

Maternal investment tactics in cooperative breeding systems



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Summary

Whenever multiple individuals contribute to the care of offspring, the optimum level of investment for each carer depends on the behaviour of the others. Previous theoretical and empirical work has largely focused on carer contributions within a single stage of a breeding attempt, neglecting the potential for investment during earlier stages to influence later care decisions. Typically, mothers have much greater control than other carers over the number and quality of offspring, and hence by altering her investment during offspring production a mother can adaptively adjust offspring phenotype to match or exploit the predicted care paradigm. In this dissertation, I use theoretical, empirical and comparative methods to investigate the influence of maternal tactics on investment rules in cooperative breeding systems, where ‘helpers’ care in addition to parents. In three chapters I model maternal control of offspring quality and offspring number across a cooperative breeding attempt, and investigate how the costliness of different reproductive stages, the kin-structure of the care group, and the consequences of offspring early-life condition influence the investment rules of carers. During offspring rearing, fair division of labour within a cooperative group can theoretically be resolved using simple turn-taking rules, leading to efficient outcomes for all carers. To test whether such a rule is employed in nature, a later chapter analyses empirical provisioning data from the chestnut-crowned babbler (*Pomatostomus ruficeps*), a cooperatively breeding bird endemic to the Australian outback. I use a Markov chain Monte Carlo approach to determine whether individuals alter their provisioning rate when other carers visit the nest, and identify both ‘passive’ and ‘active’ turn-taking behaviour. Finally, I present a comparative analysis of studies on provisioning rules in cooperatively breeding birds, and investigate whether the level of investment mothers must contribute to offspring influences the later care paradigm observed. My results indicate that maternal costs contribute to variation in both breeding group size and female provisioning behaviour. I conclude that maternal investment tactics are an underappreciated influence on carer investment rules in both the theoretical and empirical literature, and that incorporating them is crucial to understanding variation in cooperative care behaviour in nature.

Preface

This dissertation is the result of my own work, and includes nothing that is the outcome of collaboration except where specifically indicated otherwise. The text does not exceed 60 000 words, excluding tables, figures and bibliography. No part of this dissertation has been submitted to any other university in application for a higher degree.

James L. Savage

30th December 2013

Next page: Chestnut-crowned babbler (*Pomatostomus ruficeps*), from 'The Birds of Australia' (Gould 1869)



Table of Contents

Maternal investment tactics in cooperative breeding systems	
SUMMARY	I
PREFACE.....	II
TABLE OF CONTENTS	IV
ACKNOWLEDGEMENTS	VII
1: Introduction.....	1
<i>Abstract</i>	2
COOPERATION AND GAME THEORY	3
<i>Evolutionary game theory</i>	3
<i>The four fundamental cooperative games</i>	4
<i>Repeated games</i>	8
<i>Quantitative models of offspring care</i>	10
<i>Summary</i>	15
COOPERATIVE BREEDING IN BIRDS	16
<i>Prevalence and systematics</i>	17
<i>Benefits of helping</i>	19
<i>Offspring care in cooperative breeders</i>	23
<i>Classification of avian cooperative systems</i>	26
MATERNAL EFFECTS AND COOPERATION.....	31
<i>Stages of investment</i>	32
<i>Consequences of early-life investment</i>	34
<i>Maternal effects in cooperatively breeding birds</i>	36
2: Maternal costs in offspring production affect investment rules in joint rearing.....	39
<i>Abstract</i>	40
INTRODUCTION.....	41
THE MODEL	45
<i>Description</i>	45
<i>Solving the model</i>	47
<i>Comparison of analogous breeding attempts</i>	48
RESULTS.....	50

(i) <i>Productivity</i>	50
(ii) <i>Investment levels</i>	50
(iii) <i>Variable rearing costs</i>	51
DISCUSSION.....	55
3: Intra-group kinship influences maternal allocation and cooperative care behaviour	60
<i>Abstract</i>	61
INTRODUCTION.....	62
THE MODEL	65
RESULTS.....	69
(a) <i>Offspring production</i>	69
(b) <i>Offspring rearing</i>	70
(c) <i>Between- and within-group relatedness variation</i>	71
DISCUSSION.....	79
4: Maternal control of offspring size under variable rearing environments	85
<i>Abstract</i>	86
INTRODUCTION.....	87
THE MODEL	90
<i>Solving the model</i>	94
RESULTS.....	94
<i>Pre-birth investment conveys a ‘head start’</i>	94
<i>Effects of altriciality / precociality</i>	95
<i>Pre-birth investment conveys a ‘silver spoon’</i>	96
<i>Recruiting additional helpers</i>	107
DISCUSSION.....	108
5: Turn-taking in the cooperatively breeding chestnut-crowned babbler	111
<i>Abstract</i>	112
INTRODUCTION.....	113
METHODS	115
<i>Data collection</i>	115
<i>Classification of carers</i>	117
<i>Markov analysis</i>	118
<i>Model validation</i>	118

RESULTS.....	119
<i>Visit rates and turn-taking ratios</i>	119
<i>Inter-visit intervals</i>	120
<i>'Passive' or 'active' turn-taking?</i>	121
DISCUSSION.....	121
6: The influence of maternal costs on helping behaviour in cooperative birds.....	130
<i>Abstract</i>	130
INTRODUCTION.....	132
METHODS.....	134
<i>Data collection</i>	134
<i>Statistical analysis</i>	135
RESULTS.....	136
<i>Variation in cooperative care</i>	138
<i>Influence of maternal investment</i>	139
DISCUSSION.....	142
7: General discussion	145
SUMMARY OF RESULTS.....	146
CONCLUSIONS AND FUTURE WORK.....	149
References	151
Appendix A: Selection criteria for species used in comparative analysis	175
Appendix B: References for data used in comparative analysis.....	176
<i>General data sources</i>	176
<i>Species data sources</i>	176
GENERAL REFERENCES	178
SPECIES REFERENCES	178

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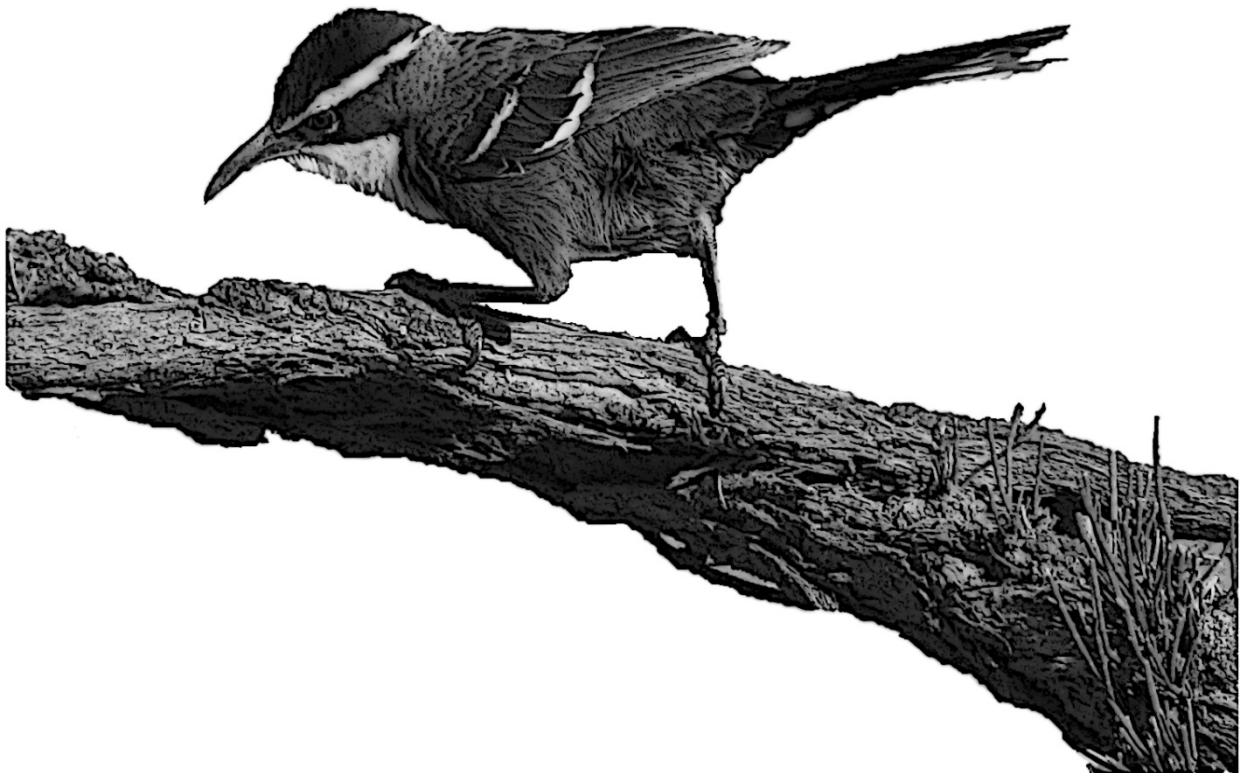
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1: Introduction



Abstract

The subject of maternal investment tactics in cooperative care systems is complex, as it exists at the interface of several larger fields, each with their own substantial literature. The evolution and maintenance of cooperative behaviour, the causes and consequences for offspring of early-life care or initial quality, and the trade-offs surrounding parental care will all influence the decisions made by a breeding female in a cooperative group. Although full reviews of all the pertinent literature would require far too much space, some context is needed for the work presented in this dissertation, and so this introduction comprises three mini-reviews of highly relevant topics to the following chapters. The first section reviews game theory and its applications to animal behaviour, unfortunately neglecting much of the expansive economics literature and many key models to focus instead on the four fundamental two-player cooperative games (and their extensions to greater numbers of individuals) in relation to cooperative offspring care. I then examine what has been modelled within the current literature on specific models of parental care, and identify areas that require further work. The second mini-review covers cooperative breeding in birds, with brief reviews of the prevalence and systematics of cooperative behaviour within birds, the potential benefits of helping, and the various possible forms of offspring care in a cooperative species. The review concludes with an attempt to broadly classify cooperative birds into fundamental types using the identity and routes to fitness of typical helpers. The final mini-review of the chapter discusses the potential scope and importance for maternal effects during parental care, with particular reference to cooperative bird species. I review the different stages of investment during the course of a breeding attempt, and the effects of differing early-life investment on later outcomes for offspring.

Cooperation and game theory

Evolutionary game theory

Game theory is a mathematical framework used to explore decision-making when individuals (or ‘players’) interact in ‘games’ which comprise, for each player, (i) a particular set of possible strategies and (ii) a set of resulting payoffs (Barron 2008). Games can be symmetrical or asymmetrical: in symmetrical games players always receive the same payoffs when adopting the same strategies (i.e. only the strategy is important, not the individual playing it). In the context of evolutionary biology, strategies are traits that are inherited rather than deliberate courses of action, and the resulting payoffs are in terms of Darwinian fitness: the reproductive success of the individual players (Sigmund & Nowak 1999). Individuals within a natural population that has played the same ‘game’ over evolutionary time will collectively approximate rational behaviour, as natural selection in an optimising process favouring individuals that consistently behave in their own best interest, although within a population not all individuals will necessarily behave optimally (Maynard Smith & Price 1973). The expected outcome of any game with rational players is that each will choose the best strategy available, given the rational strategies of the other player(s) (the ‘best response’). If the players adopt a set of strategies such that none can benefit from changing their strategies unilaterally, then that set of strategies represents a ‘Nash equilibrium’ for the game (Nash 1951).

Nash equilibria can occur with both ‘pure’ and ‘mixed’ strategies. A pure strategy defines how a player plays exactly, such that every possible situation has a well-defined move associated with it. In contrast, a mixed strategy assigns a probability to two or more pure strategies for each possible situation, and selects randomly between them each time that situation occurs. A player’s ‘strategy set’ is the set of all pure strategies available to a player; mixed strategies are in principle infinitely variable as the probabilities associated with them are continuous values. Nash (1951) proved that any game with both a finite number of players and a finite number of pure strategies has a least one Nash equilibrium if mixed strategies are allowed, and when restricted to two strategies (often termed ‘cooperate’ and ‘defect’ in games of cooperative interactions), every symmetric game has at least one pure strategy Nash equilibrium (Cheng et al. 2004).

In practical terms, Nash equilibria for particular games are found by calculating the expected payoffs to each player under every possible combination of strategies. When a game has multiple steps that are non-independent, the equilibrium must be calculated by backward induction from the final step, by calculating the Nash equilibria of the subgames that comprise each step. The result is a subgame-perfect equilibrium strategy for the entire multi-step game. Order of play is very important if information is shared between players: sequential rather than simultaneous choice of strategy may lead to entirely different optimal strategies even in single-step games. In general, simple games with restricted (often two) possible strategies are useful for being easy to analyse, while still illustrating relationships between strategy and payoff that are common to more complex games.

While finding Nash equilibria is necessary to determine the outcome of a game, another useful concept is that of Pareto optimality, which can be seen as a measure of how efficient the outcome of a game is. A particular game's outcome is Pareto optimal if there is no alternative outcome that delivers a greater payoff to at least one player with equal payoffs to all the others. In other words, no Pareto optimal outcome can be improved upon except by reducing the payoffs of one or more players. The Nash equilibrium of a game need not be Pareto optimal, as in many games players are prevented from cooperating with each other by a rational fear of being exploited by others. However, natural systems should be expected to evolve mechanisms to facilitate Pareto optimal strategies when possible, as these ultimately result in greater payoffs for everyone when games are played repeatedly (Axelrod & Hamilton 1981).

The four fundamental cooperative games

When modelling cooperation between individuals, the simplest games assume that individuals have exactly two options: 'Cooperate' (C), in which their action results in some collaborative benefit between the individual and the other player(s), and 'Defect' (D), in which no mutual benefit accrues. With this assumption there are four potential outcomes in a simple two-player game: one where both players cooperate (the 'Cc' outcome), one where both defect (Dd), and two where one cooperates and the other defects (Cd and Dc; the capital letter corresponding to the strategy of the focal player). The order in which these outcomes are preferred for players

determines what game is being played, as games in which outcomes are equivalently ordered will generate identical (pure) equilibrium strategies.

In terms of parental care, parents can choose to either provide an optimum amount of food or defence for the offspring (C), or reduce or abandon care (D). Each individual benefits from the contribution of its partner(s) (either because of an increase in productivity or a reduction in the necessary costs of rearing the offspring), and each pays a certain cost when cooperating through investing personal resources in the offspring (Williams 1966a). How this personal cost relates to outcomes for offspring is a major determinant of which fundamental game caring for offspring becomes, and hence what strategies parents should employ when jointly investing in offspring.

Cooperation between parents implies that the payoff to the focal player for outcome Cc must be greater than that for Cd, and that the payoff for Dc must always be greater than Dd, and consequently only four symmetrical two-player games are directly relevant to the study of cooperation (or offspring care), each with a characteristic payoff order. These games are the ‘prisoner’s dilemma’, the ‘hawk-dove’ game, the ‘no conflict’ or ‘soldier’s dilemma’ game, and the ‘stag hunt’ (Macy & Flache 2002; Archetti & Scheuring 2012). Which of these games a particular care behaviour falls into will have strong implications for how stable and efficient cooperation is likely to be, as games differ in how much the rational ‘best response’ strategy aligns with the Pareto optimal strategy (Table 1.1, Figure 1.1).

The prisoner’s dilemma (Tucker 1950) and its *N*-player equivalent (Hamburger 1973) (the ‘diner’s dilemma’) are the games least conducive to effective offspring care, as the Nash equilibrium is pure defection (because $D_c > C_c$ and $D_d > C_d$). Prisoner’s dilemmas result in outcomes that are Pareto-inefficient, as both players would receive a higher payoff if both cooperated, and in natural systems this should lead to selection pressure for behavioural mechanisms facilitating cooperation. Prisoner’s dilemmas are highly relevant to offspring care, as carers will almost always benefit from contributing somewhat less than their fair share, such that their partner bears a greater proportion of the total costs. Theoretical work suggests that this fear of exploitation results in inefficient investment levels (Houston & Davies 1985; McNamara et al. 1999; Johnstone et al. 2014), and empirical studies have provided evidence that this conflict between the sexes can reduce offspring fitness (Royle et al. 2002, 2006). Much research has revolved around mapping the conditions under which the prisoner’s dilemma can be resolved in more complex cases (reviewed in Doebeli & Hauert

2005), including when strategies are continuous (Killingback et al. 1999; Wahl & Nowak 1999) and/or when the game is played repeatedly between individuals (Axelrod & Hamilton 1981; Boyd 1989).

The opposite of the prisoner's dilemma is the 'no conflict' game or 'soldier's dilemma' (Clutton-Brock 2009), in which the Nash equilibrium is pure cooperation as defecting never improves an individual's payoff ($C_c > D_c$ and $C_d > D_d$). In natural cooperative interactions, soldier's dilemma-like situations might occur in group territorial defence, provided that the costs of losing the offspring or territory exceed the costs of possible injury or energetic expenditure while defending it (Heinsohn & Packer 1995). Sentinel behaviour by group members might appear altruistic (e.g. if sentinels have less foraging time) while actually directly benefiting the sentinel through greater predator awareness: if so, individuals should adopt a sentinel role whenever their energetic reserves are high enough (Bednekoff 1997). This type of cooperative relationship is often termed a 'by-product mutualism' (Bergmüller et al. 2007), as it is beneficial to all individuals concerned without requiring any deferred or indirect benefits: individuals cooperate for immediate selfish rewards, and explaining universal cooperation is straightforward.

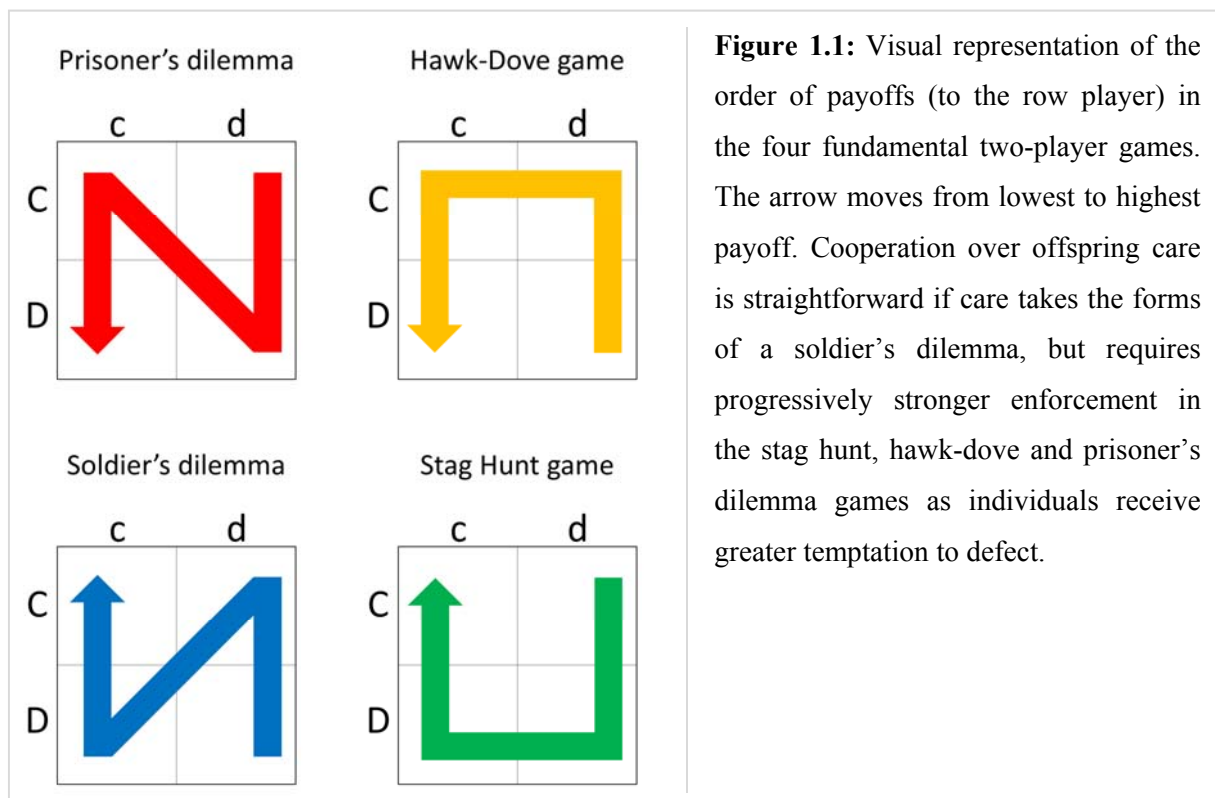
The hawk-dove game (Maynard Smith & Price 1973), also known as 'chicken' (Rapoport & Chammah 1966), or the snow-drift game (Sugden 1986), is characterised by individuals benefiting from exploiting each other, but suffering when exploitative strategies meet ($D_c > C_c$, but $C_d > D_d$), leading to a mixed equilibrium strategy. Hawk-dove games provide a good model for parental care in the cases where offspring will die should both parents fail to contribute (D_d), but where a single parent is able to raise offspring alone. If uniparental care

Game	Payoff structure	Best strategy	Behavioural example
Prisoner's dilemma	$D_c > C_c > D_d > C_d$	Always defect	Joint offspring provisioning
Hawk-dove	$D_c > C_c > C_d > D_d$	Oppose partner	Desertion → uniparental care
Soldier's dilemma	$C_c > D_c > C_d > D_d$	Always cooperate	Sentinel behaviour
Stag hunt	$C_c > D_c > D_d > C_d$	Match partner	Mobbing

Table 1.1: Summary of the four fundamental two-player care games. Cooperative behaviours such as joint offspring provisioning and adult-adult reciprocity may occur in natural systems despite conforming to a prisoner's dilemma payoff structure, as repeated interactions change the best strategy of individuals.

is possible, the partner most likely to gain further (short-term) breeding success is tempted to desert and leave the other to care for offspring (Dawkins & Carlisle 1976; McNamara et al. 2000): this deserter may, depending on the species, primarily be the male (Ezaki 1988), the female (Emlen & Wrege 2004), or be split relatively evenly between the sexes (Beissinger & Snyder 1987; Van Dijk et al. 2007) depending on cost and benefit asymmetries between the sexes.

The final fundamental game is the stag hunt (Skyrms 2001), which remains poorly studied as a model of parental care. Also known as the ‘trust dilemma’, the stag hunt describes cases where individuals benefit from cooperating but suffer if their partner defects, leading to a temptation to defect if partners are unreliable. Stag hunt games may plausibly model parental care decisions when mobbing predators, provided that individuals can effectively mob as a group with low risk (Krams et al. 2009), but suffer costs should they attempt to ‘mob’ alone. When biparental care is necessary to rear offspring, a stag hunt might similarly arise if cooperation (staying with the current partner) (Cc) is better than defection (abandoning and finding a new partner) (Dc / Dd) and both are preferable to attempting to raise offspring with a partner that will defect (Cd). In this case, cooperation is the best strategy unless your partner is likely to irrationally defect, however high mortality among carers might tempt an individual to abandon care if it suspects its partner to be at risk of ‘defecting’ through death.



Repeated games

In natural systems individuals do not normally interact with each other only once, but instead play multiple ‘rounds’ of the same game with the same individuals over the course of their lives or through an extended association such as a breeding season. If individuals can modify their behaviour in the current round of the game based on their past interactions with others, the best strategy for a player across all rounds will be influenced by not only the strategy of their partner, but also the number of rounds that will be played, and any limitations on cognition that restrict the potential complexity of strategies (Macy & Flache 2002). As with single-round two-player games, the error rate can also influence the best choice of strategy.

The iterated prisoner's dilemma is probably the best-studied multiple-round game, having been the subject of a tournament to determine the most effective strategy in a mixed population of individuals with different strategies (Axelrod & Hamilton 1981). The tournament results supported a tit-for-tat (TFT) type strategy as the most effective: individuals should be optimistic and cooperate by default, but punish partners that defect by retaliating in kind on the following round. The TFT strategy can never be exploited beyond the first round by a defecting strategy (and hence has very similar fitness when there are many rounds), and gains the maximum possible payoff when playing against itself or any other strategy that cooperates by default. If mistakes are possible then a similar but more forgiving strategy that allows a single defection before retaliating can be even more successful, as it allows cooperation to persist between retaliating strategies despite errors (at the cost of greater vulnerability to strategies that occasionally deliberately defect) (Axelrod 1984). An even better strategy in this case is ‘contrite tit-for-tat’ (CTFT) (Sugden 1986), in which the player accepts a single retaliation by its partner as punishment for an accidental defection on the previous round (Boyd 1989). When the iterated prisoner's dilemmas is extended to include continuous strategies, generous strategies capable of cooperation are also favoured (Bendor et al. 1991), although cooperative equilibria may be less stable than non-cooperative equilibria (Le & Boyd 2007).

The lessons of the iterated prisoner's dilemma apply similarly to repeated versions of the other fundamental games. The hawk-dove game generates similar best strategies to the prisoner's dilemma, with an even greater bias towards cooperative, retaliatory strategies (Carlsson & Johansson 1998; Dubois & Giraldeau 2003): as with the iterated prisoner's

dilemma, cooperative strategies are able to beat exploitative strategies by conforming to Axelrod's (1984) guidelines of being 'nice', 'forgiving', 'non-envious' and (crucially) 'retaliatory'. As one might expect, trusting strategies rapidly come to dominate in an iterated stag hunt (Fang et al. 2002), and it should be obvious that soldier's dilemmas are not influenced by iteration, as they are already fully efficient at their single-game equilibrium.

In N -player repeated games the maintenance of cooperation depends largely on whether or not individuals are able to effectively retaliate against defectors in the same way as is possible in two-player games. The 'public goods' game is an N -player game that illustrates the problem: players each own a number of tokens, and can secretly invest any number of their tokens in a common pot, the total of which is multiplied (by some value greater than 1) and then shared between all players. The maximum payoff for the group is obtained when all players invest all of their tokens, but as in the prisoner's and diner's dilemmas each player always benefits more by exploiting the contributions of the other players. The Nash equilibrium for this game is pure defection, i.e. retaining all tokens for oneself, with the result that a group of purely rational players gain the minimum (zero) payoff from the game (Frank 2010). When this game is iterated it is not possible to identify or punish a defector individually, and hence there is no way to adopt a retaliatory strategy and prevent defecting strategies from outperforming cooperative strategies. When punishment of specific defectors is possible, efficient outcomes of the public goods game can be reached, provided that defection on punishment duty is somehow prevented (Colman 2006), or if the game (or punishment regime) resembles a volunteer's dilemma (Diekmann 1985) in which only a single cooperative individual is needed to deliver benefits to the entire group (Archetti 2011; Raihani & Bshary 2011). Alternatively, cooperation might remain common if players benefit by accruing a good reputation that carries over to interactions beyond the public goods game (Milinski et al. 2002; Sylwester & Roberts 2010).

To summarize, the four possible outcome arrangements in a symmetrical, costly game of cooperation can be used to place the game into one of four 'families': the prisoner's dilemma, hawk-dove game, soldier's dilemma, and stag hunt game (Table 1.1, Figure 1.1). The division of games into these families holds both when dealing with greater numbers of players, and with more complex models of cooperative investment than the binary choice presented above. Each game can plausibly represent behavioural interactions that occur when parents cooperate to raise offspring, and the game's ordering of payoffs will alter the fundamental predictions of

which strategy to adopt: in some cases repeated interactions, directed punishment, and information about other players will be necessary to maintain cooperation, but in other cases it will always be favourable to cooperate.

Quantitative models of offspring care

When individuals cooperate to raise offspring, decisions to cooperate or defect may occur as single binary events that determine how the breeding attempt will progress (e.g. mate desertion), repeated binary events that provide opportunities for reciprocity (e.g. joining in with predator mobbing), or may be extremely frequent events, allowing a particular level of cooperation to be chosen along a continuum (e.g. provisioning rate). In addition, individuals may care for offspring alone, in pairs, or as groups, and when in groups may direct care entirely or preferentially towards their own offspring, or provide it equally to all offspring in the group. Offspring care may be restricted to a single homogenous period or encompass multiple discrete stages of care during which different carers have different roles (Clutton-Brock 1991), and these stages of care may be largely independent from each other (Van De Pol et al. 2006), or instead have important knock-on effects on future stages (Heckman 2007). However, as with simple cooperative games, it is helpful to review simple offspring care models first to establish basic principles and provide context for later extensions. The simplest models of offspring care are those wherein two individuals cooperate to raise a single brood over a single stage of development, a scenario that has justifiably received great theoretical attention due to the large number of biparental species (particularly among birds) and the relative ease of testing predictions within a single stage of care.

Ultimatum games

If we wish to allow for asymmetry between carers and near-continuous possible values of investment in offspring, possibly the simplest game that can model biparental care to some degree of accuracy is the ‘ultimatum game’ (Rubinstein 1982). This game was initially formulated to model two individuals dividing a sum of money between them, but it translates well to the dynamics of offspring care. The first player makes an offer proposing how to divide the money, and the second player can either accept the offer and receive the proposed

share, or reject the offer (resulting in both players receiving nothing). The Nash equilibrium for this game is for the first player to offer the minimum possible amount of money to the second, as there is no reason for the second player to reject any offer (greater than zero) as rejecting guarantees receiving nothing. Interestingly, when humans play repeated rounds of this game, the offers made are typically closer to 50% than to 0%, and irrational punishment of the other player (by rejecting the offer) is common if too low an offer is made (Oosterbeek et al. 2004).

Although simplistic, the ultimatum game is more appropriate in one aspect than many more complex games that model parental investment, as it is strongly asymmetric with one player acting first and thus controlling the game. In natural vertebrate systems the mother often has the ability to modify her investment in offspring size and/or number before other carers can invest, and hence she can present him with an investment ultimatum that he may have little choice but to accept. Symmetric games based only on the largely symmetric rearing period may miss important effects on offspring investment caused by this earlier asymmetry, however well they model investment within a single stage.

Sealed-bid games

The Houston-Davies or ‘sealed bid’ model (Houston & Davies 1985) treats biparental care as a game in which the parents contribute a variable (continuous) level of investment to offspring that is optimised over evolutionary time. Both gain reproductive success as a function of the total investment delivered to the offspring, reduced by the costs they pay to invest. Each parent’s investment bid is chosen without knowledge of how the other parent is investing, and cannot be changed afterwards in response to the other partner: it is optimised only over evolutionary time. The solution to the sealed-bid model suggest that an individual’s optimal bid should incompletely compensate for changes in the bid of its partner, i.e. if the partner bids higher the focal individual should decrease their bid, but not to the extent of completely offsetting the partner’s increase. A purely cooperative variant of the Houston-Davies model, in which each parent attempts to maximise their combined reproductive success, may alter this prediction as lone parents may not always invest more than they do when in a pair (McNamara et al. 2003).

Although the sealed bid model's predictions do not in fact specify response rules that are stable in behavioural time (McNamara et al. 1999), incomplete compensation to short-term changes in partner effort is nonetheless a common empirical finding. Among birds, compensatory responses to changes in partner effort have been observed in many species: a comprehensive review and meta-analysis by Harrison et al. (2009) showed that in biparental species the mean response to partner removal and partner handicap was indeed incomplete compensation.

Negotiation games

The 'negotiation' model (McNamara et al. 1999) improves upon the Houston-Davies model by explicitly accounting for the ability of each parent to respond in behavioural (as opposed to evolutionary) time to changes in the effort levels of its partner. The result is a negotiation process in which both partners modify their effort until they stabilize at a rule presenting the best return possible for them individually, given the response of their partner. Within the negotiation framework the Houston-Davies model represents a special case in which neither partner can flexibly respond to the partner from their initial bid (McNamara et al. 2003).

