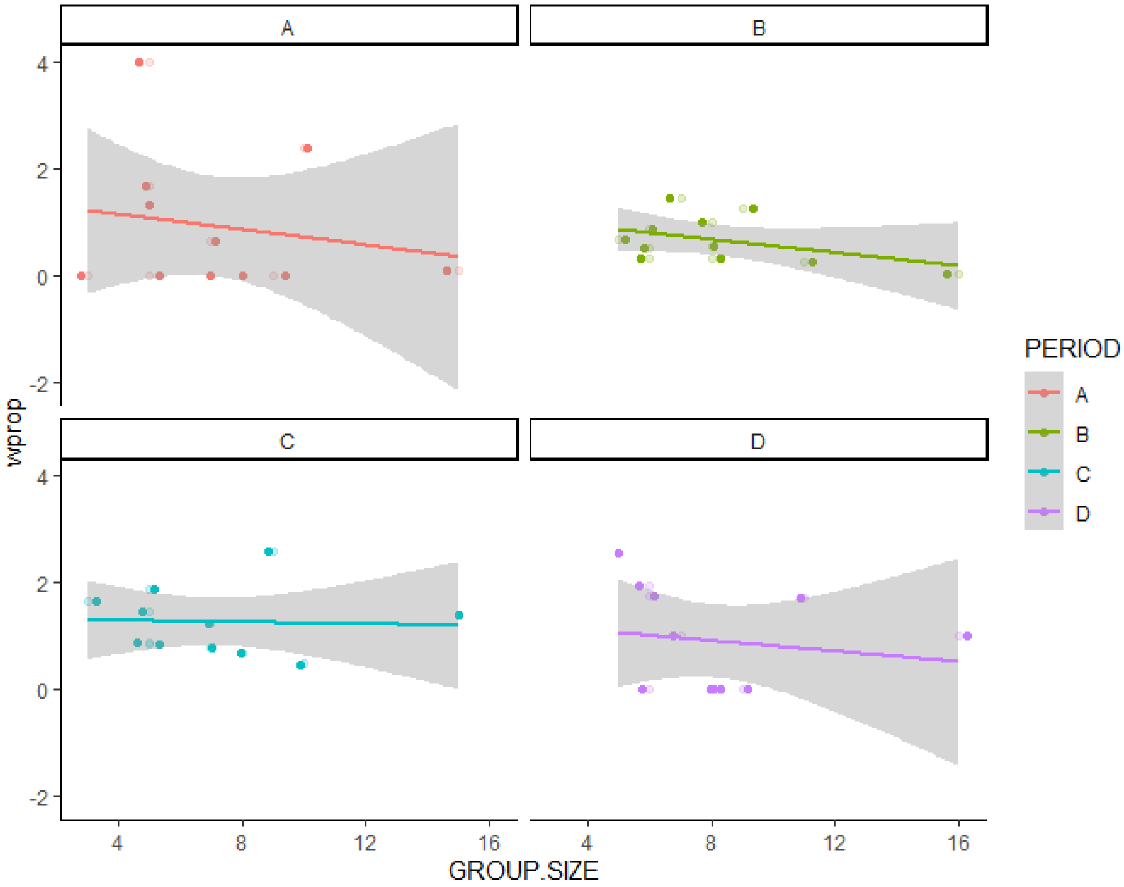

Figure 5.A3: Weighted group-grooming proportion as a function of group size in period A, B, C and D (panels). The line shows the regression and the grey area is the variance. N=44 data points, n=11 individuals