The response rules generated by the negotiation model are qualitatively similar to those of the Houston & Davies model, as both predict incomplete compensation to changes in partner effort, however in quantitative terms negotiation leads to lower predicted effort levels (McNamara et al. 2003). All empirical studies that report parental responses to changes in partner effort are implicit support for negotiation strategies over sealed bids, and further empirical evidence is found when quantitative predictions of negotiation are tested explicitly (Lendvai et al. 2009). Nevertheless, it is clear that individuals in some species do not respond to changes in effort by their partners (Schwagmeyer 2002; Tajima & Nakamura 2003; Trnka & Grim 2013), suggesting that sealed bids are also reasonable strategies to adopt in some cases. In principle, difficulties in accurately observing other individuals (or costs associated with doing so) might obviate any advantage that could be gained by attempting a responsive strategy, resulting in individuals preferring to rely largely on intrinsic knowledge to determine their investment levels.

The importance of available information in determining an individual's response rules has been demonstrated directly by Johnstone and Hinde (2006), who extended the negotiation

model to incorporate uncertainty among carers regarding offspring need. Changes in investment levels by one parent might then serve as a signal of offspring need to the other, leading to the other parent benefiting by matching (rather than compensating for) its partner's change in investment. If the sexes differ consistently in their information about brood need, this asymmetry might serve to explain the differences in behaviour between females and males that are often found in empirical studies of partner response (e.g. Duckworth 1992; Sanz et al. 2000)

Although more biologically relevant than a simple sealed-bid model, the negotiation framework is still an imperfect representation of natural behaviour. If the model is interpreted as an initial (cost-free) negotiation phase followed by an agreed-upon sealed bid (McNamara et al. 1999), then an individual capable of deception during the negotiation phase would outcompete an honest negotiator: a further extension incorporating costly initial negotiation is needed (Houston et al. 2005). Alternatively, if one interprets the negotiation as a continual response rule across an entire breeding attempt, individuals are unrealistically restricted to the same response rule throughout the care period (Lessells & McNamara 2012). Furthermore, when partners are extremely responsive to changes in each other's effort levels, negotiation can lead to offspring receiving less total investment from a pair than they would from a lone parent (McNamara et al. 2003): this is never true when parents adopt a sealed-bid strategy. More recent extensions to the negotiation framework allow for multiple bouts of negotiation over the course of a breeding attempt, to allow for response rules to change over time. While further increasing the verisimilitude of the model, repeated bouts also have the effect of further lowering parental contributions to care (Lessells & McNamara 2012), leading to sub-optimal outcomes for both parents and offspring (Johnstone et al. 2014).

Alternation rules

One possible line of investigation is to continue to look at finer scales of investment behaviour, ultimately asking how individuals organise their contributions by each quantum of care, such as a provisioning visit. By analogy to the iterated prisoner's dilemma we might expect optimal strategies analogous to 'tit-for-tat' to give the most efficient outcome for both parents, by preventing exploitation while ensuring that 'nice' contributors gain the maximum possible payoff. Recent theoretical and empirical work suggests that a simple strategy of turn-

taking by parents can efficiently organise care for young, and provides empirical evidence that great tit parents adopt such a strategy during provisioning (Johnstone et al. 2014). Parents adopt a strategy of lowering their visit rate after they visit, and raising their visit rate after their partner visits: while this is not as efficient as perfect visit alternation, it still generates more efficient care than a sealed-bid or negotiation rule (Johnstone et al. 2014). Further empirical evidence for turn-taking is currently lacking, but other studies have shown that where there is scope for intra-group conflict over food allocation, coordination of provisioning visits can improve outcomes for offspring (Shen et al. 2010), supporting further analysis of nest visits on a finer scale.

Models of cooperative systems

Models that describe offspring care by more than two individuals are extremely rare when compared to those of biparental care, and what little work exists has been restricted to only three individuals: either a pair with a single helper (Johnstone 2011) or a female with one or two helpers (Härdling et al. 2003). Although *N*-player extensions to simple games suggest that two-player and many-player games of offspring care are likely to lead to similar results, attempts to generalise models of biparental care to cooperative care are hampered by two main problems. Firstly, adding additional carers affects some of the assumptions of models used to describe biparental systems, particularly those about the level of information available to carers. In a biparental system each carer only has to observe the investment level and responses of one individual, whereas in a group of six each must observe five others, and unless visit rate increases linearly with group size each individual will be contributing less often and hence be potentially harder to observe. Secondly, helpers can differ more than parents in their relatedness to offspring and in the benefits they receive from caring for young; for example, if a helper benefits directly from their contribution to care (e.g. by gaining experience feeding chicks that improves their future direct fitness), they may have little reason to respond to the contributions of others as they are largely unconcerned with the number and fitness of offspring that are produced. Helper investment might be further complicated by preferring to rear one sex of offspring, if their benefits accrue primarily from group augmentation (Kokko et al. 2001) through the phylopatric sex; by contrast parents will normally always benefit from successfully rearing their descendants of either sex.

Summary

Understanding how individuals invest in offspring is fundamentally tied to how the payoffs of different strategies are influenced by the investment of others. Existing models of biparental care provide mostly consistent predictions for individual response rules to changes in partner effort, and these predictions are largely borne out by empirical studies. The prisoner's dilemma-like nature of contributing to care means that carer investment behaviour is not generally Pareto efficient, as both carers would increase their payoffs if both increased their investment levels, however neither is able to do so because of the threat of exploitation by their partner. Models of care that allow response rules such as turn-taking require further attention as a possible solution to this problem, as do models that incorporate multiple, potentially asymmetric stages across a breeding attempt. Two major topics have been understudied as potential influences on investment behaviour during offspring care: cooperative breeding, particularly in how non-parents should invest in contrast to parents, and maternal effects, as the majority of models have been restricted to a single investment stage.

Cooperative breeding in birds

Cooperative breeding occurs whenever more than two individuals contribute to offspring care (Cockburn 2004). This definition covers a broad range of breeding systems, including both species where all carers breed and those with true helpers (non-breeding individuals assisting a breeding pair). The presence of non-breeding carers can be used to draw a distinction between true cooperative care (Ligon & Burt 2004) and other, superficially similar systems such as cooperative polyandry (where multiple males mate with a female and assist her with offspring care) or cases where multiple pairs raise offspring together within a social group, sharing care between them. The core question in cooperative systems with non-breeding helpers is why helpers choose to forego their own reproduction to assist others, a behaviour that initially appears to run contrary to natural selection. It may be no coincidence that the first paper that drew significant attention to ‘helpers at the nest’ was a review (Skutch 1961) published shortly before the first work on kin selection suggested a mechanism for this apparently maladaptive behaviour to be beneficial (Hamilton 1964; Maynard Smith 1964). More recently, detailed explorations of the benefits and costs of cooperation have been of considerable interest to behavioural ecology as a whole, with many studies exploring the particulars of why, when and where cooperative breeding occurs.

Although all cooperative systems involve multiple individuals rearing offspring, there is great variation between species in mating system, the identities of helpers, the benefits helpers receive, the social environment, and the prevalence and intensity of cooperative care. Pairs may be monogamous (for life or sequentially), or they may be polyandrous, polygynous, or polygynandrous within or outside the social group (Cockburn 2004). Helpers may be relatives that have failed in their own breeding attempt, or they may be philopatric offspring, or subordinate breeders, or unrelated immigrants to the group (Riehl 2013). The benefits of helping may accrue by indirect fitness through relatives surviving and reproducing, or there may be direct benefits arising from experience, prestige, or group augmentation (Bergmüller et al. 2007), and when individuals in a breeding group do not benefit from caring for offspring, they may refrain from helping entirely (Emlen & Wrege 1989; Sherman 1995; Sloane 1996; Magrath & Whittingham 1997; Cockburn 1998). Most species are facultative cooperative breeders, in that pairs are capable of rearing at least some offspring successfully without helpers being present, but in others such as the white-winged chough (*Corcorax*

melanorhamphos, Heinsohn 1992), and apostlebird (*Struthidea cinerea*, Woxvold & Magrath 2005), unhelped nests universally fail. In other species (e.g. Noisy and Bell Miners; *Manorina melanocephala*, *M. melanophrys*), nests always have more than two attendants due to shared help across a large social group: these species are obligate cooperative breeders in practice, but it remains unclear whether they could rear offspring as a pair if necessary (Clarke 1988; Dow & Whitmore 1990).

Prevalence and systematics

Breeding systems involving more than a single pair rearing young have been recognised in some bird species for over a hundred years (Boland & Cockburn 2002), however this behaviour was often interpreted as multiple females laying in the same nest (e.g. North 1904). The first depiction of more than two carers attending a nest is most likely an illustration from Gould's *Birds of Australia* (1841) showing two male superb fairy-wrens simultaneously feeding a cuckoo chick. It is unsurprising that it was Australian cooperative species that were first recognised as such, as that continent contains a very high proportion of cooperative birds (Brown 1987; Russell 1989; Cockburn 2006); the relative rarity of cooperative breeding in the more populated regions of Europe and North America no doubt slowed recognition of the prevalence of the behaviour among birds as a whole.

Current estimates for the proportion of bird species exhibiting cooperative breeding are around 9% (Cockburn 2006), depending on the precise definition used: some authors count any species where a certain proportion of nests have more than two attendees (Cockburn 2006), while others attempt a definition based on non-breeding helpers (Brown 1987; Ligon & Burt 2004). Although almost all bird species worldwide are now described, outside of Europe and North America the breeding systems and life histories of many species are relatively unstudied, and many cooperative species not currently recognised as such may still exist in clades such as parrots (Psittaciformes) whose social behaviours in the wild are still poorly known. Furthermore, even well-studied pair breeding species may have unstudied populations that exhibit regular cooperative care, as in carrion crows (*Corvus corone*, Baglione et al. 2002) and house sparrows (*Passer domesticus*, Sappington 1977).

Cooperative breeding is unevenly distributed among avian lineages, suggesting a large phylogenetic component to the behaviour (Edwards & Naeem 1993; Cockburn 1998, 2006). Cooperation is more common among passerine birds than non-passerines, but varies greatly in prevalence within both groups. Certain passerine families contain only cooperative species (e.g. Maluridae, Pomatostomidae), some a range of pair-breeding and cooperative systems in fairly equal proportions (Corvidae, Aegithalidae), and some have no confirmed cooperative breeders at all (Hirundinidae, Alaudidae). Outside Passeriformes, several orders contain no cooperative breeders, including Columbiformes, Suliformes, and (until relatively recently) Psittaciformes (Cockburn 2006). Several authors have concluded that cooperative breeding is ancestral to the passerine clade, which is thought to have radiated from Gondwanaland (Ekman & Ericson 2006), and hence the high proportion of cooperative species in Australia is due to its history as the cradle of early passerine radiation. Despite its clear phylogenetic component, cooperative breeding has evolved numerous times independently within some lineages (e.g. Rallidae, Timaliidae, Meliphagidae), suggesting that it can also be an adaptive response to particular ecological conditions (Cockburn 2006).

The ecological, demographic and life-history traits that lead to cooperative breeding remain unclear, not least because all contributing factors thus identified are also shared by many pair-breeding species (Koenig & Dickinson 2004). Life-history traits such as high adult survival and a sedentary population are thought to bias species towards cooperative breeding (Arnold & Owens 1998), and of course some degree of parental care must exist for multiple individuals to contribute. In terms of ecology, diet has been suggested as a contributing factor due to the rarity of seed-eating and frugivorous cooperative breeders, and the observation that most cooperative species forage from the substrate (Ford et al. 1988); helpers that reduce offspring starvation will contribute more effectively when individual variance in food delivery is high. Alternatively, if offspring rarely starve but do benefit from active defences against potential predators (rather than passive crypsis), cooperation might increase breeding success through reducing predation risk (Rabenold 1984; McGowan & Woolfenden 1989; Innes & Johnston 1996; Hatchwell 1999). In general, ecological volatility is thought to bias animals towards cooperative breeding (Wells 2012), usually with the argument that the presence of helpers functions as a bet-hedging strategy to prevent total losses of offspring under harsh or unpredictable conditions (Rubenstein 2011). While recent analyses have suggested that the prevalence of cooperative breeding is partly explained by environmental uncertainty (Jetz & Rubenstein 2011), there still remains much potential variation to account

for (Cockburn & Russell 2011). In particular, the existence of cooperative species (and entirely cooperative clades) that have a broad habitat range throughout which cooperation persists indicates that ecological conditions cannot be the only important factor.

Benefits of helping

In a cooperative breeding system, the predicted investment behaviour of individuals is influenced by the relative values of the different options each has at the start of the breeding season. These options will generally include helping the dominant to rear offspring, dispersing to a new territory, floating (doing nothing), or competing for a breeding position, and the relative costs and benefits of each alternative will differ greatly between species (Ekman et al. 2004). In addition, environmental conditions vary in space and time, and may lead to different behaviours being favoured within a species across different populations or conditions. For tactical maternal investment to be successful in influencing helper investment, helpers must (i) have predictable responses to changes in offspring size or quality, and (ii) be sufficiently constrained from alternative beneficial behaviours that female manipulation is unlikely to make helpers abandon care. The decision of helpers to help is distinct from their decision to delay dispersal (Dickinson & Hatchwell 2004; Ekman et al. 2004), and helpers will refrain from contributing to offspring care unless by doing so they avoid some cost or receive a fitness benefit, whether it be current (within this breeding attempt) or future, and direct or indirect.

Kin selection

Helping may be a favourable alternative to breeding if it is directed towards individuals that share the helper's genetic material (Hamilton 1964; Maynard Smith 1964): helpers are expected to attempt to maximise their fitness, but personal reproduction is not the only way for an individual to increase the frequency of its genes in the population. Individuals are as closely related to full-siblings (on average) as they are to their own offspring, and so raising a full-sibling that would otherwise not have been raised delivers the same fitness benefit as raising an offspring of one's own. This indirect fitness may be preferable to attempting to breed directly if ecological constraints make founding a new group difficult (Emlen 1982), if

competition is strong and the individual is of low quality, or if the individual is young and has little breeding experience.

The condition for kin-directed helping is $r \cdot b - c > 0$ (Hamilton 1964), where b is the benefit to the recipient of help, c is the cost to the helper, and r the relatedness of the recipient to the helper (relative to the mean relatedness of individuals in the population). Helpers are hence most likely to assist close kin because a much smaller benefit is required to overcome any costs of helping a brood of full-sibs ($r = 0.5$) over half-sibs ($r = 0.25$), cousin-level relatives ($r = 0.125$) or unrelated birds ($r \approx 0$). Helping kin can be beneficial by increasing the number of offspring currently being raised, increasing offspring quality, or by reducing the costs paid by other, related carers, such that these relatives are more likely to survive and breed in future seasons (Dickinson & Hatchwell 2004). Helpers that reduce the costs to the breeding female by ‘lightening the load’ of offspring care (Crick 1992) benefit indirectly through the related offspring that she will produce in future years. However, one important caveat to kin-selected benefits is that helping to raise kin is less beneficial the greater the local competition in a system, as individuals are unlikely to benefit from rearing direct competitors for themselves or other existing kin (Murray & Gerrard 1984; West et al. 2002). As a consequence, the pattern of dispersal will influence how easily cooperation can evolve in a given species.

Breeding experience

The most obvious direct benefits of helping, beyond breeding personally, are those accruing straightforwardly from the act of helping itself, such as gaining experience of caring for offspring that can be applied to future direct breeding attempts (Selander 1964; Komdeur 1996). Helping in this manner is a by-product mutualism, provided that offspring are able to benefit from the additional care, and hence one should predict little within-group conflict over investment levels. Importantly, however, experience benefits are much less influenced by whether or not the breeding attempt is successful, which might lead to different predictions of helper investment behaviour in response to changing conditions or maternal tactics. Empirical evidence for the value of helping experience is available in some cooperative birds (Komdeur 1996; Hatchwell et al. 1999), although several negative results suggest that it is by no means a

universal effect (Dickinson et al. 1996; Khan & Walters 1997; Koenig & Walters 2011; Duval 2013).

Pay-to-stay

An alternative explanation is that offspring help in order to ‘pay rent’ or ‘pay-to-stay’ on the natal territory (Gaston 1978; Mulder & Langmore 1993; Kokko et al. 2002). When there are few positive effects of larger group size, and additional group members lead to competition for resources, delayed dispersers may be evicted by the breeding pair unless they convey a benefit to offset their associated costs. For pay-to-stay to be favourable to helpers, the dominant pair must be able to credibly threaten eviction, and staying in the natal territory must have positive effects on helper survival even after the costs of helping.

Group augmentation

Group augmentation benefits occur when rearing offspring has direct positive effects on a helper’s future fitness through improving the group’s survival, competitive, or reproductive ability (Brown 1987; Kokko et al. 2001). Under ‘passive’ group augmentation the presence of extra group members leads to better territories, better predator defence, or similar effects, however group augmentation can also be ‘active’: individuals may benefit from rearing more helpers despite no group size benefit, provided those helpers then contribute to the future breeding attempts of the donor (Wiley & Rabenold 1984; Kokko et al. 2001). As with indirect fitness benefits, the strength of group augmentation effects will depend on the difference between potential productivity with and without helpers, and group augmentation also shares with kin selection the need for a breeding attempt to be successful before any benefits can be reaped.

Social prestige

A final class of direct benefits to helping are those that revolve around accruing some form of ‘reputation’ that positively biases future interactions in the helper’s favour, often termed ‘social prestige’ or ‘image scoring’ depending on whether reciprocal investment is required to obtain the benefit (Zahavi 1995; Roberts 1998; Lotem et al. 2003; Bshary & Bergmüller

2008). Higher-prestige individuals may be more likely to attract mates or helpers when dispersing, and if helpers form a ‘queue’ for breeding status in the current group, social prestige is one way in which individual position within the queue might be determined. Prestige requires that care behaviour can function as a costly signal (Doutrelant & Covas 2007), and hence that it is observable and quantifiable by other group members. Evidence for social prestige remains scant, but explicit empirical tests have rarely been performed (McDonald et al. 2008; Nomano et al. 2013). A related benefit occurs if reputation acquired through helping can lead to direct reciprocity from the current breeders, for example if current breeders sometime become helpers at the nest of a bird that previously helped them (Ligon & Ligon 1978).

Summary

Inclusive fitness theory remains the primary explanation for cooperative care among close relatives (Abbot et al. 2011), and is important even in species with relatively low helper-offspring relatedness (e.g. $\bar{r} = 0.15$ in the long-tailed tit; *Aegithalos caudatus*, Nam et al. 2010) due to the complex relationships between individual effort, quality, future fitness, and survival probability. All direct benefits (apart from those constrained by inbreeding avoidance) are also available to related helpers, and so we should generally expect cooperation to be more common among kin than non-kin. Nevertheless, there are substantial other potential benefits that deserve attention. While it is indisputable that most cooperative species live in family groups, in a surprising number of cooperative species some or all helpers are unrelated to offspring (Riehl 2013), and in these direct benefits must exist to maintain cooperation. Fundamental differences in investment strategy will be determined by the conditions necessary to reap the benefit, not the fitness route through which it acts: both group augmentation and kin selection require offspring to be successfully reared, and hence may lead to similar strategies, while developing breeding experience is less contingent on outcomes for offspring.

The potential benefits of helping are fundamentally tied to the potential productivity and reproductive tactics of the breeding female, among other factors. If mothers can reliably raise a brood without help, and are unable to alter brood size or quality in response to the presence of helpers, direct benefits contingent on producing offspring are weak, and indirect fitness

benefits are limited to increasing maternal survival (where possible). When helpers can reduce costs paid by other carers, but brood size and quality are fixed, the benefits of helping will be high initially but decrease per helper as more helpers join the group, leading to each helper contributing only small indirect benefits. In this case we can envisage a helper choosing to help at a nest of (for example) a more distant relative because the group size allows for a greater fitness benefits. By contrast, if the mother is able to produce offspring of the number and quality optimal for the number of helpers in the group, helper benefits will remain high over a large range of group sizes. Both scenarios are likely to exist in practice (both across and within natural populations), as optimal offspring production will always be subject to the limits of fecundity of the breeder.

Offspring care in cooperative breeders

The developmental periods of many cooperative species are long, providing many opportunities for carers to invest in offspring care in multiple independent ways. Each mode of care will yield different costs and benefits to carers and offspring, different opportunities for cheating and enforcement, and different asymmetries between carers. As a result, different care behaviours may represent different fundamental cooperative games, and hence have different outcomes when conflict occurs between group members. In this section I briefly review the main types of offspring care observed in cooperative species, and the respective costs and benefits each confers.

Provisioning

A major component of reproductive investment in many species takes the form of effort expended on finding and delivering food to dependent young. This provisioning behaviour is generally required continuously until offspring become mobile (fledging age in birds), and may persist for several months afterwards as juveniles develop foraging skills. The costs of provisioning to parents have been well documented in a multitude of taxa and breeding systems (Canestrari et al. 2007; Field et al. 2007; Guindre-Parker et al. 2013), although the relationship between parental effort and survival is not entirely straightforward (Santos & Nakagawa 2012). As one might expect from the high costs that breeding females pay to

produce offspring (often also incubating alone), when only one individual enjoys reduced costs in larger group sizes, that individual is generally the breeding female (Anava et al. 2001; Browning et al. 2012b).

Because provisioning behaviour is common, near continuous, and relatively easy to observe, it has been the focus of almost all empirical studies on cooperative investment. However, despite empirical support for incomplete compensation in biparental species (Harrison et al. 2009), cooperative species fail to show consistent responses to changes in helper number. Some species compensate entirely for the presence of extra carers (Brown et al. 1978; Luck 2001), others show the expected partial compensation (Woolfenden & Fitzpatrick 1990; Wright & Dingemanse 1999), while in some no change in individual investment occurs (Mumme & Koenig 1990; Emlen & Wrege 1991). One study even reports an increase in individual investment with more carers (Valencia et al. 2006). In some species unrelated males are more likely to provision offspring, because of opportunities for mating (Magrath & Whittingham 1997), however in others there is a positive effect of helper relatedness on provisioning rate, presumably due to indirect fitness benefits (Wright et al. 2010; Browning et al. 2012a).

Although provisioning is the most common and most quantifiable form of helping, it is not necessarily the most important contribution helpers can make to offspring fitness. In scrub jays, helpers are actively prevented from provisioning nestlings, but contribute strongly to both predator mobbing and territorial defence (Burt & Peterson 1993), and in grey jays helpers only feed fledglings (Waite & Strickland 1997). In species that suffer from nest predation, but where offspring starvation is rare, parents may benefit instead from limiting the number of individuals around the nest and limiting or synchronising visits to the nest in order to reduce the likelihood of attracting predator attention (Skutch 1949; Martin et al. 2000; Raihani et al. 2010).

Predator mobbing

Another common form of parental care is mobbing of potential predators (Curio et al. 1978), and empirical studies suggest that a common cause of increased reproductive success in cooperative groups is a reduction in predation risk to offspring (Hatchwell 1999). Mobbing predators is costly due to losses of foraging time in addition to potential dangers from the

predator, however the benefits are substantial if offspring would otherwise be predated (Montgomerie & Weatherhead 1988). Collective action by many individuals is the most effective means of mobbing (Krams et al. 2009), but given the costs incurred by individuals for a shared benefit, mobbing potentially represents a public-goods type problem in which individuals are tempted to hang back, reducing overall effectiveness.

Mobbing has been studied explicitly in some cooperative species (Arnold 1999; Maklakov 2002; Graw & Manser 2007), but since it is difficult to make quantitative assessments of individual contributions to the same degree as with provisioning, and because natural mobbing is generally infrequent in comparison to offspring feeding, studies of individual contributions to mobbing remain rare. Further complications arise in attempting to measure the costs and benefit of mobbing when predators are dangerous to both adults and offspring, because mobbing may then confer immediate direct benefits on an individual by lowering personal predation risk: in these cases mobbing is by-product mutualism and hence requires no indirect or deferred benefits to explain its prevalence (Russell & Wright 2009). In addition, prolonged mobbing may actually be harmful to offspring, if it attracts more predators to the vicinity of the nest (Krams et al. 2007).

Sentinel behaviour

While group defence and vigilance are contributions to group-living rather than specific care behaviours, young offspring are considerably more vulnerable and less experienced than adults, and hence their presence may lead to additional investment by other group members. Sentinel behaviour has been well-studied in Arabian Babblers (Wright et al. 2001a, 2001b) and Florida Scrub Jays (McGowan & Woolfenden 1989; Bednekoff & Woolfenden 2003) among other species, and similarly to mobbing has been interpreted as a by-product mutualism (soldier's dilemma) rather than helping for indirect or deferred direct benefits (Bednekoff 1997, 2001). However, sentinel behaviour might also represent a stable form of costly offspring care, particularly if a single sentinel can provide benefits to a large number of relatives (or valuable group members) simultaneously (Archetti 2011; Raihani & Bshary 2011).

Classification of avian cooperative systems

Cooperative breeding is a highly variable breeding system that defies attempts at hard classification (Cockburn 1998), however a simple overlapping categorisation based on helper identity and routes to fitness is useful when making predictions about helping behaviour and maternal strategies. One approach is to use dispersal to classify species into ‘avian-’, ‘mammalian-’ and ‘insect-’ type systems (Russell & Lummaa 2009), although major variation remains within each type. Another option is to use the potential benefits helpers receive from helping, and the degree to which they have outside options, as this will determine both the level of conflict between carers and the degree of asymmetry inherent in their investment tactics. When classifying cooperative behaviour in this way, I identify five primary types of cooperative care in birds (Table 1.2): Collaborative, Redirected, Developmental, Queuing, and Altruistic. Multiple types of helper may help simultaneously, and hence particular species may represent several of the four types of cooperation simultaneously.

In ‘Collaborative’ (or ‘joint-nesting’) cooperative systems, carers are all active breeders in the current breeding attempt (Vehrencamp & Quinn 2004). Among birds, the most common example of this system is cooperative polyandry (Cockburn 2006), where a single breeding female is attended by several males who share paternity of the offspring and all contribute to offspring care. Sometimes this behaviour will be driven by female attempts to elicit extra parental care, leading to dominant males attempting to monopolise reproduction (e.g. Davies 1985), but if a pair cannot reliably raise a large brood by themselves it may benefit breeders to collaborate in exchange for greater numbers of offspring or lower personal costs (Vehrencamp 1978). Conflict between males can be reduced if males are related, as less dominant individuals can then benefit from inclusive fitness despite low paternity (Vehrencamp & Quinn 2004). Polyandrous care can occur even with greater numbers of males than there are chicks, provided secondary males have a chance of fathering some offspring (or the mating group is stable over several seasons), however the reduction in relatedness to the brood with each extra male limits the potential group size (Hartley & Davies 1994). Joint-laying, when multiple females lay in the same nest, may be asymmetric (like cooperative polyandry) with a single male (Frith & Davies 1961), or symmetric with both multiple males and multiple females collaborating to rear offspring (Jamieson 1997; Vehrencamp & Quinn 2004; Yuan et al. 2004); in these cases group sizes are potentially larger as helpers face a weaker dilution problem. The number of females will however

influence patterns of care seen during the breeding attempt, as individual females no longer have total control over investment prior to chick rearing and hence must adapt to the potential investment strategies of each other during offspring production as well as later care behaviour.

In ‘Redirected’ cooperation, helpers are failed breeders from the current season who have insufficient time or resources to breed again. These helpers typically help relatives who still have active nests, in order to boost their indirect fitness by increasing the number or condition of offspring fledged, or to ‘load lighten’ (Crick 1992) the costs of breeding for related carers (who are then more likely to survive and breed again). Redirected care requires that (i) individuals breed close enough to relatives that they can feasibly find them to begin helping, and (ii) that the benefits of group-living and helping are sufficiently low that helping before your own attempt fails is unfavourable. Compared to most other forms of cooperation, the scope for maternal tactics is limited in Redirected cooperation systems, as helpers will generally only arrive partway through the breeding attempt, and their presence is highly unpredictable. The best-studied examples of this care system are probably the long-tailed tit (*Aegithalos caudatus*, Russell & Hatchwell 2001; Hatchwell et al. 2013) and white-fronted bee-eater (*Merops bullockoides*, Emlen 1990).

In ‘Developmental’ cooperative species helpers are juvenile offspring who contribute to care prior to dispersing (Gibbons 1987). Helping to raise a new brood may benefit juveniles through indirect fitness or through the development of skills for future breeding (Selander 1964; Komdeur 1996; Sparkman et al. 2010) with few associated costs if juveniles do not yet benefit from dispersing. Eventual dispersal by the helper may happen once sexual and skill maturity are reached, or may be delayed (Ekman et al. 2004) to facilitate helping at more breeding attempts: individuals may delay dispersal because they are unable to survive or successfully breed when young, either because of low competitiveness or because adverse environmental conditions make attempting to breed unfavourable (Emlen 1982; Hatchwell & Komdeur 2000). Helper effects will be generally low in ‘developmental’ systems, as juveniles will rarely provide much care compared to experienced breeders, and neither the helper nor the parents want the helper to incur high costs before dispersing. If juveniles must be retained for an extended period to avoid high mortality, their presence may even be costly to parents (Pravosudova & Grubb 2000); in this case offspring retention can be thought of as the final stage of parental care (Ekman et al. 1994, 2004; Strickland & Waite 2001; Doerr et al. 2007). Where there are costs to retaining offspring until they can disperse successfully, helping

behaviour might be enforced by parents as ‘rent’; the offspring thus ‘pay to stay’ (Gaston 1978; Mulder & Langmore 1993; Kokko et al. 2002). The relative costs and benefits of dispersal and helping (to all carers) will combine to explain why offspring choose to (i) remain on the natal territory rather than developing elsewhere, and (ii) why they choose to help rather than simply waiting (Ekman et al. 2004).

Cooperative ‘Queuing’ systems are diverse and the best studied, representing all cases where non-breeding helpers in a persistent social group eventually succeed the current breeding pair to breed directly. Helpers are generally offspring that are philopatric indefinitely, and who help to gain either indirect fitness or direct benefits from additional breeding experience, social prestige (Zahavi 1995), group augmentation effects (Kokko et al. 2001), or ‘delayed reciprocity’ from offspring they raise (Wiley & Rabenold 1984). The mating system, individual quality, and how likely helpers are to inherit breeding status will influence whether indirect or future direct fitness benefits are dominant for particular helpers. Unrelated immigrants may also become helpers in these systems, gaining fitness through the same future direct benefits. In contrast to ‘developmental’ cooperative systems, related helpers are more likely to ‘pay-to-stay’ (Gaston 1978; Kokko & Ekman 2002) under queuing systems as helpers are both more capable of contributing, and in greater conflict with their parents who they are waiting for an opportunity to replace (Cant & Johnstone 2008).

The final type, ‘Altruistic’ cooperation, represents cases where helpers do not attempt to breed personally, and contribute to care despite little opportunity for future direct fitness. Altruistic cooperation requires helpers to be relatives, as they must gain their entire fitness indirectly through helping kin. Because indirect fitness benefits are greatest when rearing full siblings, one should expect young helpers in Altruistic systems to adopt costly helping behaviours immediately (before either member of the breeding pair changes) and hence to survive at a lower rate than breeders (e.g. Heinsohn & Cockburn 1994). This form of cooperation represents the boundary between cooperative breeding and eusociality, as the two social systems are generally divided by the presence or absence of non-reproductive castes (Crespi & Yanega 1995). The ability of a breeding female to create such helpers to improve her own lifetime productivity is a potentially important factor in the evolution of cooperation (Russell & Lummaa 2009).

Social organisation is likewise highly variable among cooperative breeders, and has the potential to influence helping decisions through the availability of outside options (Cant & Johnstone 2009). Multiple females breeding within a larger social group may lay eggs either within the same nest, in the same restricted area such as a tree or complex nest, or in separate locations some distance apart while retaining high social connectivity. When breeding units are isolated within a breeding season, they may nevertheless associate with a social group when not breeding, and this group may influence cooperation by collective decisions on when to begin breeding, or by forming the pool from which helpers are drawn. However the appropriate terminology for describing these systems is unclear, as commonly used terms (e.g. ‘colonial’ and ‘plural’) are conflated with those used to describe non-cooperative sociality, or those describing mating systems. A more rigorous and comprehensive classification system is

Cooperative system	Primary helpers	Benefits of helping	Potential for adaptive maternal tactics
Collaborative	Active breeders	Current direct fitness	Medium (one female) Low (multiple females)
Redirected	Failed breeders	Indirect fitness	Low
Developmental	Juvenile offspring	Indirect fitness Experience Pay-to-stay	Medium
Queuing	Philopatric offspring Immigrants	Indirect fitness Experience Social prestige Group augmentation	Medium
Altruistic	Philopatric offspring	Indirect fitness	High

Table 1.2: Forms of cooperation observed in birds with more than two carers at a nest. Categories are defined by the usual origin of the additional carers, and by the routes to fitness that make helping beneficial to these helpers. The potential for adaptive maternal tactics in cooperative species arises from three key factors: (i) The existence and relative value of alternative options available for helpers to gain fitness, (ii) The predictability of later care when the mother invests in offspring production, and (iii) The willingness of females to exploit helpers, influenced by helper-mother relatedness and any direct benefits of group size. For example, when helpers have other options, carer number is unpredictable, and helpers are relatives of the breeding pair (as in most ‘Redirected’ systems), exploiting helpers by altering offspring size or numbers is both difficult and potentially costly.

needed for cooperative breeders, in terms of both social and breeding organisation.

Many natural systems contain multiple helper types or social organisations and so exhibit several of the above forms of cooperation simultaneously, for example if either or both sexes exhibited ‘Developmental’ cooperation prior to dispersal and then another form of helping in their destination group. Nevertheless, in cooperative breeders the most significant differences in payoff between collaborators come about because of the differences in costs and benefits between carers, which will largely be determined by who helpers are and why they are helping. The final piece of the puzzle of how individuals should invest during cooperative care is the level of asymmetry between carers in the cooperative group, which arises through the alternative options available to helpers (Cant & Johnstone 2009), and the level of control the breeding female(s) have over early investment behaviour (Russell & Lummaa 2009). Maternal tactics can be exercised through control of offspring size and number, limited by the mother’s confidence in the future care paradigm, but the success of such tactics relies on her decisions having lasting effects on the fitness of other members of her cooperative group (Table 1.2).

Maternal effects and cooperation

Maternal effects occur when an individual's phenotype is causally influenced by the phenotype or genotype of its mother, such that evolutionary changes in the distribution of maternal traits will lead to corresponding changes in offspring traits through the causal linkage (Wolf & Wade 2009). Maternal effects may be straightforward by-products of maternal condition and physiology ('passive' effects), but can also take the form of adaptive maternal tactics to adjust offspring phenotype ('active' effects) (Badyaev 2005), and hence may influence how particular traits evolve (Bernardo 1996). In species with parental care, the scope of potential maternal effects broadens to include environmental effects during the dependent period that are mediated by the mother (Mousseau & Fox 1998a), and (while not strictly a maternal effect) strategies of mate choice by mothers will also influence offspring through genetic or environmental influences from the father. Similarly, in cooperative species in which the breeding female recruits helpers or influences their contributions to care, the entire rearing environment is mediated by the female and hence represents a maternal effect. Mothers will attempt to maximise their fitness by producing offspring of the phenotype or range of phenotypes that delivers the highest fitness to them, given the current conditions (Mousseau & Fox 1998b; Crean & Marshall 2009), and this may variously be achieved through maximising offspring fitness ('anticipatory maternal effects') or maximising maternal ability to produce further offspring while reducing individual offspring fitness ('selfish maternal effects') (Marshall & Uller 2007). Adaptive maternal strategies are expected to be most common when there is a strong relationship between strategy and fitness, when there is mother-offspring conflict in allocation decisions, and when environmental variability is high, predictable, and significantly influences the viability of alternative maternal strategies (Russell & Lummaa 2009; Hoyle & Ezard 2012).

Maternal decisions when adjusting offspring size, number or other maternally-controlled parameters are complex and variable. Changes in one reproductive parameter may influence others, as in simple size-number trade-offs affecting all offspring in a given brood (Stearns 1992; Roff 2002), potentially restricting maternal strategies. Offspring traits can be adjusted in unison, in anticipation of particular conditions, or applied differently across a single brood as a bet-hedging strategy when conditions are uncertain (Marshall & Uller 2007; Crean & Marshall 2009). In species that breed more than once, mothers must also choose what level of

resources to invest in a given bout of reproduction (Sockman et al. 2006), a decision which may be based on partner quality (Cunningham & Russell 2000) or current environmental conditions, and ‘good conditions’ of different forms may potentially lead to either reductions or increases in total investment depending on the specific costs and benefits involved (Russell & Lummaa 2009; Harris & Uller 2009).

In birds, offspring are produced by the female as eggs, which creates several different potential routes through which maternal effects can manifest. Before hatching, opportunities for mothers to adjust offspring phenotype include choosing the timing of breeding, the choice of nesting site (and quality of nest), and the pattern of incubation for eggs (Price 1998), in addition to the choice of offspring size, number, and potentially sex (Komdeur 2004). Overall energetic investment in eggs is variable (Williams 1994; Christians 2002), and differential allocation of hormones (Groothuis et al. 2005), maternal antibodies (Smith et al. 1994), antioxidants (Royle et al. 2001), or nutrients such as carotenoids (Cucco et al. 2007) to the eggs provide further mechanisms for adjusting offspring phenotype that are wholly controlled by the mother. Mothers can potentially influence offspring competition by adjusting laying order, as this often imposes a gradient of the above nutrients on the eggs (Badyaev et al. 2008), and this may influence sex determination (Rutkowska & Badyaev 2008). After egg production, females are usually primarily responsible for care during the incubation period, and when they begin incubation will also largely determine size variation within a given brood and influence offspring survival (Magrath 1990; Amundsen & Slagsvold 1998). After hatching, effects of other carers also become important as all can adjust offspring environment by altering the level of care they provide, however these adjustments are fundamentally reactionary to the initial investment chosen by the female.

Stages of investment

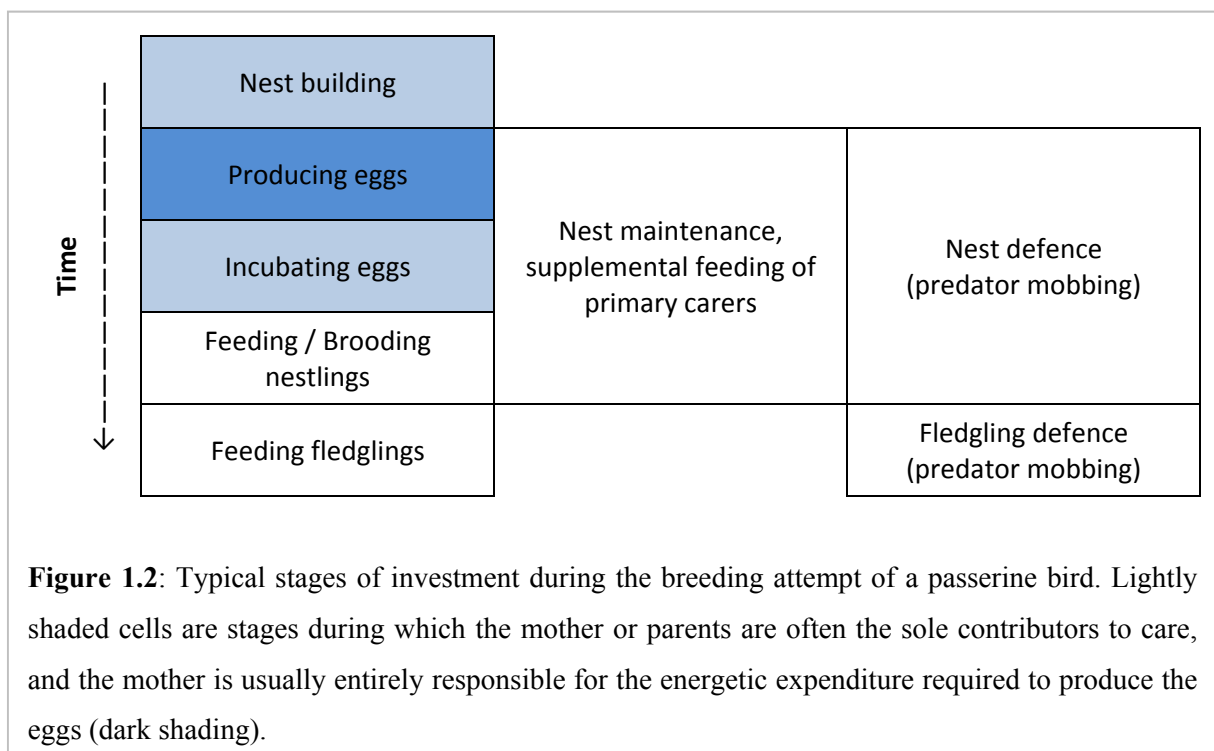
When choosing how to invest in offspring, breeding females face a trade-off between three fundamental factors: (a) How much to invest in each offspring, (b) how many offspring to produce; and (c) the level of resources to retain to improve the prospects for personal survival and future reproduction (Lack 1947; Smith & Fretwell 1974; Stearns 1992), and the decision of how much to invest in each offspring is not a single value but one that must be split appropriately between investment stages (Heaney & Monaghan 1995; Monaghan et al. 1998).

In most animals that cooperate to raise offspring, mothers must contribute investment across more stages than other carers, leading to high personal costs of reproduction when compared to other carers. Costs borne uniquely by the mother include, but are not limited to:

- Direct energetic and nutritional costs of producing eggs (Visser & Lessells 2001) or young (Clutton-Brock 1991; Schultz et al. 2008)
- Impaired agility during pregnancy (Webb 2004) or prior to egg laying (Kullberg et al. 2005).
- Energetic costs of feeding young when they rely on milk or other resources only she can provide (Lochmiller et al. 1982; Kurta et al. 1989)

In addition, costs that the female will often be exposed to more significantly than other carers include:

- Vulnerability to predation through repeated visits to, or time spent at, a static nest/den (Björklund 1990; Magnhagen 1991)
- Loss of potential foraging time spent incubating / brooding young (Visser & Lessells 2001)
- Risk of attracting predators when signalling for a mate (when compared to helpers, or in species where males do not signal) (Cushing 1985)



If investment at a particular stage is completely or primarily delivered by a single individual, that individual will pay higher costs than other carers during that stage, but can also unilaterally alter the investment delivered to offspring, and hence influence the investment behaviour of all contributors during all later stages. Consequently we would expect mothers to have considerable control over reproduction in species with parental care, and hence maternal strategies to be an important influence on investment decisions.

Birds represent an ideal model system for investigating the effects of multi-stage investment during care, as they have multiple clearly defined stages within their breeding attempts (Monaghan & Nager 1997), and often several concurrent investment behaviours within each stage (Fig 1.3). Birds also vary widely in their allocation of resources to eggs, from Procellariiformes and kiwis that produce a single egg of ~20% of maternal mass (Rahn et al. 1975; Calder et al. 1978), and tits (Paridae) where the total clutch mass can exceed maternal body mass (Robinson 2005), to cuckoos which lay eggs that are typically below 5% of maternal mass (Rahn et al. 1975). Even within species, eggs investment can vary considerably: in song sparrows, some eggs can be 70% larger than others (Arcese & Smith 1988). The incubation period, a stage not found in most mammals, can also alter in duration within species (Ricklefs & Smeraski 1983), and parental care behaviour ranges from Megapodes providing only indirect incubation to offspring after laying (Jones & Birks 1992), to obligate cooperative species with an average of ten helpers per nest (Grimes 1980). Cooperative breeding provides further scope for maternal effects, as within-species variation in care is high, and offspring are often retained in the group to help their mother raise the following brood of offspring.

Consequences of early-life investment

Two final considerations in parental care over multiple stages are that (i) investment may be more valuable to offspring at different points during the breeding season, and that (ii) the future reproductive success or development of offspring traits may be constrained by conditions encountered early in life (Lindström 1999; Lummaa & Clutton-Brock 2002; Royle et al. 2005). When compensating for low levels of early investment is difficult, it follows that the relative value of investing in offspring at later stages may be determined by how much was invested previously (Cunha & Heckman 2007). In contrast, if compensatory investment

can raise offspring of poor condition to the same size or attractiveness as those that received greater early investment (e.g. Walling et al. 2007), a straightforward trade-off emerges between investment at different stages. Which condition applies will strongly affect how maternal tactics are likely to operate with respect to changing environments or numbers of helpers.

The influences of differential maternal allocation and parental care on offspring structural traits are highly variable in birds (Price 1998). Maternal effects on offspring size are often visible in the first few days after hatching, when they may be crucial to survival (Price & Grant 1985; Williams 1994). The amount of parental care received sometimes has little effect on adult skeletal traits when estimated from diet or cross-fostering experiments in birds (Smith & Dhondt 1980; Dhondt 1982; Wiggins 1989; Smith 1993; Criscuolo et al. 2011); while in other cases a significant relationship is detected (Boag 1987; De Kogel & Prijs 1996; Tschirren et al. 2009). In general, the ability of carers to compensate for variable egg investment is likely to be contingent on good (or at least reasonable) conditions during rearing, as many species show declines in structural traits through a breeding season as conditions worsen and parental care reduces (Price 1991). Early life experience can also reduce the condition of migrating birds (assessed through fat levels) (Merilä & Svensson 1997), and zebra finches reared on a poor diet have low adult flight speed despite attaining the same size as those raised on a good diet (Criscuolo et al. 2011).

Reproductive traits are also subject to early-life conditions. In pied flycatchers, poor condition while still in the nest has lifelong consequences for the egg size that offspring produce (Potti 1999), and both zebra finches and great tits have reduced adult clutch sizes when reared in poor conditions (Haywood & Perrins 1992). Furthermore, when male secondary sexual traits are influenced by nestling conditions (Gustafsson et al. 1995; De Kogel & Prijs 1996), early conditions can have pervasive impacts on offspring reproductive success through both the ability to attract a mate and their mate's allocation to offspring sired by them. In summary, early life conditions and maternal strategies during them have potentially enormous effects on the fate of offspring, and are likely to be particularly important in cooperative species due to high variation in parental care and multiple potential routes to fitness, which may be condition-dependent.

Maternal effects in cooperatively breeding birds

Maternal effects are of great potential great importance in cooperatively breeding species, as high variation occurs in the prevalence, intensity, and utility of helping both within and between species, and this variation strongly influences both maternal and offspring routes to fitness (Russell & Lummaa 2009). In addition to the usual maternal effects during offspring development, helpers in many cooperative species are philopatric offspring from previous breeding attempts, and hence maternal interactions with them represent a further stage of potential influence (Russell & Lummaa 2009). Furthermore, the ability of mothers to influence dispersive and competitive tendencies of offspring (Marshall & Uller 2007; Groothuis & Schwabl 2008) raises the possibility for selfish maternal strategies to produce offspring in poor condition specifically to become helpers rather than breeders, and hence increase future maternal fitness. However the viability of this strategy will depend on the relationship between offspring condition and potential helping contribution, in addition to the predictability of female tenure as a dominant breeder (Russell & Lummaa 2009).

What maternal strategies should we expect in cooperative species? Firstly, if maternal-restricted costs (such as egg production) are low and all-carer costs (such as provisioning) are high, then many carers will be able to contribute effectively to the breeding attempt: even if offspring size and number are fixed, the investment from helpers will still ‘load-lighten’ (Crick 1992) the costs incurred by the breeding female. In contrast, if mothers must produce costly offspring and provide some of the following care themselves (e.g. solo incubation), and costs during provisioning are relatively low, then helpers cannot load-lighten maternal costs effectively and one might expect only small numbers of helpers to be beneficial (in the absence of direct benefits to helping). As a result, one should expect species with helpers to shift the point at which helpers can meaningfully contribute to as early in the breeding attempt as possible; either through producing offspring that are more altricial (i.e. offspring that require less initial investment and more rearing investment), or by greater involvement of helpers in earlier investment stages such as incubation. One reason why biparental care and cooperative breeding systems are more common in birds (Cockburn 2006) than in mammals (Lukas & Clutton-Brock 2012) may be the existence of the egg stage, which facilitates investment by carers other than the mother over a greater proportion of the total developmental period.

Secondly, in stable cooperative groups we should expect maternal tactics related to dispersal dynamics and breeding tenure. Under harsh conditions or when group size is below the optimum (Russell & Lummaa 2009) one might expect greater production of the sex more likely to help (Pen & Weissing 2000), and although adaptive sex allocation is generally weak (West & Sheldon 2002), evidence suggests that it does occur in cooperative breeders (Griffin et al. 2005). Likewise, below-optimum group sizes or poor conditions might result in a selfish strategy of mothers lowering investment in offspring quality to encourage them to stay and help, while under optimum group sizes mothers are more likely to adopt anticipatory strategies to maximise offspring fitness (Russell & Lummaa 2009). When dispersal is male-biased, such that mothers will potentially compete with their own offspring for breeding positions, one might expect a mixed strategy depending on tenure length and predictability, perhaps with mothers initially producing helpers to avoid competition, followed later by high-quality female offspring to inherit the breeding position. Under female-biased dispersal mothers are left with only relatives as potential mates when the breeding male dies, and hence breeding tenures are shorter as mothers typically leave or are evicted from the group upon partner death (Hannon et al. 1985; Hatchwell et al. 2000). When not rearing competitors it is likely that unselfishly producing competitive, dispersive female offspring is a good strategy, although large numbers of poor dispersers might be beneficial in an unsaturated population.

The evidence for adaptive maternal tactics in relation to group size is now substantial. Among birds, superb fairy wrens (Russell et al. 2007, 2008), carrion crows (Canestrari et al. 2011), southern lapwings (Santos & Macedo 2011), and sociable weavers (Paquet et al. 2013), have all demonstrated lower egg investment in larger groups, an effect often fully compensated for by the helpers. Cooperative cichlids have shown a similar reduction in egg size in response to larger numbers of helpers (Taborsky et al. 2007). Beyond egg size, shorter inter-clutch intervals are a common benefit of receiving help (Dickinson & Hatchwell 2004), and increases in clutch size with increasing group size have been reported in several cooperative birds (e.g. Davies & Hatchwell 1992; Lloyd et al. 2009; Klauke et al. 2013). A related strategy occurs in smooth-billed anis, where joint-laying females lay more eggs in larger groups to bias the clutch towards their own eggs (Schmaltz et al. 2008), and in colonial breeders evidence suggests that females may alter offspring quality to prepare them for a competitive rearing environment (van Dijk et al. 2013). Evidence for facultative adjustment of offspring sex ratio is also abundant (Komdeur 2004; Griffin et al. 2005; Dubois et al. 2006), however similar support for female manipulation of offspring dispersive ability is weak,

except within insects (Mousseau & Dingle 1991). One example of both tactics occurs in western bluebirds, in which females produce dispersive, competitive males under poor conditions, and non-dispersive, passive males under good conditions by adjusting sex bias in laying order (Duckworth 2009), and also adjust the sex ratio of clutches according to helper presence (Dickinson 2004).

2: Maternal costs in offspring production affect investment rules in joint rearing

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Abstract

When multiple individuals contribute to rearing the same offspring, conflict is expected to occur over the relative amounts invested by each carer. Existing models of biparental care suggest that this conflict should be resolved by partially compensating for changes by co-investors, but this has yet to be explicitly modelled in cooperative breeders over a range of carer numbers. In addition, existing models of biparental and cooperative care ignore potential variation in both the relative costs of offspring production to mothers and in maternal allocation decisions. If mothers experience particularly high costs during offspring production, this might be expected to affect their investment strategies during later offspring care. Here we show using a game-theoretical model that a range of investment tactics can result depending on the number of carers and the relative costs to the mother of the different stages within the breeding attempt. Additional carers result in no change in investment by individuals when production costs are low, as mothers can take advantage of the greater potential investment by increasing offspring number; however this tactic ultimately results in a decrease in care delivered to each offspring. Conversely, when production costs prevent the mother from increasing offspring number, our model predicts that other individuals should partially compensate for additional carers and hence offspring should each receive a greater amount of care. Our results reinforce the importance of considering investment across all stages in a breeding attempt, and provide some explanatory power for the variation in investment rules observed across cooperative species.

Introduction

Whenever an animal invests in a reproductive attempt, the amount invested represents a trade-off between the benefits accrued to the current brood of offspring and the costs to the investor in terms of survival and future reproductive potential (Williams 1966b). In breeding systems where multiple individuals contribute jointly to offspring care, carers additionally should benefit when the other(s) contribute a greater share of the total investment (Trivers 1972). In such systems, the lifetime fitness consequences for each individual investing in a breeding attempt will depend significantly on the amount invested, with the optimum amount emerging as a function of the probability of success of the attempt, the individual's relatedness to the offspring, the possibilities of current and future direct fitness gains, and by the behaviour of the other partner(s) contributing to care. The predictability of this investment by others, their likely relative contributions, and the point during the breeding attempt at which they invest will all influence an individual's investment decisions. Without understanding these varied influences on investment behaviour, the causes and consequences of caring can easily be misinterpreted, and the adaptive benefit to individuals forming a social pair or group to raise offspring will remain obscured.

Joint contribution to offspring care can arise either through biparental care, where both parents contribute to raising offspring, or through cooperative care, where at least one parent and non-parent contribute. Biparental and cooperative care systems are fundamentally similar in that they divide offspring care between individuals that benefit from caring, but in cooperative systems both the number of carers and their average relatedness to each other are typically greater. In both systems the breeding female gains a potential tactical advantage in the conflict over care through her ability to choose offspring size and number, but also often pays a greater cost because she must invest in offspring before other carers. The extent to which she can capitalize on her advantage will depend in part on these personal costs, as well as on the number and predictability of additional carers available (Russell & Lummaa 2009). Despite many theoretical analyses of investment in offspring, little attention has been given to the effects on carer investment rules of maternal tactics prior to the joint rearing period, and likewise the possible effects of multiple and variable numbers of carers has remained relatively unexplored.

Most models of biparental systems (e.g. Houston & Davies 1985; McNamara et al. 1999) suggest that the conflict over care should be resolved by each parent investing less than if raising the brood of young alone, and by responding to changes in their partner's investment with incomplete (partial) compensation, such that a change in investment by one partner (or the presence/absence of a partner) leads to a change by the other of smaller magnitude and in the opposite direction (but see Jones et al. 2002; Johnstone & Hinde 2006). This prediction has received considerable empirical support (e.g. Bart & Tornes 1989; Raadik et al. 1990; Wright & Cuthill 1990; Whittingham et al. 1994; Markman et al. 1995; Royle et al. 2002; Hinde 2005; reviewed in Harrison et al. 2009), and recent theoretical work has shown that incomplete compensation should also stabilize negotiations involving three carers (Johnstone 2011). However, support for incomplete compensation in biparental care is by no means ubiquitous (Johnstone & Hinde 2006; Harrison et al. 2009), and empirical studies investigating the effect of additional carers on individual investment levels in cooperative systems have found an even wider range of carer investment strategies. These range from carers completely compensating for the additional helper, such that there is no net increase in investment by the group as a whole (Brown et al. 1978; Legge 2000), through the expected incomplete compensation (Hatchwell & Davies 1990; Wright 1998a) to no compensation, where individual investment remains steady (Mumme & Koenig 1990; Emlen & Wrege 1991), or even an increase in individual investment (Valencia et al. 2006). In addition, within a given species, individuals can show a range of response reactions depending on their status (breeder vs. non-breeder) and/or the number of other carers in the group (Hatchwell 1999; Clutton-Brock et al. 2004; Gilchrist & Russell 2007; Browning et al. 2012b). This variation in carer responses is poorly understood, but has been suggested to reflect variation in the probability of offspring starvation: where starvation is likely, partial or no compensation is expected so that additional helpers have some positive effect on brood provisioning frequency (Hatchwell 1999). Nevertheless, it is unclear why apparent evidence for both complete and no compensation is relatively common in cooperative breeders (Cockburn 1998; Heinsohn 2004) when theoretical work generally predicts incomplete compensation. One possibility is that complete compensation arises in conjunction with a non-zero relatedness value between carers, such that additional individuals can improve the survival of related carers after brood demand is satiated. Another possibility is that the level of compensation varies depending on the costs to the breeding female of producing offspring, providing she is able to predict the number of potential helpers and adjust offspring number accordingly (Russell et al. 2008). To

our knowledge, no previous model has explored the consequences of tactical investment in offspring production by mothers, or the consequences of having variable numbers of other carers on the optimal investment strategies for each individual during offspring rearing.

As with simpler single-stage models of offspring care, when considering the influence of production costs on investment behaviour one would expect the precise amounts invested to depend upon the relative costs and benefits of care (Chase 1980; Winkler 1987), and these in turn to depend upon the number of offspring in the brood (Smith & Härdling 2000). The integration of models of optimal clutch size with those of investment in care has been largely overlooked (but see Smith & Härdling 2000), primarily because existing work suggests that females should produce a size and number of offspring that maximizes their return per unit investment regardless of the total amount invested (Smith & Fretwell 1974; Winkler & Wallin 1987). However this conclusion is based on an analysis of the tactics of a single parent, and one cannot assume that investment in offspring production and in subsequent care will be independent if other individuals can also contribute. Different numbers of offspring will elicit different levels of investment from other carers, and hence the individual choosing offspring number can potentially 'manipulate' the investment levels of others. If a breeding female is assisted by one or more individuals in raising offspring, and can adjust the number of offspring she produces in response to the presence of these helpers (e.g. Russell et al. 2003; Woxvold 2005), one must consider the evolution of offspring number and individual investment together in a single model. Smith and Härdling (2000) demonstrate the importance of considering this joint evolution and show that it can affect the stability of the mating system, however they do not address the specific investment levels or strategies that are expected under different cost parameters or numbers of carers.

The need for further theoretical work on reproductive investment is supported by the lack of consistent empirical results showing incomplete compensation (particularly in studies on cooperative breeders), which suggest that some underlying assumptions of current models need to be re-evaluated. Primary amongst these is that female investment in offspring size and number is independent of the subsequent investment by all carers, particularly given the work already linking them (Smith & Härdling 2000). Breeding females occupy a unique position in many care systems, as they are often capable of altering initial offspring size and number, and the idea that females can tactically invest in offspring in response to the number of carers has support from empirical studies (e.g. Davies & Hatchwell 1992; Taborsky et al. 2007; Russell

et al. 2007; Santos & Macedo 2011; Canestrari et al. 2011). The breeding female also may pay a greater cost than other carers, as she invests time and energy producing and caring for young before other carers are able to invest. High costs to the breeding female at this initial production stage can have significant effects on her survival or later fecundity (Heaney & Monaghan 1995; Visser & Lessells 2001), leading to a trade-off for the female between the amount invested in the pre- and post-helper stages. While females are still expected to maximize their return per unit investment in offspring care, the number of helpers and relative costs of the two stages (pre- vs. post-birth/hatching) will affect how the female should optimally divide her investment. Any complete model of investment in offspring must consider both the number of carers and the relative costs of these different stages of investment to fully understand the trade-offs involved in breeding, in addition to resolving the familiar conflict between individuals over investment. The benefits different carers gain from raising the offspring are also critically important when considering investment in a cooperative system.

The model that we introduce is a game-theoretical model of investment with variable numbers of carers (2-12) and choice of offspring number by the breeding female. Investment is divided into two stages: in the first stage (offspring production) the female pays a cost to produce her chosen number of offspring, then in the second stage (offspring rearing), she and all other carers invest in offspring care. The relative costs of the two stages are modified to explore the consequences of breeding systems in which offspring production costs are dominant compared to those in which rearing costs are dominant, i.e. in which a greater or lesser proportion of the costs incurred by the breeding female fall before or after the point at which helpers are able to invest. The relative costs of investment between the female and other carers are also manipulated to determine their effects on investment. We evaluate our results in terms of the effects of helper number and timing of costs on the numbers of offspring produced, the individual investment rules of group members, and the amount of care delivered to each offspring.

The Model

Description

Our aim is to explore the outcome in terms of productivity, total investment per offspring, and response to additional carers when the female is able to alter the number of offspring based on the number of other carers (hereafter helpers) in the group. For simplicity we assume that the breeding male, if present, has a similar payoff function to the helpers (see discussion) and hence can be grouped with them in the model. Our model is a sequential game of two steps, similar to that developed by Smith and Hårdling (2000). The female first chooses the number of offspring n , with knowledge of the number of helpers in the group z , and pays a cost derived from the number of offspring produced. Following this all carers play a simultaneous game to determine their individual investment levels. The choice of level of investment in the second step is assumed to be simultaneous and independent by all individuals, a 'sealed-bid' interaction following Houston and Davies (1985), rather than a 'negotiation' in which carers repeatedly interact in behavioral time to reach a stable investment level (as in McNamara et al. 1999, 2003; Johnstone & Hinde 2006). In general sealed-bid and negotiation models generate qualitatively similar results: for analogous models the results from sealed-bid approaches are reproduced in negotiations where individuals are inflexible in their response to each other's bids (McNamara et al. 1999). In our model we used a sealed-bid rather than negotiation approach because this allowed us to obtain analytical solutions for all numbers of carers, however individuals are assumed to be able to adjust their investment bid in the second step in response to the size of the brood set in the first step.

We first calculate the response of a breeding female and z 'helpers', (including the breeding male, if present) to a given brood size n . Breeding females choose an amount x_f to invest, and simultaneously all helpers choose an amount, termed x_h^i for the i^{th} individual. The vector of other carer investment amounts is \mathbf{x}_h where $\mathbf{x}_h = (x_h^1, x_h^2, x_h^3, \dots, x_h^{z-1}, x_h^z)$. Investment in offspring influences their survival and future reproduction, and we assume all offspring benefit equally and regardless of the particular individuals contributing. The benefit b to the brood of offspring depends on n and the total investment all individuals provide x_{tot} , where $x_{tot} = x_f + \sum_{i=1}^z x_h^i$. We assume that there is some constant minimum level of investment per

offspring x_{min} below which individual offspring gain no benefit from being helped, such that the response of b to investment is a function of $x_{tot} / n - x_{min}$.