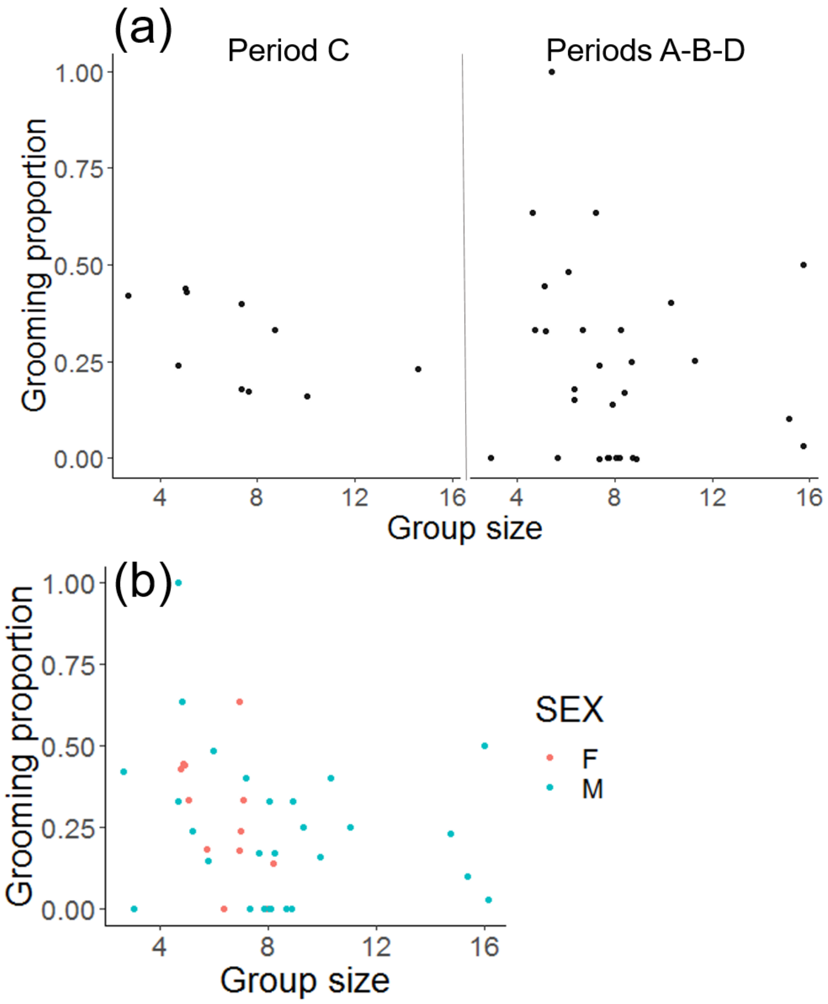

Figure 5.A4: Group-grooming proportion as a function group size and (a) period C vs. periods ABD, and (b) sex

BODY MASS

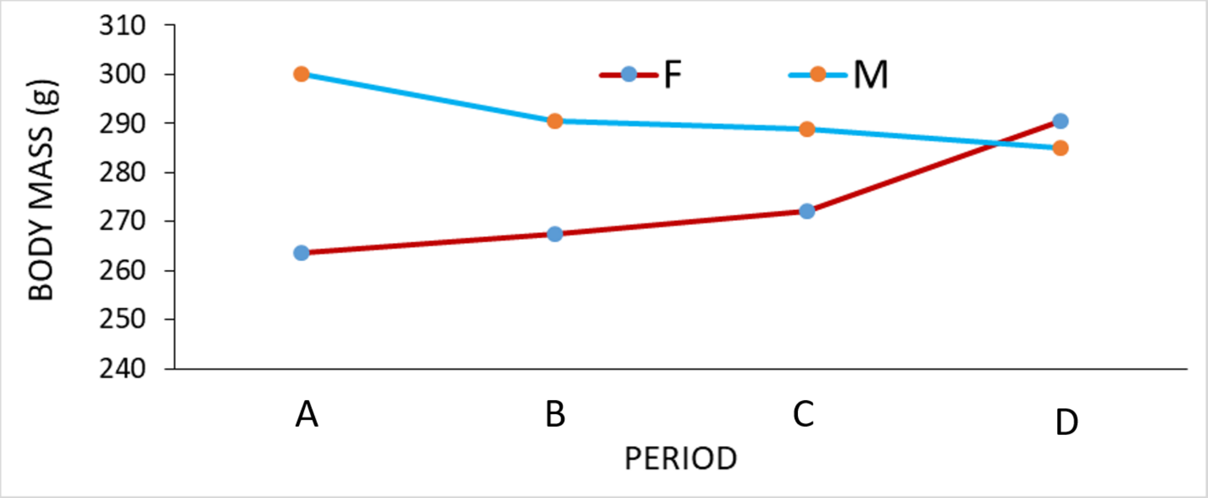

Figure 5.A5: Body mass as a function of sex and period, on average