We include a constant k_b to scale benefit as appropriate with our cost functions. We assume that the first derivative of the benefit function (b') is positive, such that increasing investment leads to increasing benefit to the offspring, but that the second derivative (b'') is negative, such that increasing investment leads to diminishing returns. Given these assumptions, for illustrative purposes we use a quadratic function that yields analytical solutions:

$$b = k_b \cdot \left(\left(\frac{x_{tot}}{n} - x_{min} \right) - \left(\frac{x_{tot}}{n} - x_{min} \right)^2 \right)$$

Reproduction is costly (Williams 1966), as it requires the investment of resources such as time or effort that otherwise would have a positive effect on future fitness. The total cost to the female c_f depends on the number of offspring she produces n , and her investment in rearing the brood x_f as well as two constants: the relative cost of offspring production k_p (which acts on n), and the relative cost of offspring rearing k_r (which acts on x_f). The total cost to the female is calculated from the sum of the costs of the two steps, an approach supported by studies demonstrating a trade-off between investment in producing and rearing broods (e.g. Heaney and Monaghan 1995). We assume that for all individuals the first derivative of the cost function (c_p) is positive, such that increasing investment leads to increasing costs, and that the second derivative (c_p) is also positive, such that costs accelerate with greater investment. Similarly, for the i^{th} other carer the cost c_h^i depends on that individual's investment level x_h^i and the relative cost of offspring rearing (k_s to allow for differences from the female's rearing costs). Unlike the female's cost function it does not depend on n as the other carers do not produce offspring themselves. As before, for simplicity we choose a quadratic function for both cost functions:

$$c_f = k_p \cdot n^2 + k_r \cdot x_f^2$$

$$c_h^i = k_s \cdot (x_h^i)^2$$

Optimization of investment levels in a given brood requires trading off the benefit an individual receives from current reproduction against the costs from reducing survival probably or future reproductive success, and must also account for the relatedness between

the investing individuals. Inclusive payoff functions for the female and helpers (respectively w_f and w_h^i for the i^{th} helper) are generated by taking the benefit individuals receive from helping and subtracting the costs individuals pay as a result of investment by themselves and by related individuals (weighted by their relatedness to the focal individual). For simplicity we assume that all other carers are equally related to the offspring, and that all individuals receive a benefit directly proportional to their relatedness to the brood (r_{fb} or r_{hb}). The breeding female and other carers are also all related equally (female-helper r_{fh} , helper-helper r_{hh}). To summarize, the inclusive payoffs are given by:

$$w_f = r_{fb} \cdot b - c_f - r_{fh} \cdot \sum_{i=1}^z c_h^i$$

$$w_h^i = r_{hb} \cdot b - c_h^i - r_{hh} \cdot \sum_{i=1}^z c_h^i$$

Solving the model

At equilibrium, neither the female nor any helper should be able to increase their payoff by altering their investment levels. Formally:

$$\frac{\partial w_f}{\partial x_f} = \frac{\partial w_h^i}{\partial x_h^i} = 0$$

There are no differences between helpers aside from their investment decisions, so the same response to investment by the rest of the group will be made by all helpers, and at equilibrium x_h^i will be identical for all i . Solving the above produces rules for x_f and x_h^i in terms of n and z at equilibrium, which are termed \hat{x}_f and \hat{x}_h respectively.

We can now calculate the optimal strategy for the female to play in the first step. The female should choose a value of n such that it maximizes her payoff w_f given that $x_f = \hat{x}_f$ and $x_h^i = \hat{x}_h$ at equilibrium. For simplicity we assume that n is large, and thus approximately continuous. Formally:

$$\frac{\partial w_f}{\partial n} = 0$$

After solving this we have rules for x_f , x_h^i and n at equilibrium that depend only on helper number z and the extrinsically specified parameters.

Comparison of analogous breeding attempts

From these rules we can plot expected investment levels by females and helpers across a range of carer numbers, and substitute them back into the original payoff equations to determine the equilibrium payoff. However, although the above results can elucidates the costs of the two stages will affect investment decisions (by manipulation of k_r and k_s versus k_p), we need a way of equating the costs of the two stages before we can meaningfully examine the effects of different cost parameters on breeding attempts. To do this, we consider the simple case of a lone female investing in offspring.

As before, we calculate the optimal investment levels by maximizing the payoff equation w_f , but this time ignoring any investment by helpers ($z = 0$, $x_h^i = 0$). With no individuals other than the female, the game simplifies and is functionally single-step; the female must simply maximize her payoff (for this simplified case relabeled w_f^0) with respect to both her investment x_f^0 and the brood size n^0 . Formally:

$$\frac{\partial w_f^0}{\partial x_f^0} = \frac{\partial w_f^0}{\partial n^0} = 0$$

Solving this equation for x_f^0 and n^0 generates equilibrium values \hat{x}_f^0 and \hat{n}^0 which can then be substituted into w_f^0 to yield an equation for female payoff that depends only on the constants of the system. Plotting production cost k_p against rearing cost k_r (Fig. 2.1) then gives us contours of equal female fitness that each represent a set of analogous breeding attempts differing only in the “balance” between the production and rearing costs. We can now alter k_p and k_r to produce conditions where the breeding attempts are dominated either by production-stage or rearing-stage costs, but where the total payoff for the attempts are the same; this allows us to make comparisons between the two kinds of breeding attempt under conditions where they are analogous.

To generate results, we chose three pairs of values for k_p and k_r that fell along a typical payoff contour. The three pairs represent a low, moderate, and high production cost respectively, and correspond to values of k_p that differ by a factor of five. The values of the other constants (see supplementary material) were chosen either for approximation to real cooperative systems (e.g. in the case of relatedness values), or so that the resulting numbers of offspring fell within a normal range for a terrestrial vertebrate. Unless otherwise specified, we assume that females and helpers have the same cost constant during the rearing stage ($k_r = k_s$), and that relatedness values are 0.25 between the helpers and offspring, helper and other helpers, and helpers and the breeding female. Throughout, 'carers' refers to all individuals including the breeding female, while 'helpers' refers to every individual except the breeding female.

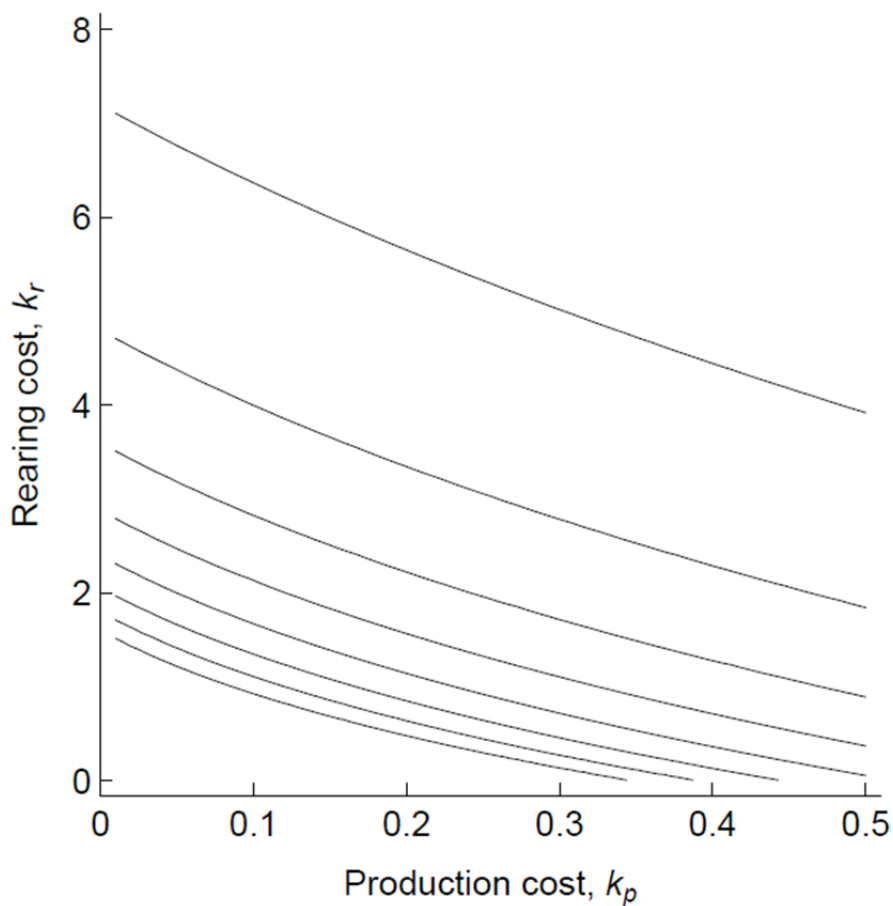


Figure 2.1: Contours of equal lone female payoff w_f^0 under varying values of production cost k_p and rearing cost k_r . Along these contours, paired values of k_p and k_r give the same payoff for a female raising a brood alone.

Results

(i) Productivity

Females produce more offspring as helper number increases (Fig. 2.2a). When the majority of costs fall in the rearing stage, offspring number and fitness are nearly linearly related to helper number, as helpers are able to contribute more effectively to the breeding attempt. In contrast, when the costs at the production stage are higher the positive effect on the payoff of having additional helpers plateaus quickly. This effect arises because the female rapidly reaches a level of initial investment in offspring that is extremely costly, and so is unable to capitalize on the presence of additional helpers by producing more offspring. This limitation on offspring production leads to a reduction in the benefit of acquiring additional helpers (to both the breeding female and existing helpers) as the number of helpers increases (Fig. 2.2b). This decrease is far more rapid, and the benefit to recruiting more helpers far lower, when production costs are relatively higher than rearing costs.

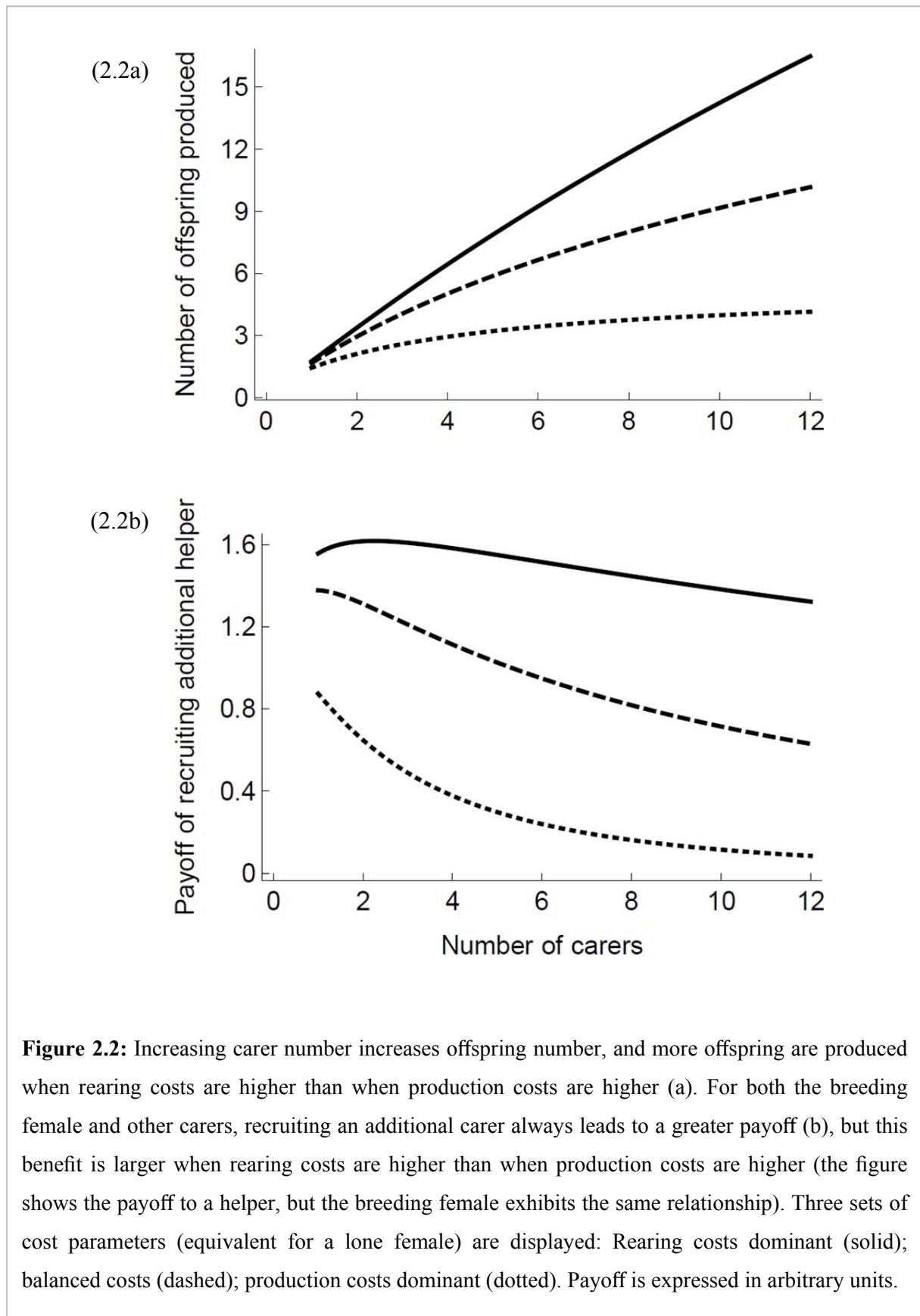
(ii) Investment levels

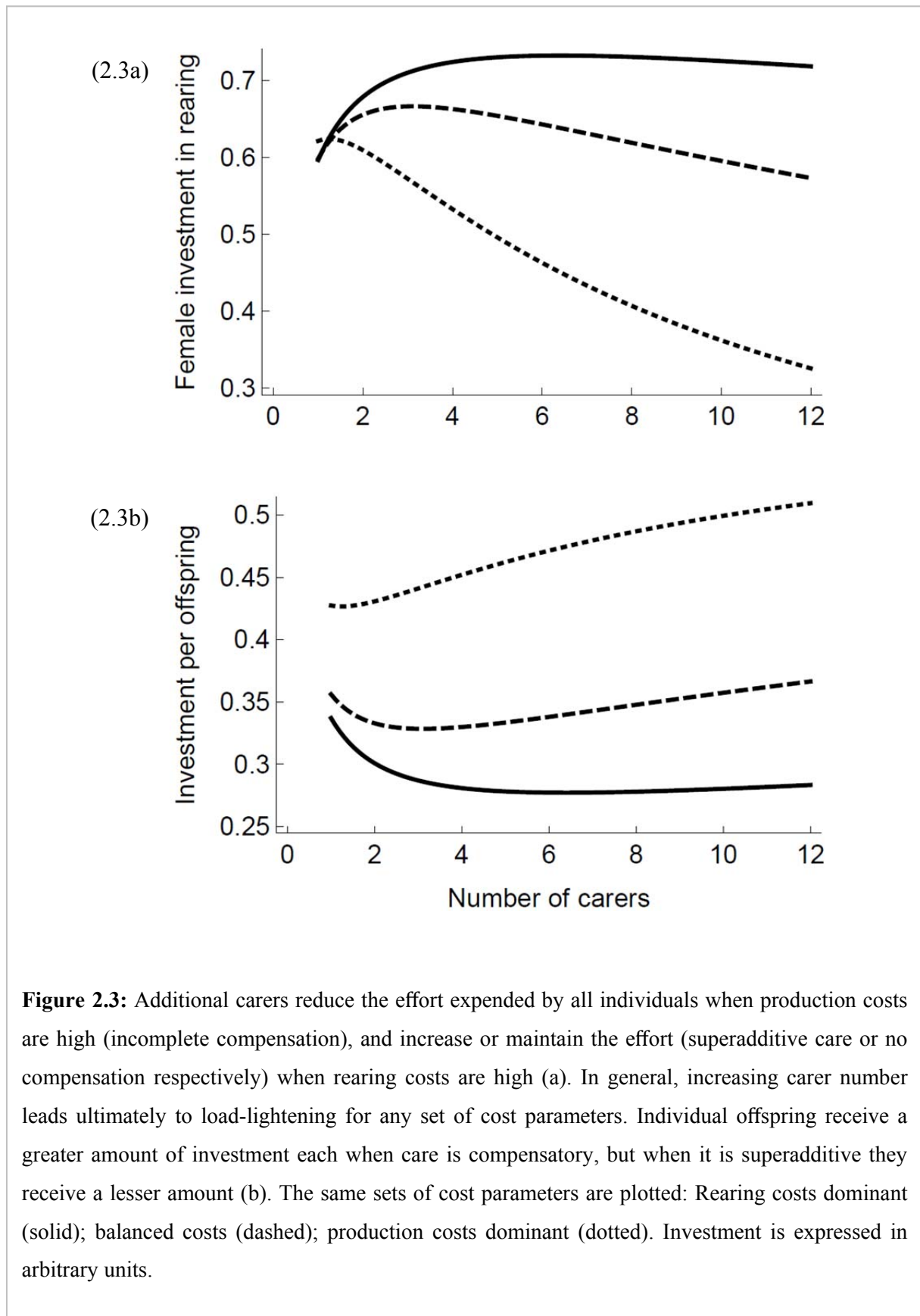
Investment levels have a more complicated dependence on helper number and the timing of costs. When there are few helpers the addition of another helper can lead to 'superadditive' investment, where all carers (helpers and breeding female) increase their individual investment in the brood (as in Valencia et al. 2006). As the number of helpers increases this positive effect on individual investment decreases, leading first to 'no compensation' (all carers maintain their individual investment, as in Wright et al. 1999) and then to compensatory care ('load-lightening'; all carers reduce their individual investment) (Fig.2.3a). The type of care received affects the amount of investment per offspring: when it is superadditive each offspring receives less investment as more helpers are added, but under compensatory care each receives more (Fig.2.3b). This apparent contradiction, whereby an increase in individual carer investment leads to lower per-offspring investment received (and *vice-versa*) is due to the greater number of offspring produced by the female in the production stage. The timing of costs is also crucial, as when rearing costs are dominant superadditive care and no compensation appear over a larger range of helper numbers, whereas dominant

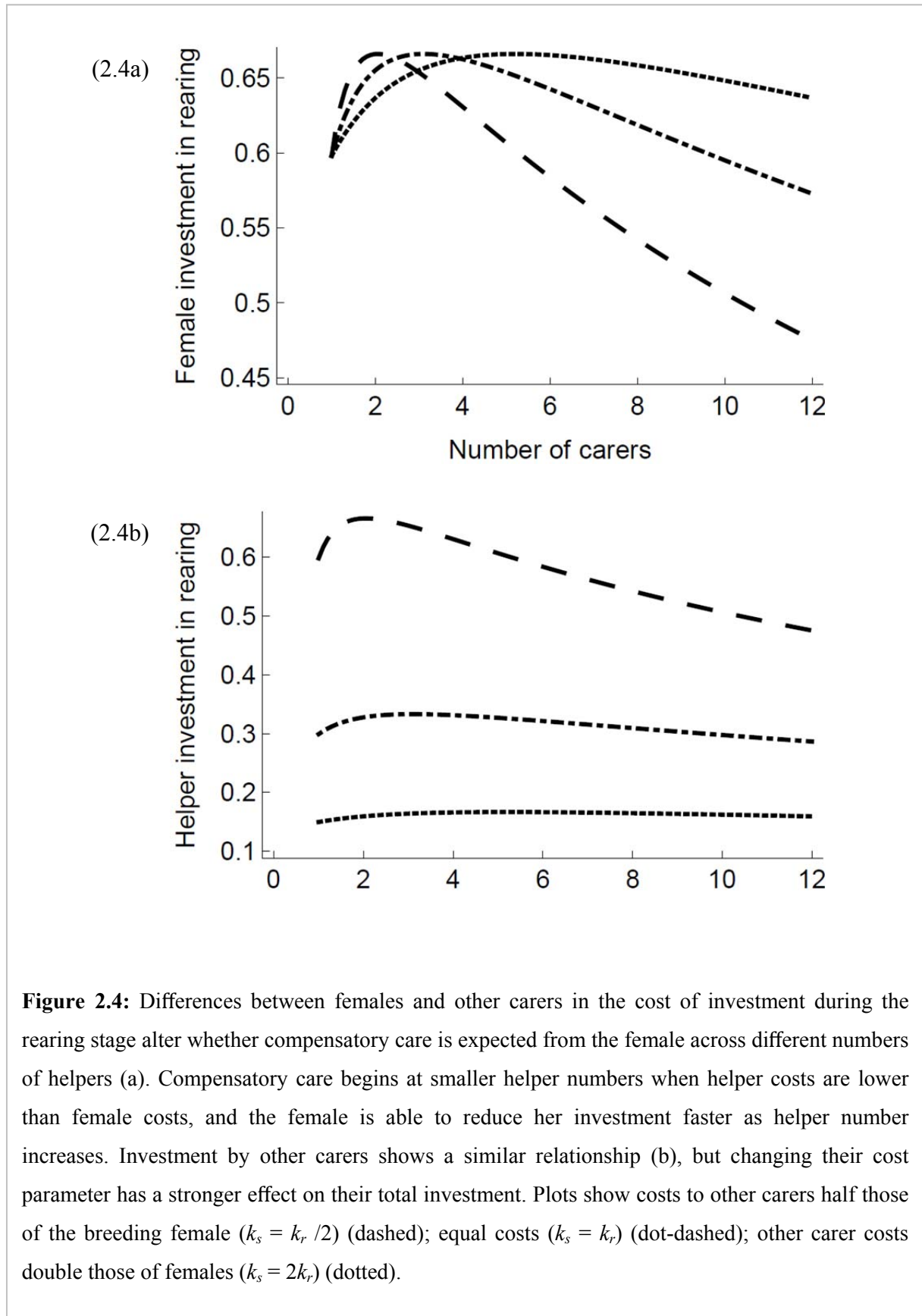
production costs favor compensatory care. In all cases the total amount of investment delivered to the brood by all carers increases as the number of carers goes up, but this total is higher when rearing costs are dominant.

(iii) Variable rearing costs

We have generally assumed above that rearing costs are the same for identical levels of investment across breeding females and helpers. This assumption will often be violated in natural systems, as helpers are frequently found to differ from breeders in their foraging ability (e.g. Heinsohn 1991; Clutton-Brock et al. 2002), and young helpers may be poorer foragers than older helpers (e.g. Heinsohn and Cockburn 1994). Breeding females may also pay a unique cost when the offspring are young (but after other individuals are able to invest), for example from brooding the young before they can self-regulate their temperature. Taking this variation into account, we see that load-lightening by the female starts at larger numbers of helpers the greater the cost to helpers relative to the female (Fig. 2.4a). As expected helpers invest far less when their costs are higher, but they too show load-lightening at greater helper numbers when their costs are higher than those of the female (Fig. 2.4b). This relationship is fairly simply explained: the poorer the ability of helpers to provide investment, the more helpers are needed to reach the female's constraint on investment at the production stage. This of course assumes that the overall 'quality' of the helpers is predictable by the female at the time offspring are produced.







Discussion

Our results suggest that when rearing costs (rather than production costs) are dominant, females are expected to produce many offspring to capitalize on the presence of helpers. As the number of other carers in the system increases, all individuals will work harder and invest more in the brood both individually and as a group (superadditive care). However this increase in investment only partially compensates for the greater number of offspring initially produced, such that each individual offspring will have less invested in it than it would have had in a smaller brood with fewer helpers. The opposite pattern is predicted when production costs are dominant. In this case females still produce more offspring with additional helpers, but to a lesser extent. Each additional helper reduces the levels of investment of all carers (load-lightening), and each individual offspring has a greater amount invested in it when there are more helpers in the system. Whichever stage of costs is dominant, 'no compensation' or 'superadditive care' is more likely to be observed when helper costs are greater than female costs. Larger groups of carers are biased towards load-lightening, as the female will always eventually be constrained by her initial investment. Our finding that investment rules are symptomatic of particular cost parameters may help to explain some of the inconsistency in empirical studies of investment, as we would not expect the same investment rules across species that differ in factors of breeding biology or life history that restrict flexibility in offspring number, predictability of helpers, or the subsequent costs of incubating, provisioning or protecting the offspring until independence.

Existing analyses (e.g. Houston & Davies 1985) predict that in biparental systems each carer should respond to the investment of the other by incompletely compensating, and thus escape part of the costs of care (load-lightening). This result holds in general for both sealed-bid and negotiation analyses (though see Jones et al. 2002; McNamara et al. 2003; Johnstone & Hinde 2006), and recent work extending negotiation to three individuals suggests it also holds for three carers (Johnstone 2011). Our analysis, however, demonstrates that these predictions hold only for a fixed brood size. They are thus relevant when predicting the response of a female to experimental removal or manipulation of her mate after offspring have been produced (e.g. Bart & Tornes 1989; Raadik et al. 1990; Duckworth 1992; Fetherston et al. 1994; Markman et al. 1995; Itzkowitz et al. 2001), but not when comparing (either within or between species) the behaviour of females who can anticipate the number of helpers at the

time of offspring production. The critical assumptions of our model are that individuals show systematic variation and respond to changes in offspring number in behavioral time, but these assumptions are supported by recent work showing tactical female investment during offspring production according to the number of carers available (Russell et al. 2003; Russell et al. 2007; Taborsky et al. 2007; Russell and Lummaa 2009; Canestrari et al. 2011; Santos and Macedo 2011). Similarly, examples from both observational studies (Magrath & Elgar 1997) and experiments (Sanz & Tinbergen 1999; Komdeur et al. 2002) show that breeding males are capable of responding to greater clutch sizes by increasing parental investment.

Inflexible brood sizes across different numbers of carers can be seen as a special case that occurs when production costs to the breeding female are very high, there is a biological constraint, or when it is very difficult to predict the amount of future help at the time of offspring production. Inflexible brood sizes lead to the female and helpers escaping more of the costs of care as carer number increases, and offspring individually doing better; this follows the pattern one would expect if extrapolating from uni- and biparental systems. However, when the female is able to modify brood size in response to a predictable number of helpers a different pattern of investment can appear. When production costs are cheap relative to those of the rearing period, our model suggests that the breeding female should take advantage of the helpers' anticipated contributions by producing more offspring (as in Davies & Hatchwell 1992; Russell et al. 2003; Woxvold 2005), rather than by fully reducing her own level of investment. Under these circumstances, producing a larger brood/litter can be viewed as a means of 'manipulation': rather than simply anticipating the care that her group will provide, a female can induce the helpers to invest more than they otherwise would have by producing more offspring. Even though she too must invest more to raise these extra offspring, she gains a net benefit due to the extra total contribution she elicits from the other carers as the size of the group increases. This female 'manipulation' is not necessarily harmful to the other carers, but this will depend on the similarity of their current and future fitness functions to those of the female; in some shorebirds, polyandrous females 'manipulate' more males to care for their offspring in a similar way, by producing additional clutches sequentially (Lank et al. 1985). From the viewpoint of the helpers, they should always respond to additional offspring by increasing investment, because they always benefit from additional offspring being reared; combined with the response of the female to predictable help this leads to a close positive relationship between group size, offspring number, and total amount of investment by the group.

In species with less flexible brood sizes, another way for the breeding female to alter initial investment would be by manipulating the amount invested in each individual offspring at the production stage according to the number of helpers, an effect shown by Russell et al. (2007), Canestrari et al. (2011), and Santos and Macedo (2011). This tactic should be expected in species that produce small numbers of offspring, as the female will be more heavily constrained by the necessity of producing a discrete number of offspring. For example, in a species that normally produces four offspring, the minimum increase (to produce a single extra offspring) represents a 25% increase in production investment, whereas a species producing twenty offspring is capable of producing an additional one and only raising its costs by 5%. The analogous theoretical predictions when dealing with tactical manipulation of investment-per-offspring, rather than offspring number, are discussed in chapter five.

In our model, low production costs can lead to individual offspring each receiving less investment when helpers are present than they would from a lone female, reproducing a theoretical result found in the biparental case by McNamara et al. (2003). In these cases the increase in helper investment only partially compensates for the greater number of offspring produced by the female to take advantage of the available help. Following this result, we predict that a positive effect of helpers on individual offspring survival and success should be more often seen when care is compensatory, but that helpers should cause females to increase the number of offspring she produces regardless of the cost parameters.

We treat all individuals other than the breeding female as equivalent in our model, but in real systems these carers will vary in their ability or willingness to deliver care due to factors such as age (and hence experience) (Heinsohn & Cockburn 1994; Langen 1996) or relatedness to the brood (leading to different indirect benefits) (Emlen & Wrege 1991; Nam et al. 2011; Browning et al. 2012a). Lowering relatedness between helpers and offspring should decrease helper investment if indirect benefits are important, and less experienced helpers will likely pay higher costs, also leading to reduced investment. However in most systems there will be an inverse relationship between relatedness and experience as older individuals are more likely to have lived through a change in the breeding pair; this will lead to similarity in the payoff functions of helpers as the effects on investment work in opposite directions. The breeding male is a potential exception to the above rule as he will normally possess both high relatedness to the brood and significant experience, however studies typically indicate that breeding males do follow the same investment patterns as non-breeders during offspring

rearing (Wright 1998b; McDonald et al. 2009). In our model the term that governs how individual payoff is affected by the costs incurred by other group members is referred to as 'relatedness', but could equally well represent any direct benefit where an individual's fitness is linked to the fitness or survival of other group members.

Our results suggest that cooperation should evolve more easily when a greater proportion of the costs of reproduction can be removed from the breeding female, as this allows more carers to invest effectively in offspring. As we have seen, when the female's costs are higher in the production stage the effect of additional carers on productivity quickly plateaus, whereas when they are lower the number of offspring produced is nearly linear with carer number, at least over the ranges considered. Conversely, the more potential carers that are available, the greater the advantage to shifting the earliest point that carers can invest towards the beginning of the breeding attempt, thus biasing the 'balance' of the attempt towards rearing costs. This could be achieved (for example) by producing young that are smaller and less well developed (assuming they can be fed by any individual), by developing mechanisms for other carers to share the costs of guarding or caring for eggs, or by provisioning the female during incubation or gestation to transfer away some of her production-stage costs.

Given that the effect of additional carers on female payoff is always positive, help should never be refused by the breeding female unless additional factors such as resource competition become important. This means that group size is likely to be driven by the relative values of the alternative options available to the other carers, especially when ecological factors are not acting to reduce the fitness of larger groups. In many systems we would expect there to be a certain payoff below which one or more alternative options (e.g. dispersal, floating, or challenging for breeding) becomes favourable, causing the helper to leave the system. Further theoretical work incorporating group formation and outside options would be needed to determine stable group sizes in a mixed population of breeders and helpers with varying relatedness. Although our model is framed in terms of helpers gaining indirect fitness benefits from offspring, the abstract relationship between offspring benefit and helper benefit equally well describes helpers accruing direct fitness benefits, provided that these direct benefits are contingent on the success of the breeding attempt in the same way indirect benefits would be. For example, the outcomes expected when helpers accrue fitness through augmenting group size fit well with our model, as this relies on offspring surviving and contributing to the future fitness of the helper. By contrast, our model is less useful for

systems where selection for helping is based largely on ‘help-for-experience’ (Selander 1964); ‘pay-to-stay’ (Gaston 1978) or ‘social prestige’ (Zahavi 1995), because in such systems helper benefits are based on the act (rather than consequences) of helping.

Future empirical studies in pair- and cooperatively-breeding species would benefit from considering the mounting evidence that maternal investment can vary significantly according to partner quality (Krist 2011; Horváthová et al. 2012) and/or group size (Russell & Lummaa 2009). As with any multi-stage investment system, focusing on decisions within individual stages in isolation may produce confusing or contradictory results if individuals can shift investment between stages as parameters change, or in response to the behaviour of others (Russell et al. 2008). Further theoretical work is needed to understand the effects on investment levels of restricted (but non-zero) investment by helpers at early stages. While we have focused here on effects of maternal variation in offspring number, one might also expect aspects such as offspring size, sex ratio, hatching synchrony and timing of reproduction to influence investment decisions in a cooperative group (Russell & Lummaa 2009).

3: Intra-group kinship influences maternal allocation and cooperative care behaviour

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Abstract

In any system where multiple individuals jointly contribute to rearing offspring, conflict is expected to arise over the relative contributions of each carer. Existing theoretical work on the conflict over care has: (a) rarely considered the influence of tactical investment during offspring production on later contributions to offspring rearing; (b) concentrated mainly on biparental care, rather than cooperatively caring groups comprising both parents and helpers; and (c) typically ignored relatedness between carers as a potential influence on investment behaviour. We use a game-theoretical approach to explore the effects of female production tactics and differing group relatedness structures on the expected rearing investment contributed by breeding females, breeding males, and helpers in cooperative groups. Our results suggest that the breeding female should pay higher costs overall when helpful helpers are present, as she produces additional offspring to take advantage of the available care. We find that helpers related to offspring through the breeding female rather than the breeding male should contribute less to care, and decrease their contribution as group size increases, because the female refrains from producing additional offspring to exploit them. Finally, within-group variation in helper relatedness also affects individual helper investment rules by inflating the differences between the contributions to care of dissimilar helpers. Our findings underline the importance of considering maternal investment decisions during offspring production to understand investment across the entire breeding attempt, and provide empirically testable predictions concerning the interplay between maternal, paternal and helper investment and how these are modified by different relatedness structures.

Introduction

In many animals, the successful development of offspring requires resources from parents beyond those delivered pre-hatching/prenatally. Offspring receiving such resources can obtain them from one parent only (uniparental care), both parents (biparental care) or at least one parent and non-parent (cooperative care). Understanding the patterns of resource investment in developing young by parents and non-parents is a central component of life-history theory (Williams 1966; Stearns 1992). Despite this, few attempts have been made to model the investment rules of carers across different stages within a breeding attempt (see Shen et al. 2011 for a two-carer example), even though changes to investment levels at an early stage in a breeding attempt are known theoretically and empirically to influence later behaviour of all carers (Smith and Härdling 2000; Russell et al. 2007) as well as estimations of carer investment rules (Russell et al. 2008). In addition, few studies have explored how the indirect fitness consequences of relatedness among carers should influence investment in a cooperative group (Johnstone 2011).

In uniparental care systems, the predicted maternal investment strategy within a given reproductive attempt is relatively straightforward, as it is only influenced by the relationships between current investment, and both current and future contributions to overall fitness (Williams 1966b). When another carer is added, contributions to care become more complex because the optimal investment strategy of one parent is also influenced by that of the other, as each will benefit when the other takes on a greater proportion of the costs of care (Trivers 1974). Assuming carers have similar information about offspring need (Johnstone and Hinde 2006), the usual prediction of biparental care models is that parental investment should be reduced to incompletely compensate for that provided by the other partner (Houston and Davies 1985; McNamara et al. 1999); although threshold effects (Jones et al. 2002) or very high responsiveness to partners (McNamara et al. 2003) can lead to other response rules. Cooperative care systems further complicate the possible investment strategies, not only because the parent(s) and non-parent(s) may accrue different benefits when contributing to offspring care (Hatchwell 2009), but because both the number of non-parents (hereafter helpers) and their relatedness to each other and to offspring can vary both within and between species (Russell and Lummaa 2009). This complexity may explain why empirical tests of provisioning rules are largely supportive of incomplete compensation in biparental species

(Harrison et al. 2009), whilst cooperative species have been found to exhibit almost every conceivable response to the presence of other carers (Hatchwell 1999; Heinsohn 2004). To date, few theoretical frameworks have been provided in which to understand this variation.

Using a comparative approach, Hatchwell (1999) found that in cooperatively breeding birds a significant proportion of the striking variation in investment rules could be explained by the probability of offspring starvation. In bird species in which nestling starvation is rare, parents are more likely to reduce their personal costs by compensating for the additional investment from helpers, while in species with frequent nestling starvation, additive care is more common (where each additional carer increases the overall investment to the brood). In a three-player negotiation model, Johnstone (2011) showed that this result could be accounted for by different rearing cost functions: where such functions are more strongly accelerating (i.e. conditions are harsher and offspring payoffs lower), all carers tend towards maintaining investment levels such that offspring receive the largest possible amount of resources. In addition, Johnstone (2011) suggested an important role for intra-group relatedness in determining response rules: when rearing cost functions are similar for both parents, the presence of a helper leads to the parent that is less related to the helper compensating for changes in helper effort more strongly. However, both the above studies have important limitations.

Firstly, breeding females vary dramatically in their initial investment in offspring production, both within and between species (Russell and Lummaa 2009), and this investment is likely to significantly influence maternal care allocations during offspring rearing, and by extension the contributions of other carers (Clutton-Brock et al. 2004; Gilchrist and Russell 2007). Previous studies have rarely considered a role of maternal investment during offspring production on carer investment optima during offspring rearing, and those that have (e.g. Shen et al. 2011) seldom gave control of offspring number to the breeding female. However, growing evidence suggests that breeding females are capable of modifying the number and/or quality of offspring produced when they can predict the likely contributions of other carers (Davies et al. 1992; Russell et al. 2003; Woxvold and Magrath 2005; Russell et al. 2007; Taborsky et al. 2007; Canestrari et al. 2011; Santos and Macedo 2011; Paquet et al. 2013). In a recent game-theoretic model, Savage et al. (2013) showed that high production costs (relative to rearing costs) should lead to reductions in individual investment with additional carers, because in such cases breeding females produce fewer offspring, which consequently

need less investment during the rearing period. However, this model was limited by treating the breeding male as identical to other helpers, and by neglecting to explore the effects of intra-group relatedness on allocations of care.

Secondly, while Johnstone (2011) considered relatedness structure between the breeding pair and a single helper, the potential effects of having multiple helpers of varying relatedness were not explored. It is rarely the case that cooperatively breeding groups are restricted to parents with a single helper, yet few attempts have been made to predict how individuals will respond to each other in larger, interrelated cooperative groups: at most, three individuals have been considered (Härdling et al. 2003; Johnstone 2011). The relatedness between helpers and breeders within cooperative groups can vary considerably both between and within species, because although cooperative breeding typically arises within a family context (Emlen 1995; Hatchwell 2009), helpers may be related to both parents, one parent (after the other dies/disperses or following group immigration) or neither parent (when both are replaced from outside the group or when the helper is a lone immigrant) (Stacey and Koenig 1990; Dickinson and Hatchwell 2004). Variation in kin-structure is likely to influence helper provisioning rules (and by association the parental rules) because related helpers will gain a greater benefit from reducing the costs of each other's contributions than will unrelated helpers, either because related helpers that survive to become breeders will provide each other with indirect fitness, or because related helpers are more likely to agree on the levels of investment to deliver to future broods of offspring (West-Eberhard 1975).

For the present study we define a cooperative breeding system as any in which non-breeding helpers contribute to rearing the offspring of others. In addition, for the purposes of our model, we assume that all helpers behave similarly with no significant task specialization or qualitative differences in investment strategy, as is commonly the case in cooperative breeders (Clutton-Brock et al. 2003; Cockburn 2004; Russell 2004). We present a game-theoretical model of a cooperative breeding system in which the breeding female can choose the number of offspring she produces with knowledge of the number of helpers that will assist in rearing them. We then explore the effects of varying the number of helpers and the relatedness differences among breeding females, breeding males, helpers and offspring on: (i) the expected payoffs; (ii) provisioning rules; and (iii) individual levels of investment in the system. We show that several different results should be expected for the same level of intra-group relatedness, depending on the number of carers contributing, but that higher intra-group

relatedness should largely lead to reductions in individual investment by all carers when additional carers are added to a given system.

The Model

We model the breeding attempt as a two-step sequential game, following Smith and Hårdling (2000) and Savage et al. (2013). In the first step, the breeding female chooses the number of offspring to produce, with knowledge of the number of carers that will contribute to the breeding attempt, and pays a personal cost for producing each offspring. Following this, the entire group plays a “sealed bid” investment game (Houston and Davies 1985) to determine the investment levels of each individual contributing to care. The sealed-bid approach simplifies the analysis considerably over “negotiation” approaches (as in McNamara et al. 1999, 2003; Johnstone and Hinde 2006; Johnstone 2011), and the predictions of the two modelling frameworks are qualitatively similar, particularly when individual responsiveness to other carers is low or moderate (McNamara et al. 2003). We use the same cost and benefit functions as Savage et al. (2013) (see below), but rather than focusing on the effects of costs incurred at different stages of reproduction (production and rearing), we instead explore the effects of relatedness structure on individual contributions to care. We consider three different classes of carer: the breeding female, the breeding male, and a variable number of helpers. The helpers may be related to the breeding female, the breeding male, or both, and we also explore cases in which two different types of helper contribute to care within the same breeding attempt.

We model the cooperative breeding group as an interrelated set of individuals comprising two parents (breeding female and breeding male) and H helpers (focusing on $0 \leq H \leq 10$, which encapsulates the majority of mean group sizes across cooperative vertebrates; Russell and Lummaa 2009). The breeding female and breeding male are assumed to be unrelated to each other, and each related to their offspring by $r = 0.5$. Helpers are assumed to be related to the offspring and to each other (r_{ho} and r_{hh} respectively) by values between 0 and 0.5. Helpers can be related to offspring through either the breeding female, breeding male, or both, and so female-helper and male-helper relatedness (r_{fh} and r_{mh} respectively) are also assumed to vary between 0 and 0.5. In natural systems the paired relatedness values between an interrelated

group of helpers, offspring, and breeders will never be fully independent, so in several cases we alter r_{ho} , r_{fh} , r_{mh} and r_{hh} together as a single variable termed “group relatedness” (r_g) to focus are results on realistic parameters. In other cases we hold one variable constant and explore the effects of varying another, for example when quantifying the differences between half-sibling helpers ($r_{ho}=0.25$) related through each parent ($0 \leq r_{fh} \leq 0.5$).

We assume that all group members are able to respond to the number of offspring produced by the female in the first (offspring production) step by adjusting their level of investment in the second (offspring rearing) step. We treat all helpers of the same type (e.g. female-related half-siblings) as identical, ignoring potential consequences of variation among helpers in ability to deliver care. To find stable levels of investment for all individuals, we first calculate the response of the breeding female, both types of helper and breeding male to a given brood size n . The breeding female chooses a level of investment x_f , and simultaneously the breeding male and helpers choose a level of investment, designated x_m for the male and x_h^i for the i^{th} helper. We assume that offspring benefit from investment through an increase in survival probability and future reproductive opportunities, and that total investment is divided equally among all offspring. As such, the benefit b to offspring depends only on n and the total investment all individuals provide, x_{sum} , where:

$$x_{sum} = x_f + x_m + \sum_{i=1}^H x_h^i .$$

To more realistically approximate the development of offspring we define a minimum level of investment per offspring x_{min} below which offspring survival is not possible and hence carers gain no benefit from investment. Consequently, b responds to investment as a function of $(x_{sum} / n) - x_{min}$. We assume that the first derivative of the benefit function must be positive, such that greater investment leads to greater benefit to the offspring, but that the second derivative must be negative, such that there are diminishing returns on increasing investment. To obtain precise results we use a simple illustrative function that satisfies these assumptions (over the appropriate range of values) and yields an analytical solution:

$$b = k_b \cdot \left(\left(\frac{x_{sum}}{n} - x_{min} \right) - \left(\frac{x_{sum}}{n} - x_{min} \right)^2 \right)$$

Individuals pay a cost c for investing in offspring, determined entirely by their own individual level of investment. We define the total cost to the female c_f as a function of both the number of offspring produced by the female n , and her level of investment in rearing the brood x_f . To account for variability in the costliness of producing and rearing offspring, the relative costs of offspring production and rearing are manipulated by defining two constants k_p and k_r , which act on n and x_f respectively. The final cost c_f to the female is the sum of the costs incurred over the two steps, as in natural systems both production and rearing of offspring is costly and often necessitates a trade-off by females (Monaghan et al. 1998). We assume that the first derivative of the cost function (c') is positive for all individuals, such that costs increase with greater investment, and that the second derivative (c'') is also positive, such that costs accelerate as investment increases. As before, a simple quadratic function is used as an illustrative example:

$$c_f = (k_p \cdot n^2 + k_r \cdot x_f^2)$$

Similarly, for the i^{th} helper the cost c_h^i depends on the helper's investment level x_h^i and the relative cost of offspring rearing (a new constant k_s , to allow for potential differences from the female's rearing costs). We also define the cost c_m for the male in terms of his investment x_m and a constant k_m . Unlike the female's cost function neither the helpers' nor the male's cost functions depend on n , as the other carers do not produce offspring themselves.

$$c_h^i = (k_s \cdot x_h^{i2})$$

$$c_m = (k_m \cdot x_m^2)$$

We assume that each individual chooses its level of investment so as to maximize a weighted sum (w) of the benefit to the offspring minus its personal costs and the costs incurred by the other carers in the group, where the weighting of each term corresponds to the relatedness to the focal individual of the individual incurring the cost or benefit. At this point differences in relatedness values between different classes of helper become important, so we define two helper classes h_1 and h_2 , with H_A and H_B helpers in each class ($H = H_A + H_B$), and allow their investment x_h^i to differ (x_{h1}^i and x_{h2}^i). The relatedness values between all types of carer are assumed to be reciprocal, and are shortened to the form r_{xy} , where x and y are abbreviations of the focal carer types (e.g. r_{fh1} for the relatedness value between females and class 1 helpers), or the form r_{xo} for the relatedness between carer type x and the offspring. Breeding females

and breeding males are assumed to be unrelated. To summarize, the maximands (respectively w_f , w_m , w_{h1}^i and w_{h2}^j for the i^{th} helper of class h_1 and j^{th} of class h_2) are given by:

$$\begin{aligned}
w_f &= r_{fo} \cdot b - c_f - r_{fh1} \cdot \sum_{i=1}^{H_A} c_h^i(x_{h1}^i) - r_{fh2} \cdot \sum_{j=1}^{H_B} c_h^j(x_{h2}^j) \\
w_m &= r_{mo} \cdot b - c_m - r_{mh1} \cdot \sum_{i=1}^{H_A} c_h^i(x_{h1}^i) - r_{mh2} \cdot \sum_{j=1}^{H_B} c_h^j(x_{h2}^j) \\
w_{h1}^i &= r_{h1o} \cdot b - c_h^i - r_{fh1} \cdot c_f - r_{mh1} \cdot c_m - r_{h1h1} \cdot \sum_{i=1}^{H_A-1} c_h^i(x_{h1}^i) - r_{h1h2} \cdot \sum_{j=1}^{H_B} c_h^j(x_{h2}^j) \\
w_{h2}^j &= r_{h2o} \cdot b - c_h^j - r_{fh2} \cdot c_f - r_{mh2} \cdot c_m - r_{h2h2} \cdot \sum_{j=1}^{H_B-1} c_h^j(x_{h2}^j) - r_{h2h1} \cdot \sum_{i=1}^{H_A} c_h^i(x_{h1}^i)
\end{aligned}$$

At equilibrium no individual can increase their payoff by altering their investment levels, i.e.:

$$\frac{\partial w_f}{\partial x_f} = \frac{\partial w_m}{\partial x_m} = \frac{\partial w_{h1}^i}{\partial x_{h1}^i} = \frac{\partial w_{h2}^j}{\partial x_{h2}^j} = 0$$

Solving the above produces rules specifying x_f , x_m , x_{h1}^i and x_{h2}^j in terms of n and H at equilibrium, which are termed, \hat{x}_f , \hat{x}_m , \hat{x}_{h1}^i and \hat{x}_{h2}^j respectively. Within each helper class there are no intrinsic differences between the helpers in our model, so each should make the same response to investment by the rest of the group, and hence at equilibrium x_{h1}^i and x_{h2}^j are each identical for all i or for all j .

We are now able to calculate the optimal number of offspring for the breeding female to produce in the first step of the model, taking into account the impact of her choice on the subsequent investment decisions of all group members. The female should choose a value of n such that it maximizes w_f , given that $x_f = \hat{x}_f(n)$, $x_m = \hat{x}_m(n)$, $x_{h1}^i = \hat{x}_{h1}^i(n)$ and $x_{h2}^j = \hat{x}_{h2}^j(n)$ at equilibrium. For simplicity, we treat n as a continuous variable (a reasonable approximation when n is large). Formally, at equilibrium:

$$\frac{\partial w_f}{\partial n} = 0$$

This leads to equilibrium rules for x_f , x_m , x_{h1}^i , x_{h2}^j and n at equilibrium that depend only on helper number H and the extrinsically specified cost parameters (k_b , k_p , k_r , k_s , k_l). All solutions

were generated and subsequent plots produced in Wolfram Mathematica (v7.01, Wolfram Research 2008).

To plot results we chose values for the constants such that investment levels ranged between 0 and 1, and such that numbers of offspring approximated a natural range for a terrestrial vertebrate. This leads to a relationship of approximately $k_r = 20 k_p$. We also assume that all individuals have the same cost constants through the rearing stage ($k_r = k_s = k_t$), such that everyone pays the same costs for delivering the same level of investment to the brood (see Savage et al. 2013) for an exploration of differences in this parameter between helpers and females, and for the effects of varying the $k_r : k_p$ ratio).

Results

(a) Offspring production

Our model predicts that patterns of relatedness within groups should have a strong influence on the number of offspring the breeding female produces. Breeding females should always increase investment in offspring production as the number of available helpers increases, but the magnitude of this increase is determined by both the female's relatedness to the helpers (r_{fh}) and the helpers' relatedness to the offspring (r_{ho}). Male-helper (r_{mh}) and helper-helper (r_{hh}) relatedness values have no effect on the equilibrium levels of investment by the female, male or helpers, and hence no effect on the investment per offspring delivered by the group. As cooperative groups often consist of individuals who are interrelated to some degree (aside from the breeding pair), in some cases we assume that r_{fh} and r_{ho} vary together as a single parameter (group relatedness, r_g). Under this condition, females in highly interrelated groups ($r_g=0.5$) show greater investment in offspring production than those in moderately ($r_g=0.25$) or distantly interrelated groups ($r_g=0.125$) (Fig. 3.1a). This effect largely arises because helpers that are closely related to offspring are willing to invest more during the rearing period, and the female is able to produce more offspring accordingly.

When r_{fh} and r_{ho} are instead altered independently (i.e. when comparing male-related helpers to female-related helpers), female investment behaviour is less straightforward because the

two parameters affect offspring production in opposite directions. Greater helper-offspring relatedness encourages greater investment by the female (as above) because the helpers will contribute more to care, but females also reduce investment in offspring production as female-helper relatedness increases. Breeding females invest more in offspring production when they are less closely related to helpers (assuming r_{ho} is constant) because they benefit from reducing the costs borne by related individuals during the breeding attempt (Fig. 3.1b). In essence, the benefit the female receives from rearing greater numbers of offspring is lessened by the impact on the costs and survival probability of related helpers. Consequently, a breeding female should invest maximally in offspring production when the other carers are closely related to the offspring but distantly related to her, as she has no negative fitness consequences from extracting more investment from them. The breeding male represents a class of carer that fulfils the above conditions for maximal female investment (high relatedness to offspring, zero to female), and as such his presence or absence has a greater effect on the female's tactics during offspring production than does that of any single helper: all helpers that are related to offspring as closely as the breeding male are also offspring of the breeding female (Fig. 3.1c).

(b) Offspring rearing

Variation in offspring production by the breeding female under differing patterns of relatedness and different numbers of helpers has knock-on effects on the investment by all carers during offspring rearing. As above, we initially assume that r_{fh} and r_{ho} vary together as the single parameter “group relatedness” (r_g). When group relatedness and helper number increase, the female increases offspring production to take advantage of the available care, but eventually the personal costs she incurs from doing so prohibit further increases. At this point the only effect of contributions from extra helpers is to reduce costs to each other and the costs borne by the breeding female, and the benefits individuals derive from doing this will depend on the level of group relatedness. In closely-related groups, compensatory care with additional helpers is predicted across all group sizes, as the female reaches her constraints on offspring production more quickly with harder-working helpers, and all individuals benefit from reducing the costs paid by each other. In less closely-related groups, no compensation for extra helpers is seen at first, as the female modifies her investment in offspring production

in response to the number of carers, but it eventually appears when sufficient helpers are present (Fig. 3.2a).

Unsurprisingly there is also a positive effect of group relatedness on helper investment levels, with close relatives ($r_g=0.5$) investing more than those of intermediate relatedness (0.25) and those in turn investing more than distant relatives (0.125). Helpers also reduce individual investment when there are many helpers and group relatedness is high, but maintain largely static investment levels across differing group sizes when group relatedness is low (Fig. 3.2b). As before, when female-helper relatedness is allowed to vary independently of helper-offspring relatedness, the effect of higher r_{fh} is to lower the investment by the female (Fig. 3.2c). This arises because of the lower rearing investment required to support the reduced number of offspring produced in the first step, and as with offspring production suggests that female-unrelated helpers should behave more like the breeding male than female-related helpers, and have a more similar effect to on group investment behaviour.

(c) Between- and within-group relatedness variation

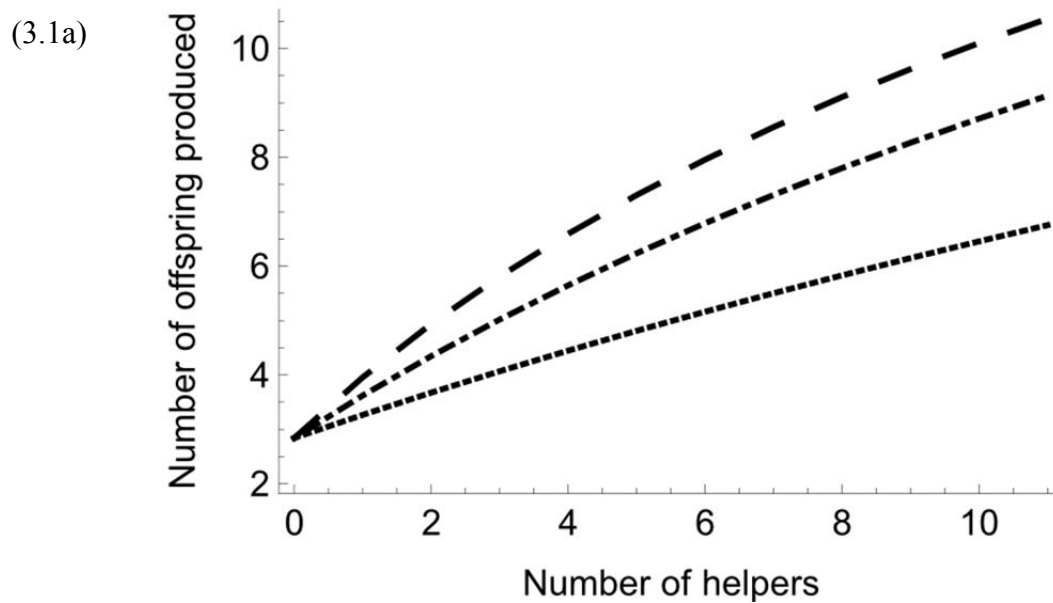
In natural systems helpers may be related to offspring through the breeding female or breeding male, and because of the fitness dependency between related carers this distinction is important even when helper-offspring relatedness is identical. Comparing groups in which all helpers are similar, full-sibling helpers invest more than half-sibling helpers due to greater benefits, but among half-sibling helpers those that are breeding-female-related invest less than those that are breeding-male-related, because the female produces less offspring in the first step when helpers related to her are present (Fig. 3.3a). Full-sib helpers reduce investment as group size increases in order to escape the costs of care, because the female is already at or close to her limit of offspring production. In contrast half-sib helpers largely maintain investment levels over a range of group sizes because the female can still invest more in offspring production in response to extra helpers.

A similar pattern can be observed when comparing the outcomes for individual offspring across group relatedness structures (Fig. 3.3b). Investment-per-offspring increases with helper number when helpers are closely related to the female, but does not when helpers are unrelated to her and group size is small. This is because the female produces fewer offspring

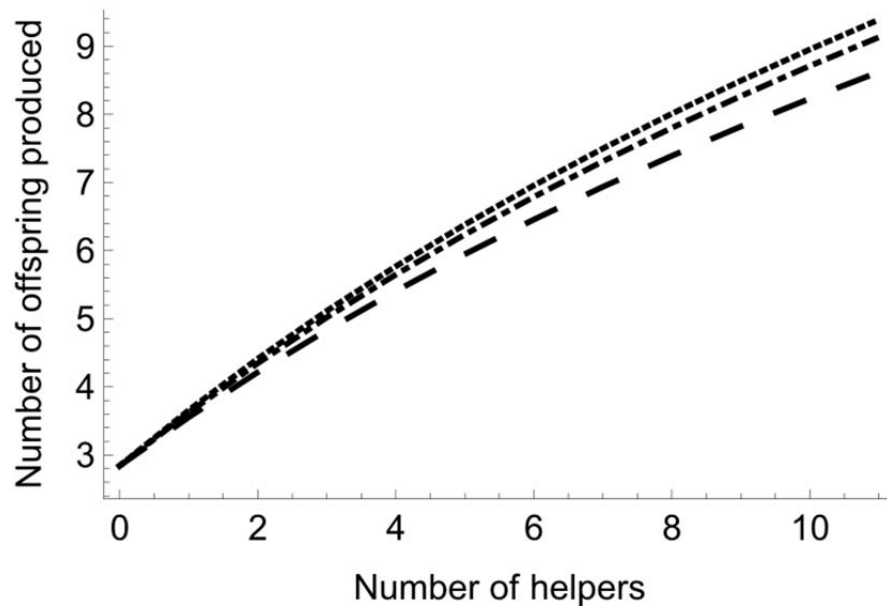
in total when she has a small number of related helpers than when she has a small number of unrelated helpers, so the total investment has to be divided into fewer portions by the offspring. With the female being more willing to exploit unrelated than related helpers, each additional unrelated helper leads to a large increase in offspring production, and although all carers increase their investment levels to provide for these additional offspring, this increase may not fully compensate for the greater total investment required; this leads to each offspring receiving less care. In contrast, when a related helper is added to a group the female makes a more modest increase in offspring production, and consequently the presence of an extra carer leads to total investment by the group outpacing the number of offspring, and each individual offspring receiving more care.

When helpers vary in relatedness within a group, each helper still responds independently to the number of offspring produced as a function of its own costs and its relatedness to the offspring and other carers, and the female tunes offspring production to the sum of potential investment across all the helpers. Consequently we find that investment in a mixed-relatedness helper group should be equivalent to investment in a homogenous helper group that possesses the same relatedness values between all carers and offspring as the mean values of the mixed group. However, it is instructive to compare the investment by a particular type of helper within a homogenous group of its own helper type with the investment by the same helper in a mixed group in which other helper types are also present. In these cases mean relatedness values to the female and offspring will vary between the groups compared, so the female strategy and investment levels of all carers will differ. We find that full-sib helpers invest more in mixed groups where half-sib helpers are also present than in homogenous groups where all helpers are full-sibs, as there is less investment by the rest of the helper group. Conversely, half-sib helpers invest less in a mixed group as the female is less willing to exploit them by producing additional offspring when there are full-sib helpers present that will provide the majority of the care (Fig. 3.3c). As a consequence, between-group differences in relatedness have less influence on individual investment levels than within-group differences: full-sib and half-sib helpers differ in investment level more when both are present in the same group than in groups with only one type of helper.

Figure 3.1: (a) Females produce more offspring with more helpers, but are expected to respond to closely related helpers by increasing offspring production further. The plot shows offspring production for close ($r_g = 0.5$, dashed), intermediate ($r_g = 0.25$, dot-dashed), or distant ($r_g = 0.125$, dotted) relatedness between group members. (b) When only relatedness between females and helpers is considered, close relatedness leads to lower investment by females at the rearing stage due to costs being shared. In the graph, helper-offspring relatedness is fixed at 0.25 and offspring production is plotted for different levels of female-helper relatedness ($r_{fh} = 0.5$ (dashed), 0.25 (dot-dashed), 0.125 (dotted)). (c) A male is both closely related to offspring and distantly related to the female, and therefore exerts a stronger influence on female production than does a single helper. Lines show offspring production in groups with a male and helpful ($r_{ho} = 0.5$) helpers (solid), with a male and unhelpful ($r_{ho} = 0.125$) helpers (dot-dashed), with helpful helpers but no male (dashed), and with unhelpful helpers with no male (dotted)



(3.1b)



(3.1c)

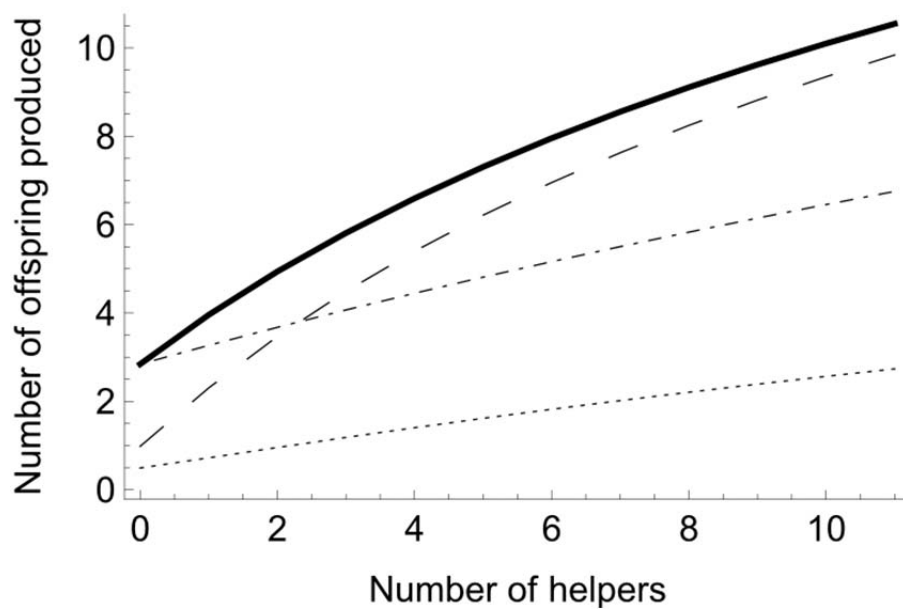
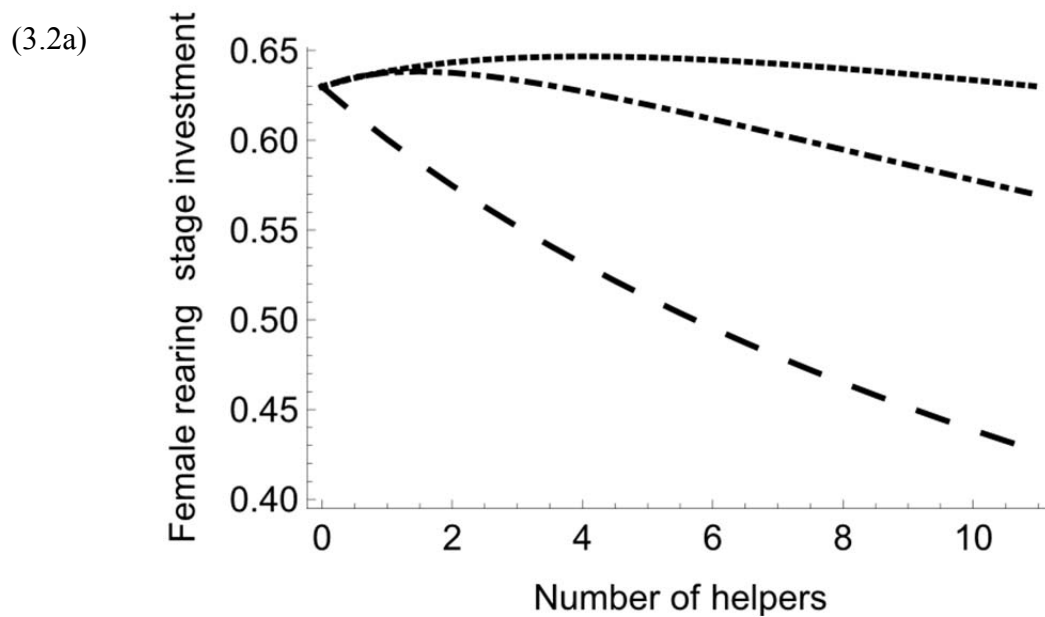
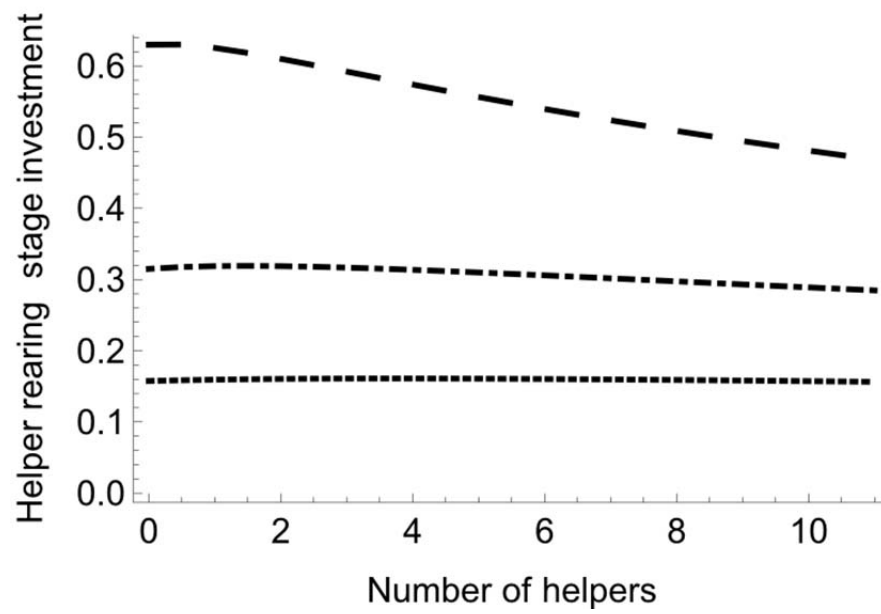


Figure 3.2: (a) Females reduce rearing-stage investment when they have helpful helpers (high group relatedness), as they benefit more by overproducing in the first step due to the greater available amount of care. (b) Helpers invest more in closely related offspring, and exhibit a greater reduction in individual contribution at high helper numbers. Plots show helper investment for close ($r_g = 0.5$, dashed), intermediate ($r_g = 0.25$, dot-dashed), or distant ($r_g = 0.125$, dotted) relatedness between group members. (c) When only relatedness between females and helpers varies, there is a reduction in care by females when helpers are related to her, as she benefits less from extracting more investment from them. Helper-offspring relatedness is fixed at $r_{ho} = 0.25$ and the female rearing-stage investment plotted for different levels of female-helper relatedness: ($r_{fh} = 0.5$ (dashed), 0.25 (dot-dashed), 0.125 (dotted))



(3.2b)



(3.2c)

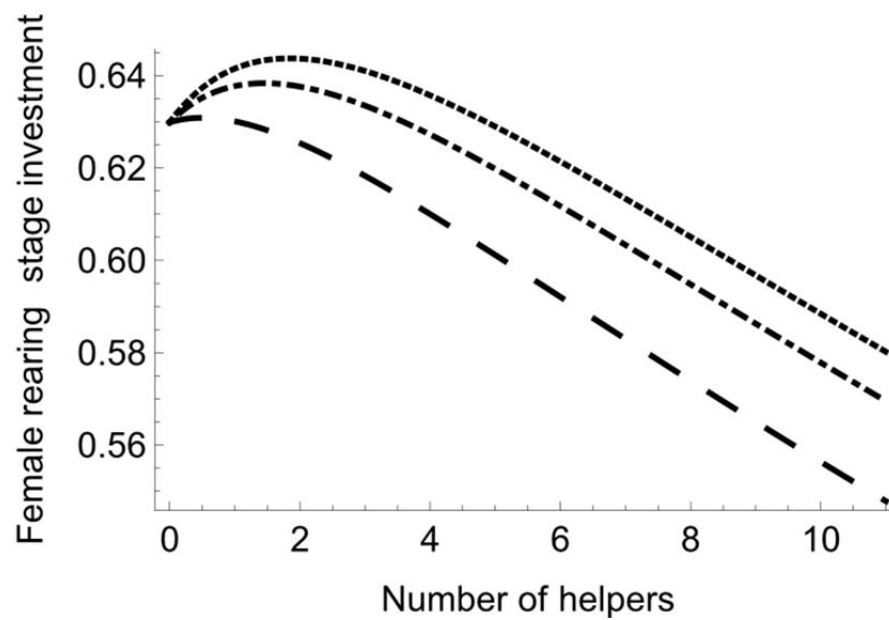
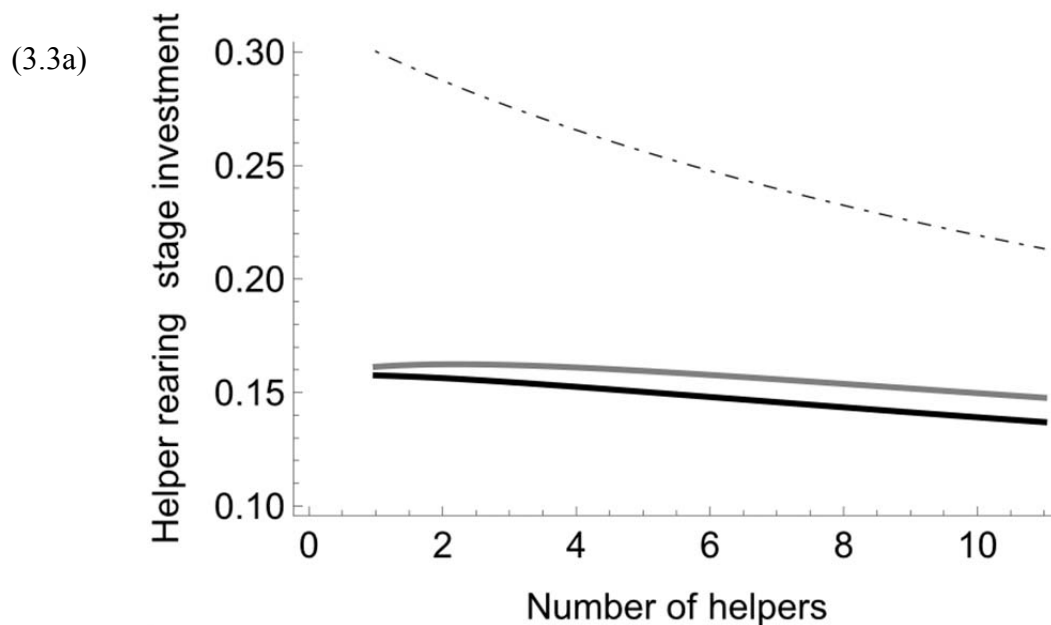
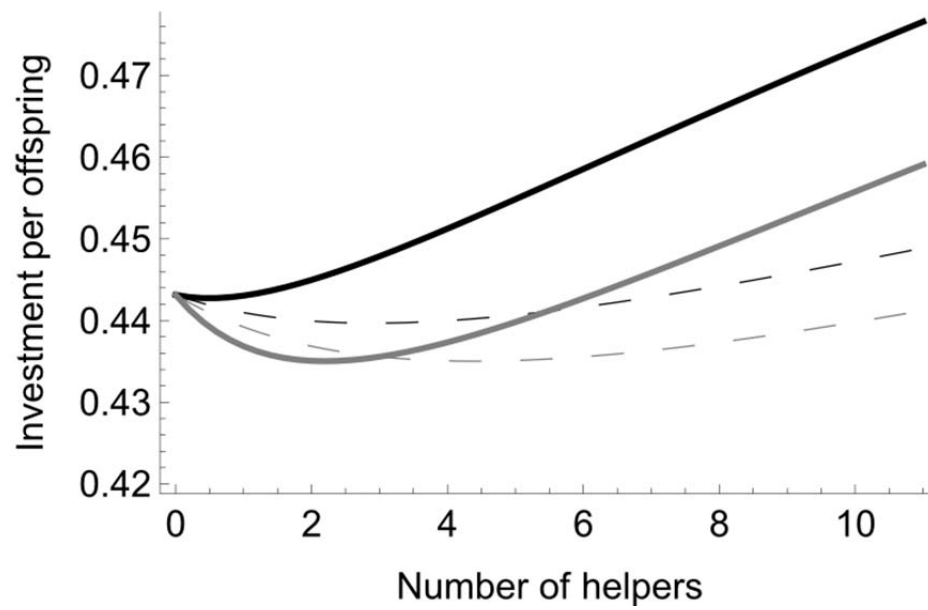


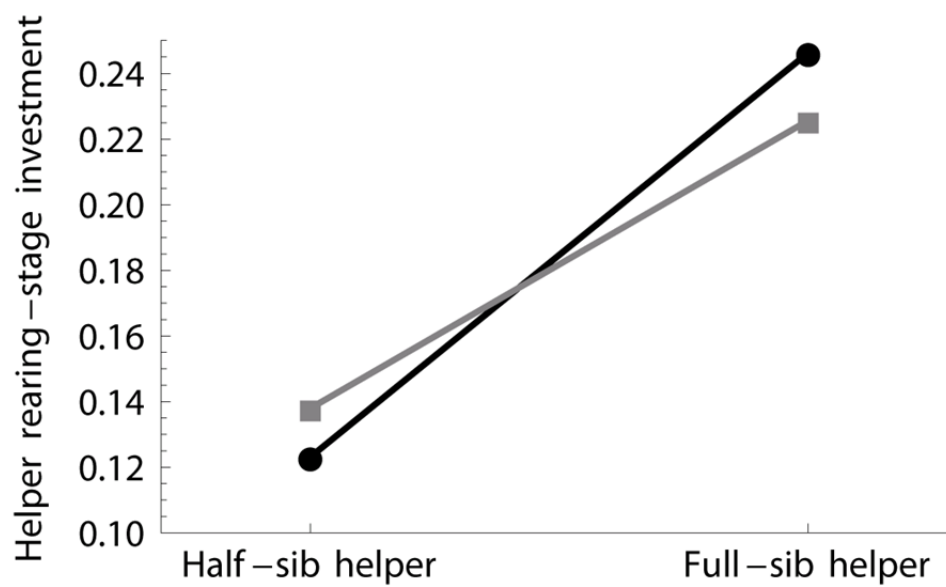
Figure 3.3: (a) Helper investment in groups where helpers are full-siblings to offspring is greater than in groups where helpers are half-siblings, and when group size increases individual reductions in care are more pronounced. In addition, because of a reduction in production-stage investment by the breeding female, helpers invest less in groups where they are closely related to the female. (b) Individual offspring benefit from additional helpers that are closely related to the breeding female, particularly when both r_{fh} and r_{hc} (i.e. r_g) are high. When r_{fh} is low, offspring may do less well individually as group size increases, because the female produces more offspring in total to exploit the helpers. Plots show investment-per-offspring for groups with half-sib helpers (solid lines) and distantly-related ($r_{fo} = 0.125$) helpers (dashed lines) that are either closely related ($r_{fh} = 0.5$, black), or unrelated ($r_{fh} = 0$, grey) to the breeding female. The black dot-dashed line represents the investment level of a full-sib helper related to both parents and offspring by 0.5. (c) Within-group variation in relatedness has a greater influence on helper investment levels than does between-group variation. Half-sib helpers invest less in mixed groups than in homogenous groups in which all helpers are half-sibs, whereas full-sib helpers invest more in mixed groups than in homogenous groups in which all helpers are full-sibs. The plot shows helper investment levels for full-sib and half-sib helpers in mixed groups (black, 3 full-sib and 3 male-related half-sib helpers), and homogenous groups (grey, 6 helpers that are either full-sibs or male-related half-sibs)



(3.3b)



(3.3c)



Discussion

Although there is accumulating evidence that females tactically adjust their level of investment according to socio-ecological conditions, relatively little theoretical work exists on the subject. As such, our work extends previous models in two key ways. Firstly, it allows for flexible maternal investment in offspring as a function of the number and relatedness of available carers, treating helpers and the breeding male separately. Secondly, it explores the effects of variable helper numbers and different relatedness levels on carer investment patterns during offspring rearing. Our results suggest that intra-group relatedness will have a significant influence on the provisioning rules and levels of investment observed in cooperative breeding systems. Broadly, female productivity increases as a function of increasing intra-group relatedness due to the increased benefits to helpers of investing heavily in more related offspring. However, the effect of helpers on female productivity was found to be lower than the effect of the breeding male, because, in contrast to related helpers,

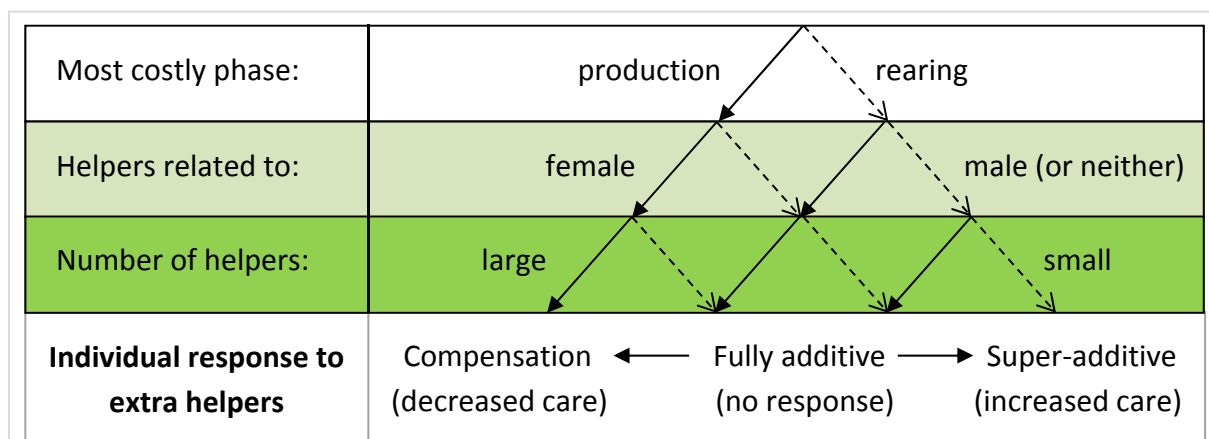


Figure 3.4: Predicted investment rules across different helper numbers within cooperative groups, based on the distribution of costs to the breeding female, the relatedness of helpers to the breeding female, and the current number of helpers. Reduction of individual carer investment as helper number increases (i.e. compensation or “load-lightening”) is expected when (1) offspring production is relatively more costly to the female than offspring rearing (Savage et al. 2013a; Chapter 2), (2) when the breeding female is closely related to the helpers (or directly benefits from their survival), and (3) when the current number of helpers is large. When the above conditions fail to hold, carers are predicted to respond to extra helpers either by maintaining current investment levels (fully additive care), or in extreme cases by increasing their individual investment level (super-additive care): this is due to the female tactically increasing offspring number to take advantage of the extra available care.

the breeding female has no indirect fitness stake in his survival. In addition, the circumstances under which carers reduce investment when more helpers are present are strongly influenced by intra-group relatedness, as extracting investment from related individuals is less beneficial. Our results have implications for provisioning rules on multiple levels, from differences between biparental, polyandrous, and cooperative care systems, to the influences of dispersal strategy and breeding tenure on group provisioning and investment over time (Fig. 3.4).

The effects of maternal tactics on individual provisioning rules are particularly clear when our results are compared with previous theoretical work modelling investment in offspring during a single reproductive stage. In contrast to a female with (up to) two helpers rearing young (Härdling et al. 2003), we do not always see a reduction in individual carer investment as group size increases: if the female can increase her production of offspring, carers may maintain or even increase their investment. In addition, in our model total female costs are higher (rather than lower) with full-sib helpers, as the female increases offspring number to take account of the greater potential help. Our model contrasts similarly with previous work on a breeding pair and single helper rearing young (Johnstone 2011), as we find that carers reduce their individual investment less when the female has tactical control of offspring number. However we support Johnstone's (2011) finding that females will pay lower costs with related helpers than with helpers related only to their partner provided that the helpers' relatedness to the offspring is the same. Modelling investment as a two-stage process and with a range of group sizes shows that carer investment strategies can strongly deviate from those predicted by analyses of the rearing stage in isolation, particularly when group size also varies, and can additionally be modified by the relatedness structure of the group (see Russell et al. 2008 for some supporting empirical evidence).

Our prediction that individuals should provision differently according to relatedness patterns in the group has consequences for comparing provisioning rules in cooperative breeding systems to those in biparental systems. Biparental care is well-analysed, and whether sealed-bids (Houston and Davies 1985), negotiation (McNamara et al. 1999; Johnstone and Hinde 2006; Johnstone 2011), or sequential negotiation (Lessells & McNamara 2012) are used to determine investment levels, the results generally predict partial compensation in the presence of a partner (though see McNamara et al. 2003; Johnstone and Hinde 2006). Cooperative systems (when considered theoretically at all) have often been regarded as direct extensions of the biparental case, with simply more individuals that invest in offspring according to their

own costs in the same way as the parents; only rarely has theoretical work explicitly addressed investment consequences of variation in inter-carer relatedness (Härdling et al. 2003; Johnstone 2011). However, under our model, a biparental system differs significantly from a cooperative one in investment behaviour, as biparental systems contain only unrelated carers while cooperative ones usually display some degree of interrelatedness. In particular, the relatedness between the carers modifies how much females are willing to exploit the other carers by modifying their own investment across offspring production and rearing. As a consequence, we predict that provisioning rules in biparental systems will differ from those in cooperative systems when indirect fitness relationships exist among carers, for example by the breeding female exhibiting weaker responses to the presence/absence of another carer in cooperative systems.

Intra-group variation in relatedness patterns in cooperative breeders might help to explain the significant variation in observed carer provisioning rules. While investigations into parental provisioning rules in biparental care systems tend to provide support for expected incomplete compensation (Harrison et al. 2009), this is less commonly the case in cooperative breeders (Hatchwell 1999; Heinsohn 2004). For example, of the 27 cooperative bird species in Hatchwell's (1999) comparative analysis on provisioning rules, helpers were associated with reductions in provisioning rate of both parents (44%), one parent only (30%) or neither parent (26%). This variation was shown to be attributable to variation in nestling starvation: carers tend to reduce investment when carer numbers increase if nestling starvation is rare, but maintain investment where nestling starvation is common (Hatchwell 1999). However, all else being equal, our model also suggests that individual reductions in rearing-stage investment when there are more carers ("load-lightening") should be a common empirical finding over a wide range group sizes when females and helpers in a group are closely interrelated. By contrast, when females and helpers are more distantly interrelated, their investment levels should remain largely constant regardless of group size because females alter offspring production to extract the maximum possible investment from all carers. Consequently, our model could provide part of the mechanism behind Hatchwell's (1999) findings: the observed inter-species differences in nestling starvation may arise in part from the consequences of variable maternal investment in offspring production, group size, group kin-structure, and the interplay between them.

That said, an emerging pattern in many cooperatively breeding vertebrates is that different categories of carers react differently to the presence of co-carers. For example, in meerkats (*Suricata suricatta*) breeders of both sexes reduce their investment in pup-feeding with increasing group size, while non-breeders maintain their levels (Clutton-Brock et al. 2004). Such results are not consistent with the above hypothesis regarding offspring starvation risk (Hatchwell 1999), and have instead been interpreted as breeders benefiting more than helpers from saving resources for future reproduction, particularly in species where the probability of attaining breeder status is low (Clutton-Brock et al. 2004; Browning et al. 2012). Our results suggest that an additional explanation might be the costs of offspring production and relatedness differences between carers in the group. In particular, females constrained from or selected against producing more offspring when helper number increases are expected to reduce their investment, while helpers investing at lower levels largely maintain their contributions to better support the offspring. If enough helpers are available at the rearing stage, every group member benefits from a greater proportion of the female's investment being made at the initial stage. In groups with helpers closely related to the breeding female, one would expect greater reductions in investment as helper number increases, as a consequence of the female being unwilling to foist additional costs on to the helpers by increasing offspring production. Studies have yet to consider how carers of differing relatedness to each other should respond to changes in group size, but our model predicts several possible effects, including differences in investment in mixed group relative to homogenous groups, and a greater similarity of investment behaviour between the breeding male and helpers related to offspring through him, compared to those related through the breeding female.

While some caution is required due to the lack of demographic and ecological considerations in our model, our results also have implications for how female investment should vary across species with the system of dispersal and length of breeding tenure. When females are unrelated to helpers but helpers still contribute heavily to care we predict an exploitative strategy with females producing more offspring to extract more investment from the other carers. In contrast, a female with closely related helpers should produce fewer offspring, causing an overall reduction in the costs all carers pay. Given that the former case will usually arise when females are dispersive and the latter when females are philopatric, we predict that in general birds should respond more strongly than mammals to changes in helper numbers by altering offspring numbers, except in species with sex-biased dispersal opposite to the norm

(Greenwood 1980). Exploitative strategies should be most prominent in newly immigrated breeding females, because through their breeding tenure they will become increasingly related to their helpers (Johnstone & Cant 2010). Mathematical models and empirical work show that such effects could have significant consequences on reproductive skew in humans (Cant & Johnstone 2008; Lahdenperä et al. 2012), but the consequences for cooperative breeding animals remain untested. Although potentially difficult to implement, a demographically explicit version of our model could provide more complex predictions about investment behaviour, as helpers might (for example) be expected to adjust their contributions to care based on their own sex, the sex of the offspring, and the sex bias in dispersal, because of the potential for kin competition (Johnstone & Cant 2008). Similarly, we have ignored variation in the costs of cooperation when compared to alternative options for helpers, which is likely to modify the degree to which females can extract additional investment from helpers as group size changes.

Finally, despite our framing of the model in terms of indirect fitness benefits, the link between helpers and offspring in our analysis has implications for any scenario in which helpers have an interest in the survival of the offspring and other group members. For example, under group augmentation (Kokko et al. 2001), helpers benefit by successfully raising additional offspring to boost their own direct fitness, and hence within a single breeding attempt the benefits from helping are similar to those generated by inclusive fitness relationships. We suggest that our model is a fair approximation for this type of direct fitness benefit, particularly for smaller values of intra-group “relatedness”, which would be more accurately termed fitness interdependence in the case of directly benefiting helpers (see Roberts 2005). The analogy also holds for between-carer inclusive fitness relationships: individuals concerned with augmenting group size will be averse to other carers paying high costs, as raising additional group members is of limited benefit if current group members perish in the process. We would expect carers benefiting through group augmentation to maintain investment patterns through time regardless of changes in breeder identity, with the benefit attached to group augmentation replacing “group relatedness”, i.e. the breeding female should reduce her contribution at the rearing stage when augmentation benefits are high, focusing instead on producing additional offspring. Given the current lack of empirical research on the topic, we suggest that future work on cooperative care systems should investigate how provisioning rules are influenced by variation in the benefits of group size for different classes of individual.

To summarize, maternal control of offspring production and inter-carer relatedness can both have strong influences on the expected provisioning rules in biparental and cooperative systems. Such rules include the numbers of offspring produced, the response to additional carers, and quantitative investment levels during provisioning; and we can make empirical predictions about how the rules might be expected to vary within and between species (Fig. 3.4). Our results underline the importance of incorporating tactical female investment when modelling the conflict over care: when a female is able to predict the number and helpfulness of other carers in advance of producing offspring, her ability to manipulate the initial investment can lead to different behaviours among other members of the group than if her investment were fixed. Consequently individual investment decisions cannot be meaningfully analysed in isolation, either from other carers or from the other stages in which individuals can contribute (Smith and Härdling 2000; Savage et al. 2013), and understanding the investment decisions of any group that cooperates to rear offspring ultimately depends on the integration of models of offspring number, offspring size, carer number, carer relationships, and alternative carer options. In addition, the biology of the particular species in question will affect the relative costs and constraints of producing offspring compared to rearing them (Savage et al. 2013a), further complicating the issue by altering the proportion of total costs helpers are able to contribute to. Future empirical work should monitor investment across all possible stages of a breeding attempt whenever feasible, as without this wider context investment behaviour can easily be misconstrued (Russell et al. 2008). Similarly, theoretical work that focuses entirely on fine-scale investment within a single stage of a breeding attempt might be expected to have limited relevance outside of its stated context.

4: Maternal control of offspring size under variable rearing environments



Abstract

In species where the number of individuals contributing to offspring care can vary, an individual's investment strategy should depend on the size of the breeding group and the relative contributions of each carer. In many care systems the mother has greater control over the number and/or quality of offspring than the other group members, and hence can benefit by adjusting her pre-birth investment in offspring production to match the expected care available from others. Increased quality of offspring at birth can have several possible effects on later investment, depending on whether higher-quality offspring require more or less care during rearing, and whether they have a higher potential fitness if reared successfully. We argue that variable maternal tactics should be most apparent in care systems such as cooperative breeding where there is great variation in the level of care available, a position supported by empirical findings suggesting that mothers can both reduce and increase pre-birth investment under different contexts. Existing theoretical work on carer investment rules has largely focused on biparental care, and on modelling offspring provisioning in isolation from other stages of investment, and hence has been unable to explore the causes and consequences of tactical maternal investment in cooperative breeders. Furthermore, the potential for investment at one stage to influence the value of investment at another has hitherto received little attention within the literature on parental care. We present a game-theoretical model incorporating cooperative rearing and female control of pre-birth investment, wherein maternal investment either substitutes for later investment (allowing compensation for differing conditions) or alters the value of later investment ('complementary' investment). We show that very different patterns of care can arise depending on whether an increase in pre-birth investment reduces the need for investment during the rearing period, or instead primes offspring to benefit more from post-birth care.

Introduction

Classic life-history theory dictates that mothers should vary their investment in reproduction according to current ecological conditions and the potential for future reproduction (Williams 1966b; Stearns 1992), and that this investment can be used to produce either large numbers of small offspring or small numbers of large offspring, generating an offspring size-number trade-off (Lack 1947; Williams 2001; Roff 2002). More recently, evidence has accumulated that mothers can also tactically vary their level of investment in each offspring prior to birth, independently of the number of offspring produced, to better match the potential benefits of current conditions (Fox et al. 1997; Cunningham & Russell 2000; Verboven et al. 2003). When offspring fitness is determined by the total investment in them across all stages of their development, mothers can tactically increase pre-birth investment to compensate for poorer rearing conditions (e.g. Bolund et al. 2009), or reduce it to transfer costs to other carers (e.g. Russell et al. 2007); however the assumption that investment can be substituted across stages may not always apply. For example, offspring that are larger at birth may be more likely to survive development, or more likely to become dominant as adults (Royle et al. 2005), altering the value of investing in them during the rearing period. Similarly, if larger offspring also require more food, higher pre-birth investment may require higher post-birth investment if the potential benefit is to be realized. The potential for this ‘dynamic complementarity’ (*sensu* Heckman 2007) between the value of investment across developmental stages has hitherto been largely overlooked in the literature on parental care.

When investment is substitutable between pre- and post-birth development stages, one should expect mothers to compensate for better rearing environments by reducing pre-birth investment, as this transfers more of the costs of reproduction to the stage during which investment is less costly than normal (assuming that better rearing conditions impose lower costs on carers). One context in which mothers should commonly reduce pre-birth investment under favourable conditions is in cooperative breeding systems, in which offspring are reared by one or more ‘helpers’ in addition to the parents (Russell & Lummaa 2009). Cooperative systems provide an excellent test of adaptive plasticity in maternal allocation strategies because the consequences of current ecology on maternal fitness are highly variable and yet predictable (Russell & Lummaa 2009). Larger groups are more capable of delivering food to the breeding female and/or offspring than smaller groups, and so mothers gain higher

breeding success with more helpers, but groups are not static: the number of helpers available will vary both spatially and temporally. While there is some suggestive evidence that increasing groups size sometimes leads to increased investment in cooperative breeders (Russell et al. 2003; Hodge et al. 2009), the majority of studies have reported a reduction in pre-birth investment with increasing group size, usually without a corresponding change in the number of offspring produced (Taborsky et al. 2007; Russell et al. 2007; Santos & Macedo 2011; Canestrari et al. 2011; Paquet et al. 2013).

Two suggested explanations for females reducing pre-birth investment under favourable conditions are the helper compensation (Russell et al. 2007) and reduced predation (Taborsky et al. 2007) hypotheses. Russell et al. (2007) supported the direct substitutability of investment across development by showing that superb-fairy wren (*Malurus cyaneus*) mothers benefit from investing less in egg nutrients when in the presence of helpers, because helpers fully compensate for maternal reductions, leading to increased maternal survival probability to the following year. Taborsky et al. (2007) showed that mothers laid smaller eggs with experimentally elevated group sizes in a cooperative cichlid (*Neolamprologus pulcher*), and suggested that smaller fry are less vulnerable to predation when in larger groups, a hypothesis that can be extended to cover other passive benefits to having larger numbers of helpers. In this case, the female is also compensating for good conditions, indicating a lack of complementarity between offspring quality (in this case size) and later care. Nevertheless, no formal model exists to explain when females should benefit from reducing pre-birth investment in the presence of helpers (as in most cases outlined), or why variation in maternal pre-birth investment might occur under different numbers of helpers across species (e.g. Russell et al. 2003, 2007; Koenig et al. 2009).

Under ecological conditions that differ from the average, altering pre-birth investment in offspring benefits mothers by more closely approximating the optimum for current conditions (Burley 1981; Uller 2008). In birds, for example, mothers sometimes lay larger eggs (and hence take on higher costs) when currently paired with males that are more ‘attractive’ than the population average (Krist 2009; Pryke & Griffith 2009), rather than laying larger eggs to compensate for poor males (Bolund et al. 2009). The viability of these alternative strategies revolves around the balance between current and future fitness: if the offspring of attractive males are themselves more attractive, and the mother is unlikely to mate with similarly attractive males in the future, she may benefit from increasing current investment despite an

attendant reduction in her probability of survival (Sheldon 2000). However, when offspring attract more investment during both pre- and post-birth development because attractive males provides more care (rather than because they pass on genes for ‘attractiveness’), there is a strong implication that pre-birth investment is complementary, not substitutable, with post-birth investment.

Traditional models of offspring care have generally assumed that investment during offspring production must trade-off with that during offspring rearing (Smith & Fretwell 1974), but ignored other potential effects of pre-birth investment and the possibility for mothers to tactically adjust pre-birth investment in anticipation of varying levels of help during the rearing period (Savage et al. 2013a). In light of the empirical findings suggesting the existence (but not ubiquity) of tactical maternal investment, more theoretical work is needed to explore the potential consequences for carer investment rules and outcomes for offspring. Across species, reducing investment at early stages of development may have an enormous effect on the final fitness of an individual (Suomi 1999; Knudsen 1999), or may be largely irrelevant in comparison to the rearing environment (Van De Pol et al. 2006). In either case, substituting investment may not always be possible, hence limiting the scope for maternal tactics. Furthermore, if offspring that are higher-quality at birth receive lasting advantages, the level of investment delivered at an early stage will directly change the benefits of caring for offspring at later stages (Heckman 2007), potentially altering investment strategies in a complex manner as the availability of care changes. Another potential concern is the necessity of following up early investment (Heckman 2007): if higher-quality offspring require high rearing investment for their fitness to be realized (for example because they need more food), investment again fails to be substitutable between stages.

In this chapter, we present a formal model of how females breeding in cooperative groups should alter their pre-birth investment in offspring as group size changes. We hypothesise that the key influence on maternal strategy is the relationship between pre-birth investment and later outcomes for offspring, with this determining whether mothers enjoying good conditions should invest more to exploit current conditions, or save resources to boost their future survival probability. We suggest that females should reduce pre-birth investment as group size increases if the primary benefit to offspring is through giving them a ‘head start’ (i.e. when pre-birth and rearing investment are perfectly substitutable). Previous work by Hatchwell (1999) has shown that in cooperative species parents compensate for the presence

of helpers by reducing their provisioning rate, but only when nestling starvation is rare, and we suggest that a similar argument can be applied to pre-birth investment when it has no special effects on offspring fitness. Conversely, we predict mothers should increase pre-birth investment with group size when higher early investment leads to lasting advantages for offspring, providing a ‘silver spoon’ that complements future investment.

The Model

We model a cooperative breeding attempt as a two-step process with a breeding pair and a variable number of helpers. The female first chooses the amount of investment delivered pre-birth, and then the whole group plays a standard ‘sealed bid’ investment game (*sensu* Houston & Davies 1985) to determine their individual investment levels during the offspring rearing period. Our model follows a similar structure to Savage et al. (2013a), but concerns female control of offspring quality with the number of offspring fixed, rather than giving the breeding female choice of offspring number with quality being fixed. Empirical studies support the assumption by generally reporting no adjustment of offspring number when offspring quality is found to vary (e.g. Russell et al. 2007; Taborsky et al. 2007; Santos & Macedo 2011; Canestrari et al. 2011). All calculations and plots were made using Wolfram Mathematica (v7.01, Wolfram Research).

The cooperative group consists of H helpers and a breeding pair (female and male). All group members choose their level of investment in offspring care during the second, rearing step with full knowledge of the investment made by the female during the first, offspring production step; in empirical terms they are assumed to be able to judge offspring quality accurately at the beginning of the rearing period. The breeding female and male are related to helpers by the relatedness parameters r_{fh} and r_{mh} respectively, are unrelated to each other, and are each related to the offspring by $r_{fo} = r_{mo} = 0.5$. Helpers are assumed to be identical to each other in their cost parameters and relatedness to other group members, and are related to each other by r_{hh} and to the offspring by r_{ho} .

To find stable investment levels for all individuals during the rearing period, we first calculate the response of all individuals to any quality of offspring the female could produce. All

individuals simultaneously choose an investment level x during the rearing stage, termed x_f, x_m and x_h^i for the female, male and i^{th} helper respectively. Cost parameters (k_q, k_f, k_m, k_h) specify the relative costs of the female quality investment and the female, male and helper rearing investments respectively. The total costs incurred by the breeding female are assumed to be a function of her investment in offspring quality at production q and her later investment during offspring rearing x_f . Males and helpers only contribute during offspring rearing, so their costs are simply a function of their rearing-stage investments. For all carers, costs accelerate with increasing investment:

$$c_f = (k_q \cdot q^2 + k_f \cdot x_f^2)$$

$$c_m = (k_m \cdot x_m^2)$$

$$c_h^i = (k_h \cdot x_h^{i2})$$

Offspring are assumed to share the investment of the carers equally, and as such are modelled as a unit. We assume that the resulting fitness of offspring after both investment stages is a function of the mother's pre-birth investment in offspring quality (q) and the combined rearing investment (x_{com}), which is the sum of the rearing contributions of the female, male, and all helpers:

$$x_{com} = x_f + x_m + \sum_{i=1}^H x_h^i$$

We assume that greater pre-birth quality either reduces or increases the amount of rearing investment that is required by the offspring; the former if investment is substitutable, leading to high-quality offspring gaining a developmental 'head start' over others, and the latter if high-quality offspring are larger and thus require more food. To represent this q is multiplied by a constant k_a , where $k_a \in \{-1, 1\}$. The relative importance of different stages of development varies greatly across animals with parental care, and as a consequence maternal investment in initial offspring quality and investment during offspring rearing need not be equally necessary or valuable to offspring. To model this we introduce a parameter ν ($0 < \nu < 1$) that modifies the value to the offspring of the delivered investment at each stage. High values of ν represent a sensitive or critical period during early development that can

only be effectively supported by maternal investment, or (alternatively) an unimportant rearing period, as might occur in a highly precocial species. Low values of v represent cases where early variation in investment is largely unimportant, or where offspring are highly altricial and hence are influenced far more by investment during the rearing period.

Offspring are assumed to benefit from care only above a minimum level of usable investment x_{\min} . The first derivative of the offspring benefit function is assumed to be positive above this threshold, such that greater investment benefits offspring, while the second derivative is negative, implying diminishing returns on investment. For simplicity we use a quadratic function, weighted by benefit parameter k_b . This function is then multiplied by a factor $(1+q)^n$ where $n \in \{0,1\}$ to represent two possible influence of offspring quality on final offspring fitness: when $n=0$ changing offspring quality only influences the amount of rearing investment needed, whereas $n=1$ represents a ‘silver spoon’ situation where offspring that are higher quality at birth are more valuable for a given level of later investment. Our aim in choosing these two functions is to compare cases in which greater maternal pre-birth investment (i) increases or (ii) reduces the marginal value of future investment during the rearing period. To this end we pair the ‘silver spoon’ value of $n=1$ with large offspring being hungrier ($k_a = -1$) when generating results, to better contrast with the ‘head start’ case in which low-quality offspring can potentially catch up with high-quality offspring during the rearing period ($n=0, k_a = 1$). Using a quadratic function to render the solutions analytically solvable, the two offspring benefit functions for the ‘head start’ and ‘silver spoon’ cases ($b_{HS}(q, x_{com})$ and $b_{SS}(q, x_{com})$) are hence given by:

$$b_{HS}(q, x_{com}) = k_b \cdot \left(\left((1-v) \cdot x_{com} + v \cdot q - x_{\min} \right) - \left((1-v) \cdot x_{com} + v \cdot q - x_{\min} \right)^2 \right)$$

$$b_{SS}(q, x_{com}) = k_b \cdot \left(\left((1-v) \cdot x_{com} - v \cdot q - x_{\min} \right) - \left((1-v) \cdot x_{com} - v \cdot q - x_{\min} \right)^2 \right) \cdot (1+q)$$

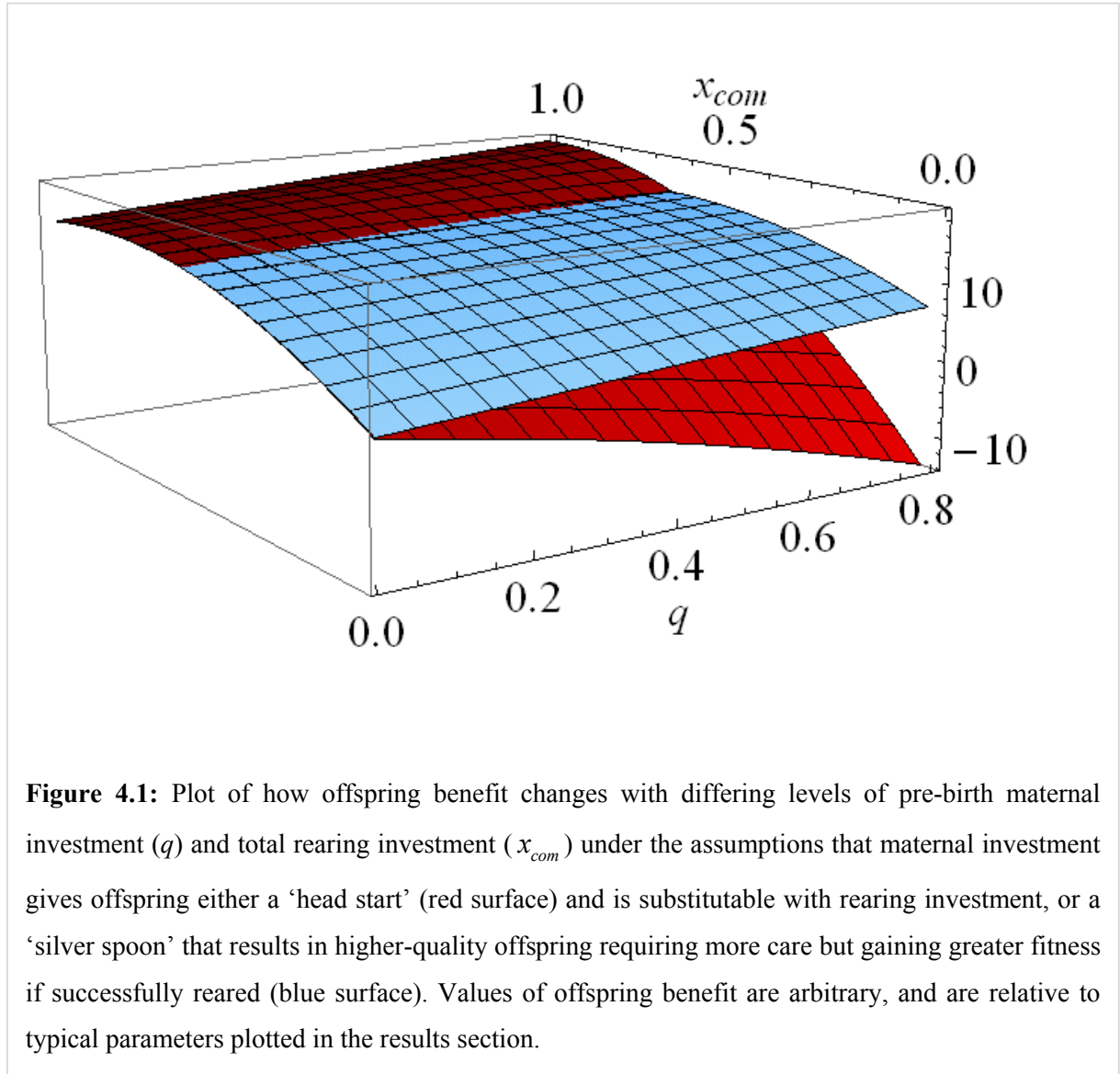
To assist in visualising the differences between the ‘silver spoon’ and ‘head start’ offspring benefit functions, we generate plots of how offspring benefit changes under different levels of q and x_{com} with typical model parameters (Figure 4.1).

To find optimal investment rules for all carers, we assume that each attempts to maximise a weighted sum of the benefit to the offspring, weighted by relatedness to the carer, minus their own costs of care, minus the costs borne by other related carers, again weighted by relatedness to the carer:

$$w_f = r_{fo} \cdot b(q, x_{com}) - c_f - r_{fh} \cdot \sum_{i=1}^H c_h^i$$

$$w_m = r_{mo} \cdot b(q, x_{com}) - c_m - r_{mh} \cdot \sum_{i=1}^H c_h^i$$

$$w_h^j = r_{ho} \cdot b(q, x_{com}) - c_h^j - r_{fh} \cdot c_f - r_{hh} \cdot \sum_{i=1}^{H-1} c_h^i$$



Solving the model

All carers make a simultaneous choice of investment level after the initial stage, based on the level of offspring quality q chosen by the female. At equilibrium no carers should be able to alter their maximands by changing their investment levels, i.e.:

$$\frac{\partial w_f}{\partial x_f} = \frac{\partial w_m}{\partial x_m} = \frac{\partial w_h^i}{\partial x_h^i} = 0$$

The resulting equilibrium investment rules are termed \hat{x}_f , \hat{x}_m and \hat{x}_h^i for the female, male and helpers respectively; all helpers are assumed to behave identically as they all have the same cost and benefit functions. These investment rules depend only on the quality variable q and the model parameters, so at equilibrium:

$$x_f = \hat{x}_f(q), x_m = \hat{x}_m(q), x_h^i = \hat{x}_h^i(q)$$

Finally, we substitute the above equilibrium investment rules back into the female maximand to determine her optimum choice of offspring quality in the first step. At equilibrium the female should not be able to increase her maximand by altering q :

$$\frac{\partial w_f(\hat{x}_f(q), \hat{x}_m(q), \hat{x}_h^i(q))}{\partial q} = 0$$

Solving the above gives us rules for q , x_f , x_m and x_h at equilibrium that depend only on the extrinsically specified cost, benefit, and relatedness parameters.

Results

Pre-birth investment conveys a ‘head start’

We first consider cases in which initial female investment in offspring quality is both additive with later rearing investment and of similar value, so that it gives offspring a ‘head start’ towards reaching a given level of total investment ($k_a = 1, n = 0, v = 0.5$). Under these

circumstances, the model predicts that breeding females should reduce investment in offspring quality when greater numbers of helpers are present (Fig. 4.2a), as they are then able to reduce their personal costs without major negative effects to the offspring, thanks to compensation by other carers. Carers are all predicted to reduce their rearing-stage investment with increasing helper number, demonstrating ‘load-lightening’ (Crick 1992), with the decline being most noticeable with full-sibling helpers, because these invest the most in small groups (Fig. 4.2b). The breeding male behaves similarly to a full-sibling helper during the rearing period, although his presence or absence has a greater influence on maternal strategy than does a single full-sibling helper, because the mother avoids exploiting related carers to the same degree as those to whom she is unrelated.

The total amount of investment delivered by all carers during the rearing period increases with helper number (Fig. 4.2c), and is slightly greater for helpers related to offspring through the breeding male than for those related through the breeding female, due to the female adopting a more exploitative pre-birth investment strategy when helpers are unrelated to her. The increase in rearing investment with group size is largely masked by the reduction in pre-birth investment by the female, leading to little change in total investment delivered to offspring (Fig. 4.2d). Together these results support the helper compensation hypothesis, which suggests that females should reduce early-stage investment in offspring when in larger groups because helpers are able to compensate, and that this can conceal the positive effects of helpers on offspring when the rearing period is studied in isolation.

Effects of altriciality / precociality

Under generic ‘head start’ conditions ($k_a = 1, n = 0$), we can change the value parameter ν to compare investment rules between systems in which pre-birth investment or post-birth investment are relatively more valuable to the offspring. An intermediate value of ν (≈ 0.5) represents investment during either stage being equally effective in altering offspring benefit, while high (≈ 0.9) and low (≈ 0.1) values of ν represent highly precocial and highly altricial species respectively (high ν could also represent species in which early-life investment is particularly critical to successful development). The relative effectiveness of investment between the two stages strongly influences the patterns of investment seen, with female investment in offspring quality predictably peaking when her early investment is highly

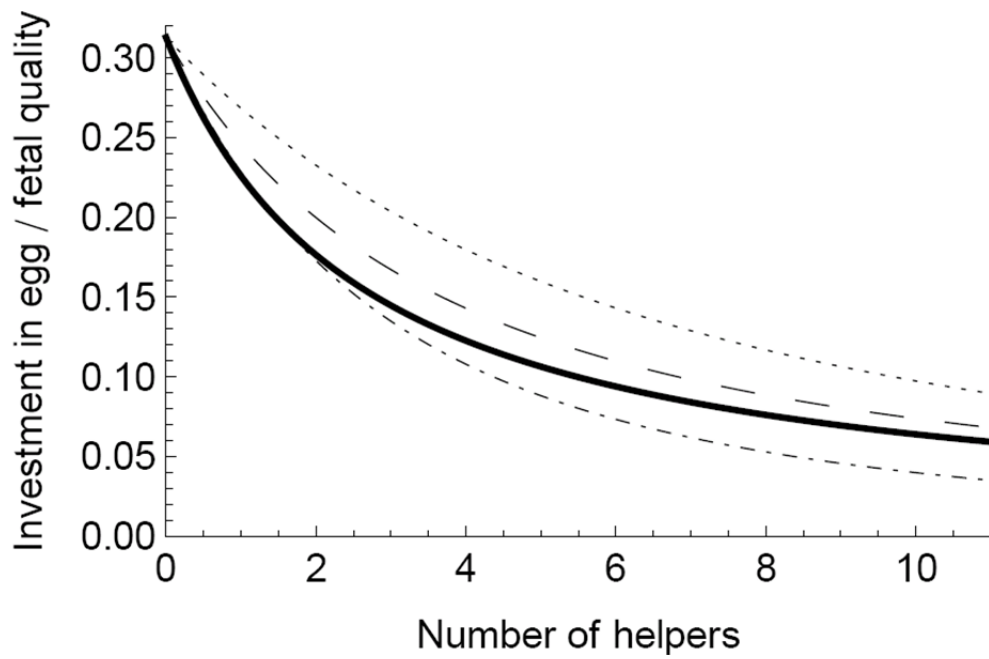
valuable (Fig 4.3a). Individual helpers invest more in small groups than in large groups, and when moving along the altricial-precocial continuum helpers initially invest more when rearing investment is less effective (in order to continue delivering similar benefits to offspring), but eventually reduce investment when the meagre benefits to offspring can no longer offset the costs incurred by carers (Fig. 4.3b). Total rearing investment delivered to offspring peaks at the point on the altricial-precocial continuum where rearing investment is only moderately effective, as the greater requirements of the offspring elicit greater contributions from the carers provided that the group is large enough to support them (Fig. 3c).

Pre-birth investment conveys a ‘silver spoon’

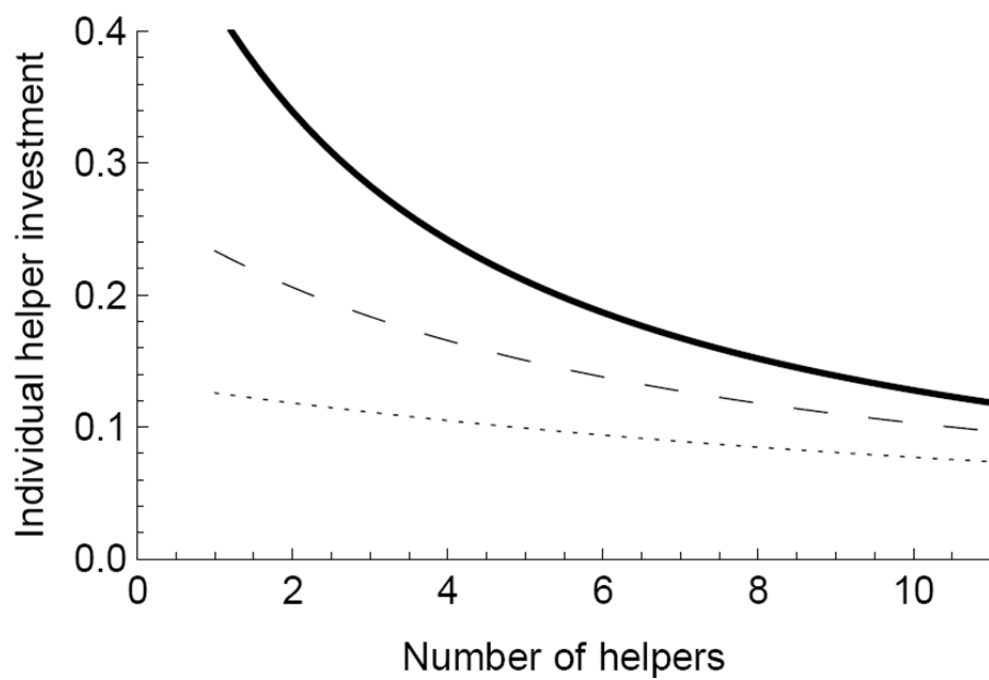
When higher-quality offspring require more investment during rearing, but do better in adulthood if their needs are met ($k_a = -1, n = 1$), breeding females increase their pre-birth investment in offspring quality as helper number increases (Fig. 4.4a). This effect occurs because more helpers can more easily feed larger, higher-quality offspring and hence take advantage of the greater potential benefit that arises when they are sufficiently provisioned. Higher investment in initial offspring quality leads to higher rearing investment to offset the hungrier chicks and to deliver the greater potential benefit of the ‘silver spoon’, and as a consequence maternal pre-birth investment is highest when the care group comprises half-sibling helpers that are related to offspring through the breeding male, because the mother avoids taxing related carers with high costs (Fig. 4.4a).

As with ‘head start’ conditions, under ‘silver spoon’ conditions helpers of all types reduce their individual investment as group size increases (‘load-lightening’)(Fig. 4.4b), although this may be a negligible reduction in groups with distantly-related helpers. As a result, total rearing investment by the group still increases with group size, but in contrast to ‘head start’ conditions groups comprising breeding-male-related half-sibs match or exceed the investment of full-sib helper groups (Fig. 4.4c). Total investment in offspring increases more obviously with group size under ‘silver spoon’ than under ‘head start’ (Fig. 4.4d) conditions, because of the lack of maternal / helper compensation and greater potential benefits of high group size.

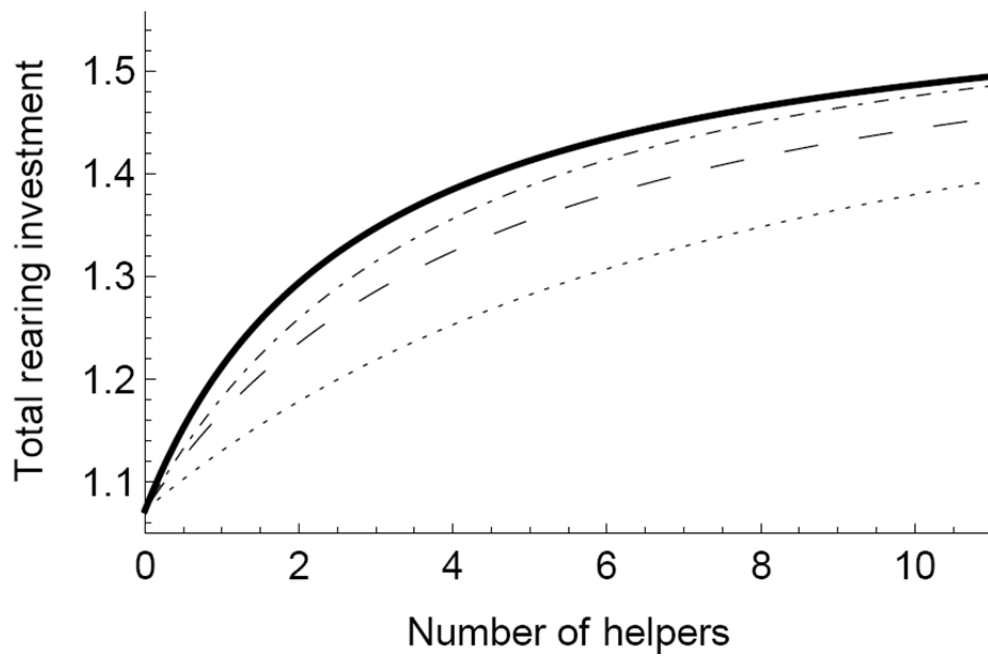
(4.2a)



(4.2b)



(4.2c)



(4.2d)

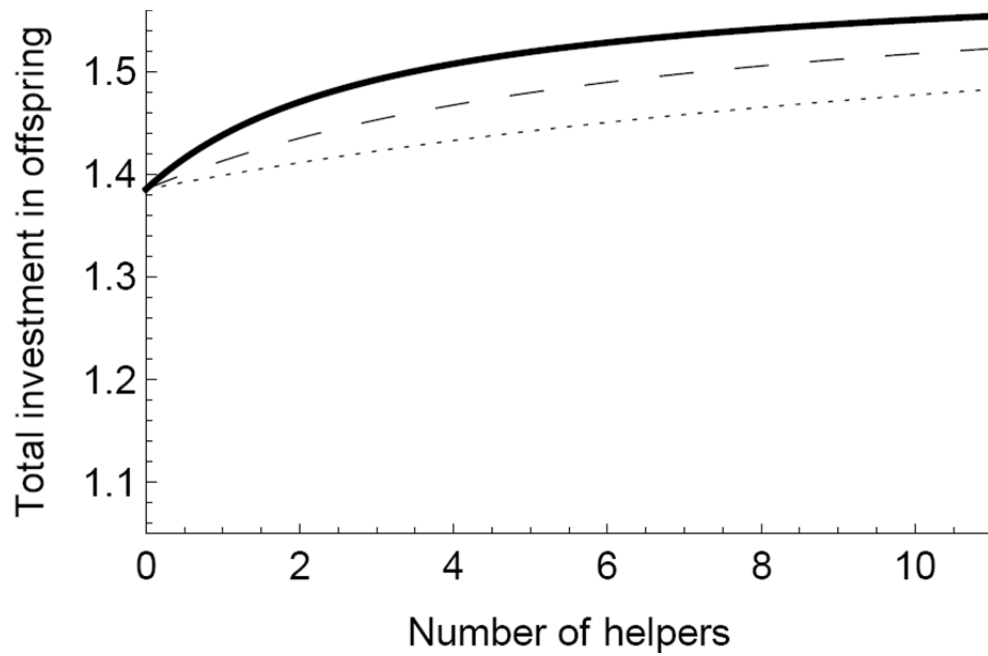
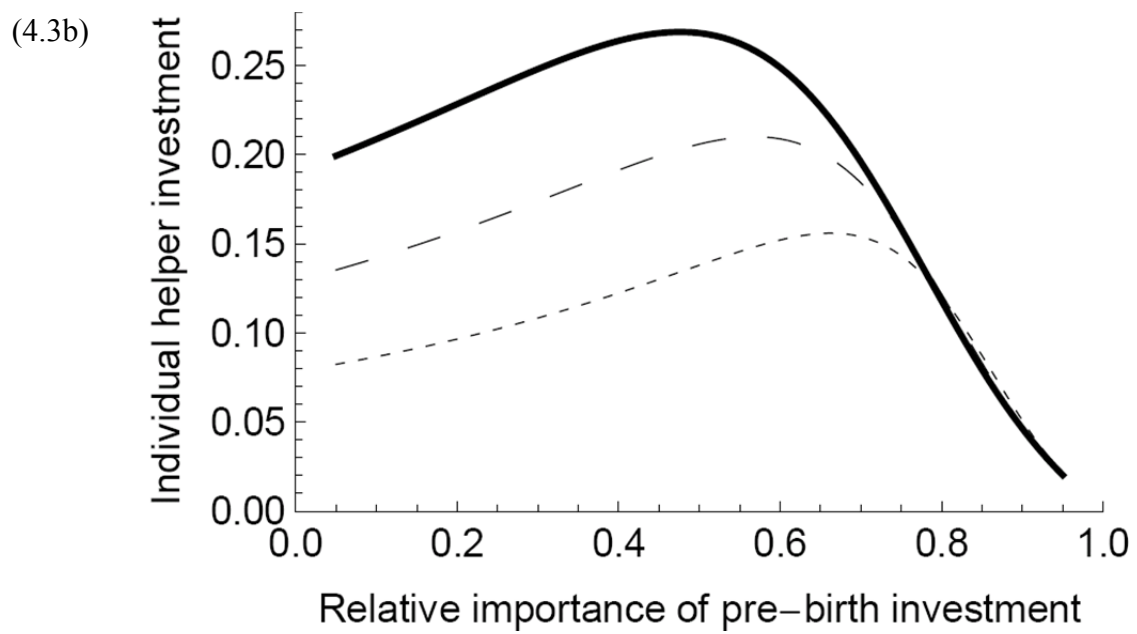
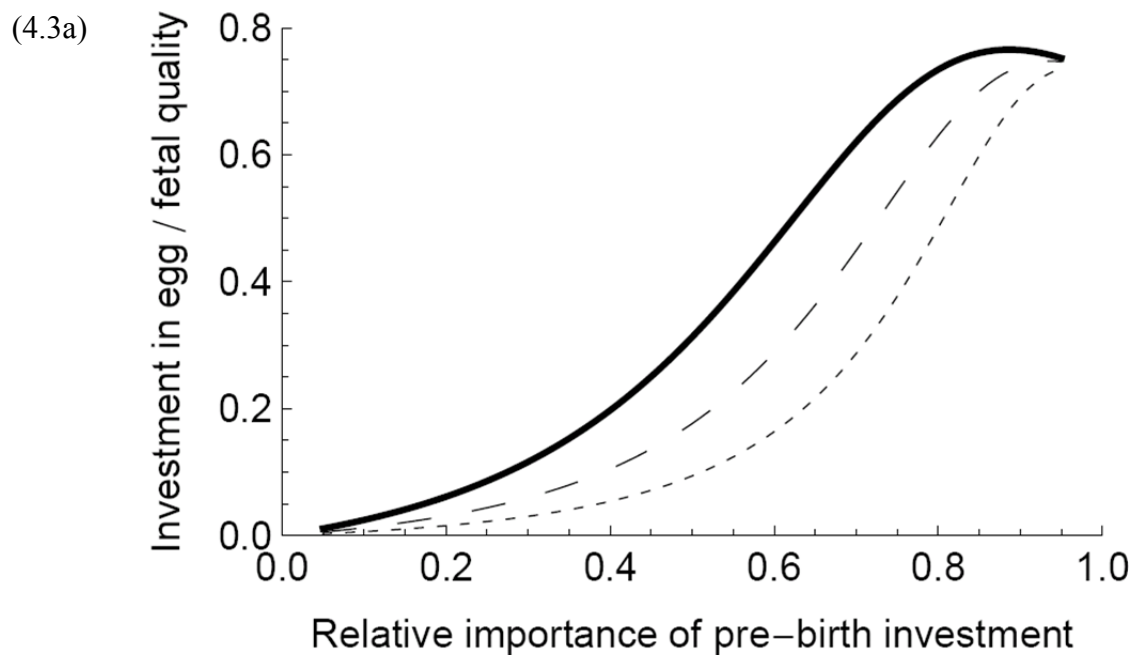
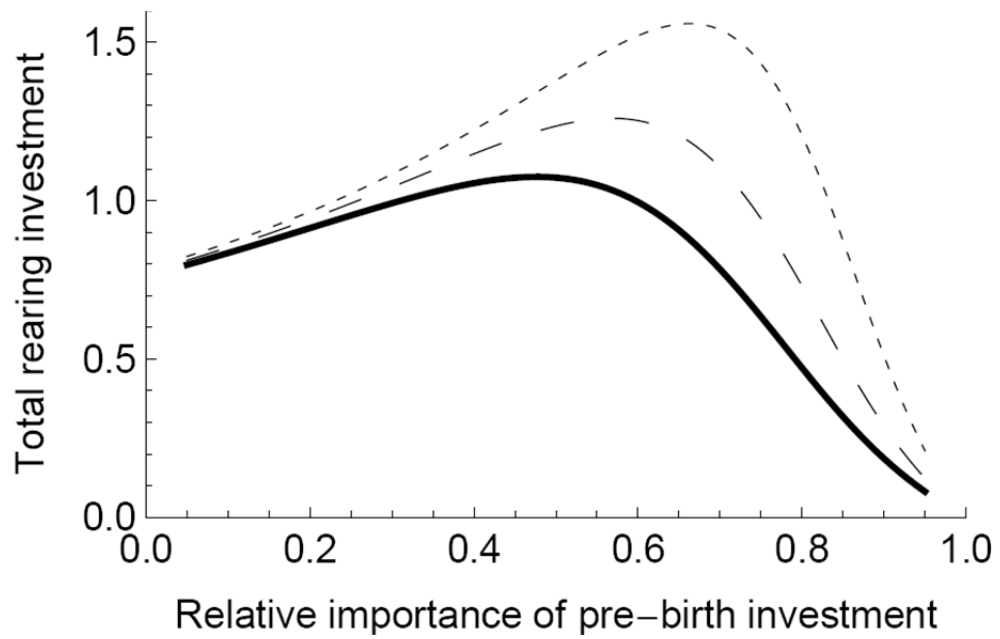


Figure 4.2: (a): Under substitutable ‘head start’ investment conditions, maternal pre-birth investment decreases with increasing group size, as helpers are able to take on a greater proportion of the total investment required by offspring. Breeding females invest less with helpers that are full-siblings to the offspring (solid line) than with half-sibs (dashed = maternally-related; dot-dashed = paternally-related) or cousins (dotted), because closely-related helpers are more willing to deliver more care later in the breeding attempt. (b): Individual helper rearing investment declines with group size as helpers ‘load lighten’ each other; this decline is more obvious the more closely related helpers are to offspring as distantly-related helpers always invest little and thus have little scope to reduce costs (in this plot the paternally-related half-sib line is omitted for clarity, as it very closely overlaps maternally-related half-sibs). (c): The total investment delivered to offspring during the rearing period increases with group size as helpers compensate for the lowered investment of the mother; full-sibling helpers lead to greater total investment than half-sibs or cousins. (d): Total investment in offspring over the breeding attempt (initial female investment + rearing investment) increases with group size regardless of the type of helpers in the group, and despite the reduction in female investment, but the effect is very small as a proportion of total investment delivered and hence might be overlooked empirically. Values of investment levels are arbitrary.



(4.3c)



(4.3d)

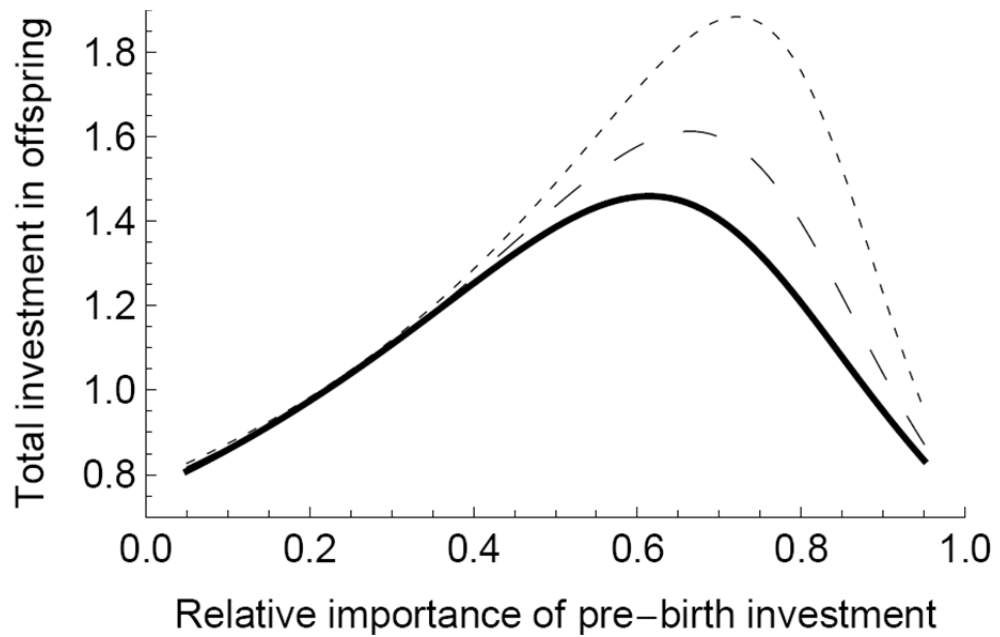
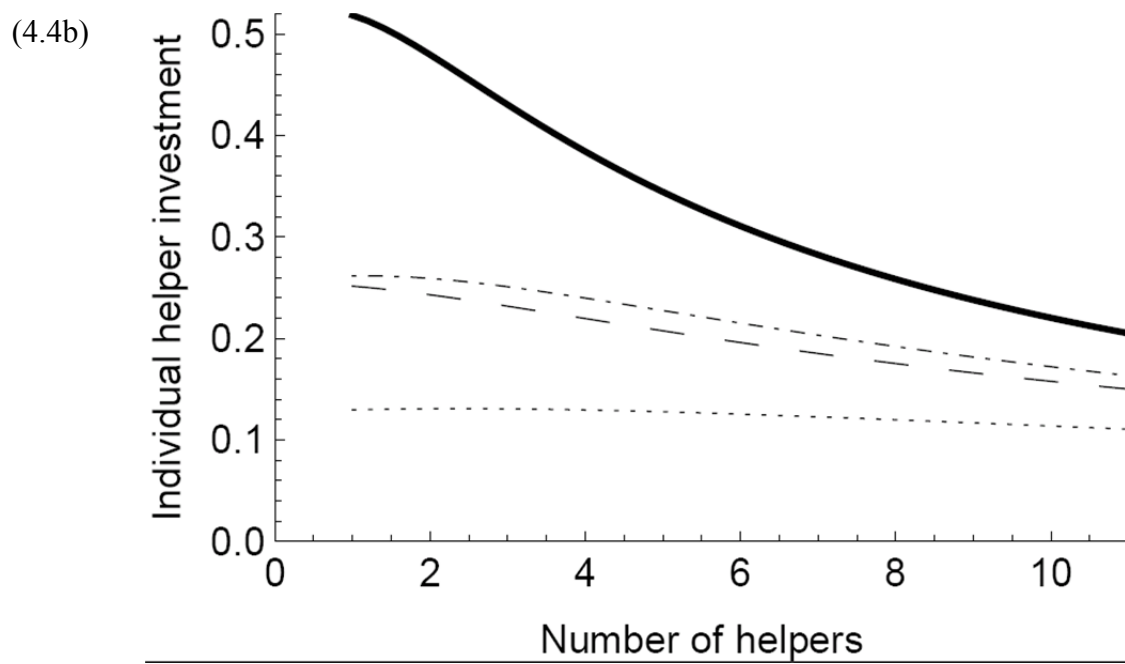
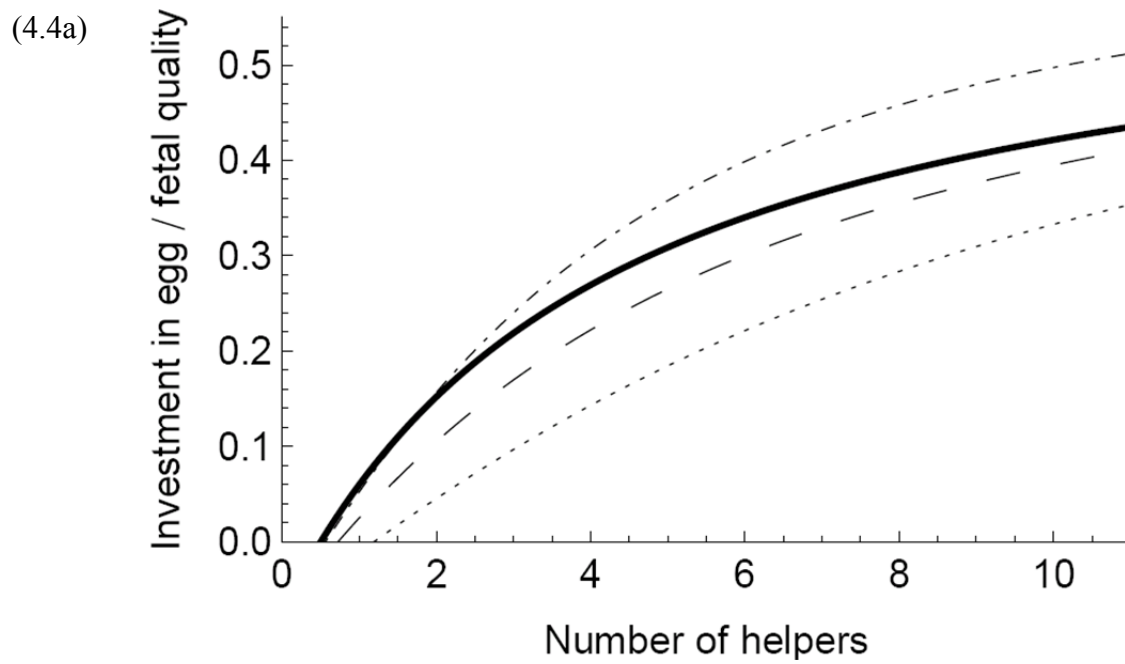
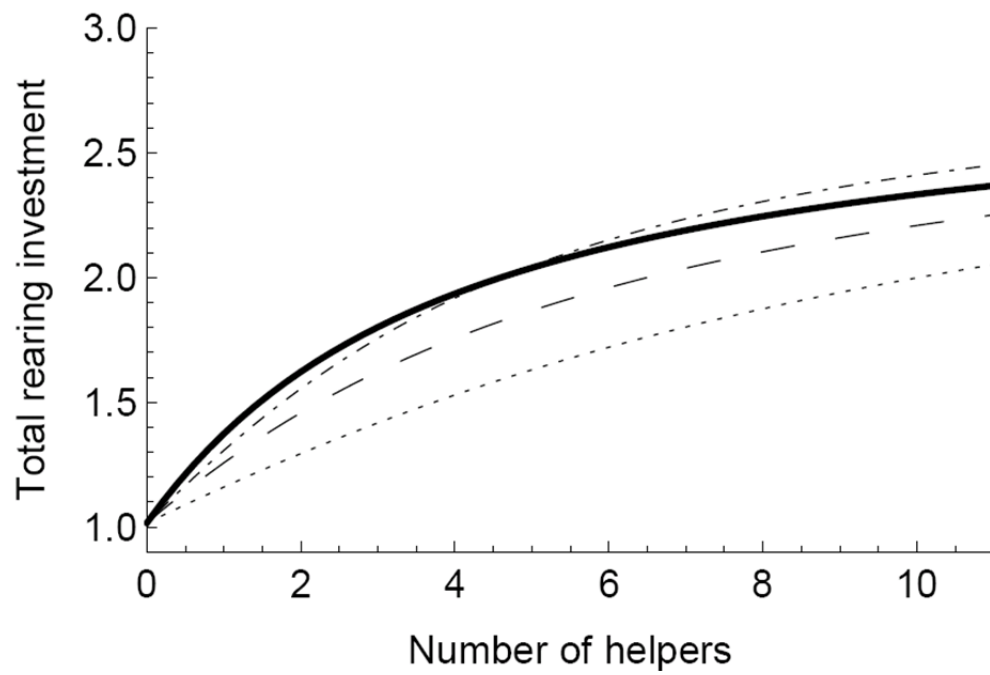


Figure 4.3: (a): Under ‘head start’ conditions, investment in offspring quality is generally greater when early-stage maternal investment is more valuable to young (precocial species), but decreases with extremely important early investment as other carers struggle to deliver any benefits and the female cannot efficiently split her costs between the stages. Quality investment decreases with increasing group size (3 = solid line, 6 = large dashes, 9 = small dashes), but peaks when early investment is more valuable in larger groups. (b): Helper investment is greatest when investment is similarly valuable across the stages, and larger groups peak when rearing investment is less valuable. Helpers generally work harder in small groups (solid line) than intermediate (large dashed) or large (small dashed) groups, but only when rearing investment is similarly or more valuable than early investment: when early investment is critical and rearing investment unimportant more helpers have little effect. (c): Total rearing investment is lower in smaller groups than in larger groups, but diverges more and peaks at higher levels of precociality in larger groups: this is because large groups can support the high investment levels needed to benefit offspring meaningfully even when unit investment is of low value. (d): Total investment in offspring is largely invariant with group size when pre-birth investment is unimportant, when maternal investment is highly valuable large groups deliver substantially more investment to offspring.



(4.4c)



(4.4d)

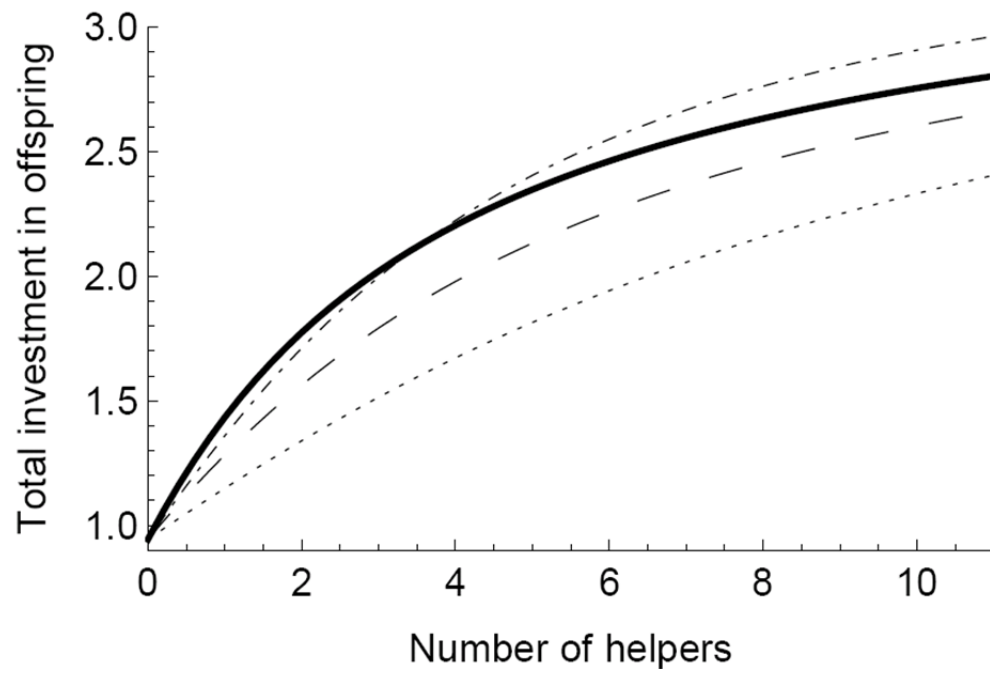
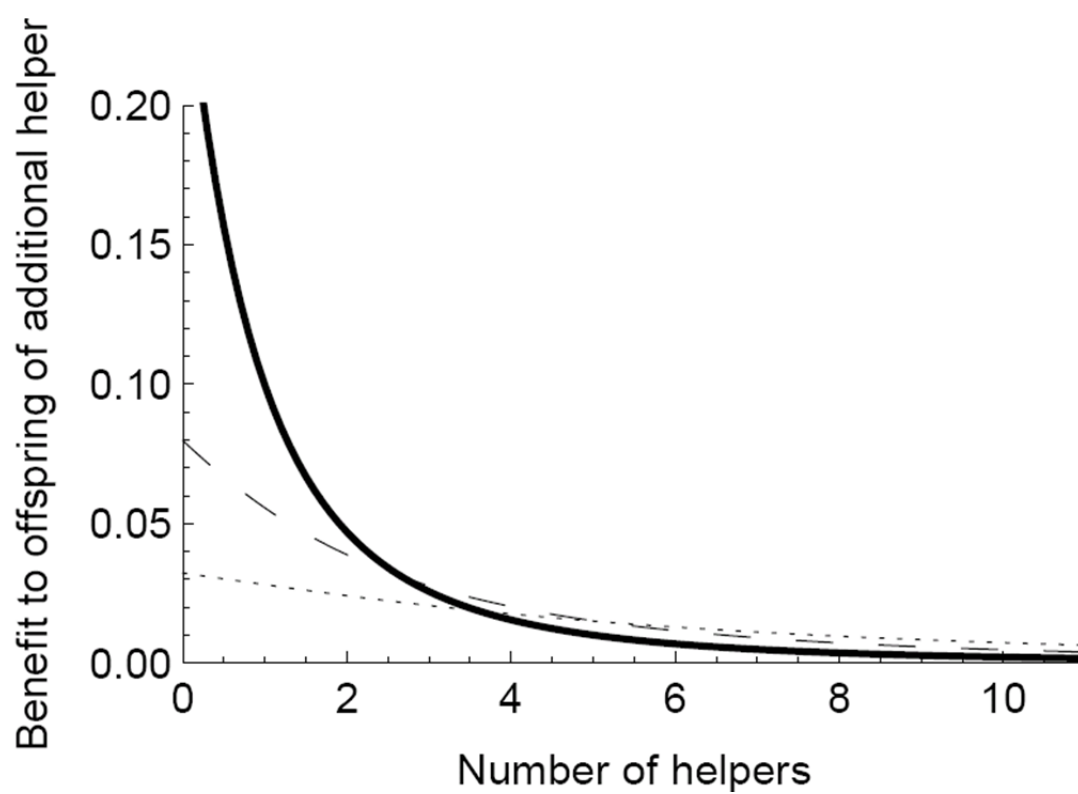


Figure 4.4: (a) When larger offspring require more food but gain greater benefits from investment (a ‘silver spoon’), mothers increase investment in offspring quality as group size increases. The increase is largest when helpers are half-siblings to offspring and unrelated to the mother (dot-dashed line), however mothers invest less with half-sib helpers related through her (dashed) than with full-sib helpers (solid). (b): All helpers load-lighten with increasing group size, with closely related helpers reducing the most. Groups with paternally-related half-sibs contribute slightly more than those with maternally-related half-sibs due to the female adopting a more exploitative pre-birth investment strategy. (c): Total investment by all carers during offspring rearing is greatest with paternally-related half-sib helpers, as the female is willing to extract greater investment from them; full-sib, maternal half-sib, and cousin helpers generate progressively less total investment. (d) Total investment in offspring increases with group size more substantially than under ‘head start’ conditions, but still plateaus at large group sizes. A large group delivers the largest total investment in offspring when all helpers are paternally related half-sibs, whereas in smaller groups full-sib helpers generate the most total investment.

(4.5a)



(4.5b)

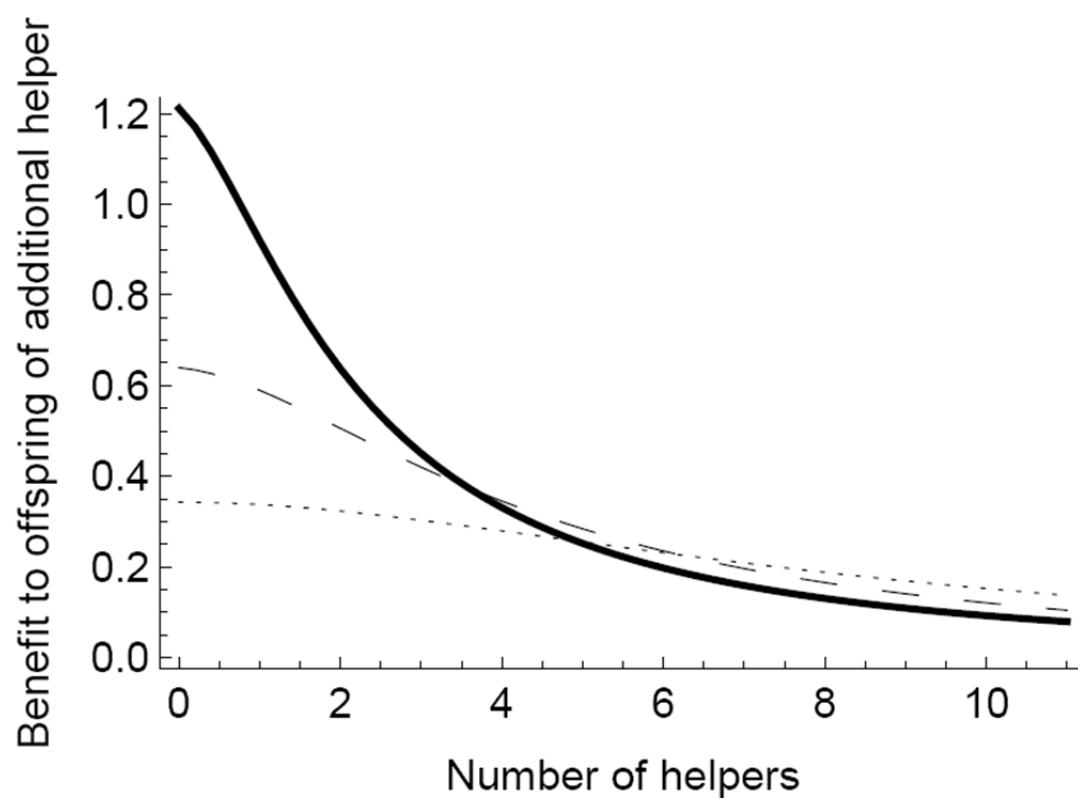


Figure 4.5: (a): Under ‘head start’ conditions, offspring benefit most from an additional helper when in small groups, but this effect is much stronger with full-sibling helpers (solid line) than it is with half-sib (dashed) or cousin (dotted) helpers. In large groups with less-helpful helpers, offspring benefit more from the recruitment of an additional helper than when in similarly sized groups with full-sib helpers, as the current total investment in offspring is lower. (b) The benefit to offspring of adding an extra helper varies similarly under ‘silver spoon’ conditions as under ‘head start’ conditions, but is of greater magnitude due the multiplicative effect of the mother boosting offspring quality. However, the differences in offspring benefit between adding a full-sib helper (solid line) and adding a cousin helper (dotted line) are much smaller under ‘silver spoon’ than under ‘head start’, and substantial benefits to recruiting helpers persist even in large groups.

Recruiting additional helpers

The benefit accrued by offspring from adding another helper to the group varies depending on whether ‘head start’ or ‘silver spoon’ conditions apply. Under ‘head start’ the benefit is greater for small groups than for large groups, and greater when helpers are more closely related to offspring as they are more willing to provide care (Fig. 4.5a). The level of altriciality also has an influence: when rearing investment is largely unimportant to offspring (i.e. in precocial species), the presence of an additional helper predictably conveys little benefit to the offspring, as the new helper is unable to meaningfully change the effective investment received. However offspring in highly altricial species benefit less from an additional helper than do offspring in moderately altricial species, because (i) small groups can deliver high benefits to offspring when rearing investment is highly effective, leaving little for additional helpers to do besides load-lightening, and (ii) the female is unable to split her costs efficiently between both investment stages when her investment in offspring quality is essentially meaningless (Fig. 4.5b).

Under ‘silver spoon’ conditions (Fig. 4.5c), the benefits to offspring of recruiting an additional helper are much greater than under ‘head start’, as helpers can contribute to offspring benefit even in large groups. The extra available care during the rearing period can be directed (via increased maternal pre-birth investment) towards larger, hungrier, but potentially more valuable offspring, rather than simply reducing the costs of other carers through load-lightening. As with ‘head start’ conditions the benefits are greatest with small

groups and with closely-related helpers, however under ‘silver spoon’ conditions the difference between adding a closely- or distantly-related helper is reduced.

Discussion

We find clear differences in how offspring benefit from care, and in the investment strategies adopted by carers, depending on whether maternal pre-birth investment is substitutable or complementary with later investment. Mothers are expected to reduce pre-birth investment under good conditions when their investment gives offspring a ‘head start’, as this transfers more of the costs to the stage that is less costly than usual. In contrast, when pre-birth investment provides a ‘silver spoon’ that leads to potentially greater offspring fitness if they are reared successfully, mothers should take advantage of good conditions by increasing pre-birth investment. Better rearing conditions can arise through greater numbers of helpers available to assist with rearing, as we explore here, but equally applies to pair-breeding species where the ability of males to assist with care varies: if better males simply provide more care, females should compensate by reducing pre-birth investment, but if they provide lasting benefits that are only realised in high-quality offspring, mothers might be expected to increase pre-birth investment when paired with a high-quality mate.

Our results provide support for the concealed helper effects hypothesis proposed by Russell et al. (2007) in cases where pre-birth investment is substitutable with investment during the rearing period when all carers can contribute (the ‘head start’ condition). Females are predicted to reduce their investment in offspring quality when more helpers are present, and helpers to respond by increasing investment in offspring rearing, leading to the total amount of care delivered to offspring remaining similar across a large range of group sizes. This female tactic raises the possibility that empirical studies focusing on the rearing period alone might erroneously conclude that large numbers of helpers can deliver additional investment to offspring without any positive effect, when in reality the helpers are greatly reducing the overall costs paid by the breeding female.

Concealed helper effects should therefore arise whenever investment is substitutable across investment stages, but in practice aspects of ecology or life-history may limit the scope for maternal tactics in particular species. In particular, maternal tactics will be less important

when (a) group size or helper helpfulness is unpredictable at the time when the mother produces the offspring (i.e. there is an unknown supply of care), or similarly (b) when conditions during the breeding attempt are unpredictable, which might make the costs of delivering care difficult to forecast. In some systems (c) the final quality of offspring may be unaffected by early investment (e.g. Van De Pol *et al.* 2006), represented in our model by a very low v , and in others (d) extra carers may only contribute by reducing predation or defending territory (Burt & Peterson 1993) rather than removing quantitative costs of care from the breeding pair: in both (c) and (d) the female should always produce the minimum viable quality of young. In addition, maximal investment in the quality of young should be expected when (e) breeding females are unlikely to breed again, and hence will benefit little from increasing their own survival probability beyond the breeding season (Clutton-Brock 1984). As we show in our model, complementary investment across investment stages leads to different tactics, but the above factors remain important.

The relative benefit to the breeding female of trading off offspring quality against personal costs will vary depending on the breeding system, because in species with strong competition for breeding positions it may be especially valuable to produce very high-quality offspring when the opportunity arises, as only high-quality individuals are likely to reproduce. A similar effect could also arise more proximally when offspring must compete for survival with other broods at an early age (e.g. Van Dijk *et al.* 2013). If rearing the highest-quality offspring is only possible when offspring are born at high quality, the potential benefits lead to the female increasing pre-birth investment under good conditions as her contribution boosts the value of investment delivered during the rearing period. In our model, this ‘silver spoon’ relationship (‘dynamic complementarity’ *sensu* Heckman 2007) indeed leads to female pre-birth investment matching rather than compensating for current conditions. For example, if body mass at birth has a multiplicative effect on the likelihood of becoming a dominant breeder assuming adequate food during rearing, mothers might favour high pre-birth investment even when it is costly and not intrinsically valuable (or is even harmful, if larger offspring require more food) without follow-up investment by the group. Conversely, if offspring of low quality at birth are produced and investment is complementary, one might expect parents to reduce investment during rearing rather than attempting to compensate, as the offspring are unlikely to become breeders regardless of the level of rearing investment provided.

More theoretical work is needed on how tactical maternal investment can modify investment rules and outcomes for offspring in cooperative groups. Along with previous work on female manipulation of offspring number (Savage et al. 2013a, 2013b), we have shown that maternal investment in offspring quality can drastically alter investment rules in cooperative species. However, even when assuming a simple trade-off between offspring number and quality it is difficult to predict the expected investment strategies if females can alter both factors simultaneously. Offspring size is often used as a proxy for offspring quality, but although size-number relationships have been widely explored across many taxa (Kaufman & Kaufman 1987; Smith et al. 1989; Sinervo & Licht 1991; Roff 2002; Walker et al. 2008), changes in one factor may have complex effects on the other, making the assumption of simple size-number trade-offs unreliable (Lepage et al. 1998; Brown & Shine 2009). Most valuable as an addition to current theory would be a demographic approach to modelling a cooperative breeding system, incorporating dispersal patterns and potential alternative options for helpers in addition to maternal control of offspring size and/or number. This would facilitate cross-species comparisons of investment strategy by exploring intra-group relatedness, the costliness of different breeding stages, and helper investment decisions within a more flexible model framework. In addition, dynamic complementarity effects between development stages require further attention as a potential explanation for the range of maternal investment tactics seen in nature.

5: Turn-taking in the cooperatively breeding chestnut-crowned babbler



Abstract

When multiple individuals contribute to rearing a brood of offspring, efficient delivery of resources is difficult because each benefits if the other(s) provide a greater share of the total investment required. A recent study has suggested that when individuals can monitor the investment of others, a simple strategy of turn-taking can resolve this problem, and has provided evidence for ‘alternation’ between great tit parents feeding their young. Such strategies might prove more difficult for cooperatively breeding birds, in part because the greater number of carers in such species makes it more difficult for them to monitor one another’s behaviour and hence to maintain turn-taking. To test whether turn-taking occurs in a natural cooperative system, we use a continuous time Markov model to deduce the provisioning rules governing investment in the chestnut-crowned babbler (*Pomatostomus ruficeps*), an endemic Australian cooperatively-breeding bird with variable group size. Our analysis reveals that a high degree of turn-taking occurs between group members, such that individual birds are far more likely to visit following other individuals than to make a repeat visit themselves. We show using a randomisation test that part of this turn-taking arises through the distribution of individual inter-visit intervals (‘passive’ turn-taking) and part through individuals deliberately responding to the investment of others (‘active’ turn-taking). We conclude that turn-taking in babblers is a consequence of both deliberate response rules and foraging ecology, with the latter effect arising from the existence of a typical minimum time required to forage and travel to and from the nest. Our work underlines the importance of considering both the social and ecological context when investigating parental care behaviour in nature, and demonstrates that turn-taking is a feasible way to organise investment across a range of cooperative group sizes.

Introduction

Individuals who cooperate to raise offspring face several problems when attempting to provision their young efficiently. Firstly, care is costly (Williams 1966b), so each individual stands to gain if other carers contribute a greater share of the required provisioning. Secondly, each individual has only partial knowledge of the provisioning behaviour of other individuals, which results in uncertainty about both the relative contributions of other carers and the current needs of the offspring. Both of these factors influence the provisioning decisions of carers, and the uncertainty becomes progressively greater as the number of individuals contributing to care increases.

Existing theory on offspring care has focused on the total amount of care delivered and on the response of carers to a change in the amount delivered by others. Models have typically adopted either 'sealed bid' (Houston & Davies 1985) or 'negotiation' (McNamara et al. 1999; Lessells & McNamara 2012) approaches to find the optimum investment level (or response rule, in negotiation models) for each carer during the breeding attempt. Both methods produce qualitatively similar results, generally predicting incomplete compensation for changes in partner investment (McNamara et al. 1999), although additional considerations such as asymmetric information about the offspring among carers (Johnstone & Hinde 2006) or threshold effects such as partner desertion (Jones et al. 2002) can lead to alternative predictions. Empirical support for incomplete compensation is strong in biparental species (reviewed in Harrison et al. 2009), but significantly weaker in cooperative species where non-breeding individuals also contribute to care (Hatchwell 1999).

The solutions to sealed-bid and negotiation models do not generally lead to the best possible outcome for carers as a group, since their joint payoffs could be increased by all carers simultaneously raising their investment (Johnstone et al. 2014). In effect, carers are trapped in a many-player Prisoner's dilemma-like situation (Glance & Huberman 1994) in which each carer benefits from 'defecting' (by reducing care) for a marginal increase in their personal payoff, despite the resulting overall loss in payoff when all individuals adopt this strategy. When individuals are highly responsive to changes in investment by others, negotiation may even result in offspring receiving less investment from two cooperating parents than from a lone parent (McNamara et al. 2003). Nevertheless, existing work suggests that cooperation can be maintained if repeated interactions allow individuals to reward cooperators and/or

police exploiters/defectors (Axelrod & Hamilton 1981; Frank 2003), relying on simple mechanisms such as group knowledge of the contributions provided by others (Keser & Van Winden 2000). The tendency of individuals to invest more in a common project if others invest similarly is known from studies on humans to assist in optimally providing for a common good (Fischbacher et al. 2001; Frey & Meier 2004), but evidence for it in animal studies is lacking, possibly due to limitations in cognition (West et al. 2007).

In many natural systems investment in offspring takes the form of collective provisioning by all carers, which is split into many discrete events wherein a single carer brings food to the offspring. These repeated events provide an opportunity for individuals to minimize potential cheating by applying a turn-taking strategy to offspring care: if individuals reduce their provisioning rate after they visit, and increase it after others visit, all carers will broadly contribute the same amount over the breeding attempt. Perfect turn-taking is unlikely to occur in natural systems due to imperfect information and stochastic factors, however any significant response to other carers will improve investment efficiency (Johnstone et al. 2014). Recent work on great tits (*Parus major*) has provided evidence that such reciprocal investment rules are used to regulate provisioning of young, and that this strategy can provide a solution increasing the fitness of both parents, provided provisioning by one parent can be observed by the other (Johnstone et al. 2014).

Here, we extend the approach of (Johnstone et al. 2014) to analyse investment in groups with larger numbers of carers, using a continuous-time Markov-Chain Monte-Carlo (MCMC) model (Bremaud 2001; Harcourt et al. 2010) to analyse nest provisioning data from the cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*). Chestnut-crowned babblers are medium-sized (50g) endemic Australian passerines that breed in groups of 2-15 (mean ≈ 6), with helpers that provision at the nest in addition to the breeding pair (Russell et al. 2010; Browning et al. 2012a). Babbler groups forage together within stable home ranges (Portelli et al. 2009), and often return to the nest area as a group when individuals provision (pers. obs.), providing ample opportunity for individuals to observe the contributions of others. Babblers do not ‘cheat’ by pretending to deliver food to offspring (Young et al. 2013), and their contributions are not driven by considerations of social prestige (Nomano et al. 2013). As such, babblers provide an appropriate model system to investigate fine-scale response rules in the provisioning of offspring, including turn-taking strategies. Markov-chain models have previously been used with success to describe animal behavioural

rules in several contexts (Harcourt et al. 2009, 2010; Patterson et al. 2009; Johnstone et al. 2014), and we demonstrate here that they are also applicable to studying the fine-scale organization of provisioning in cooperative breeders.

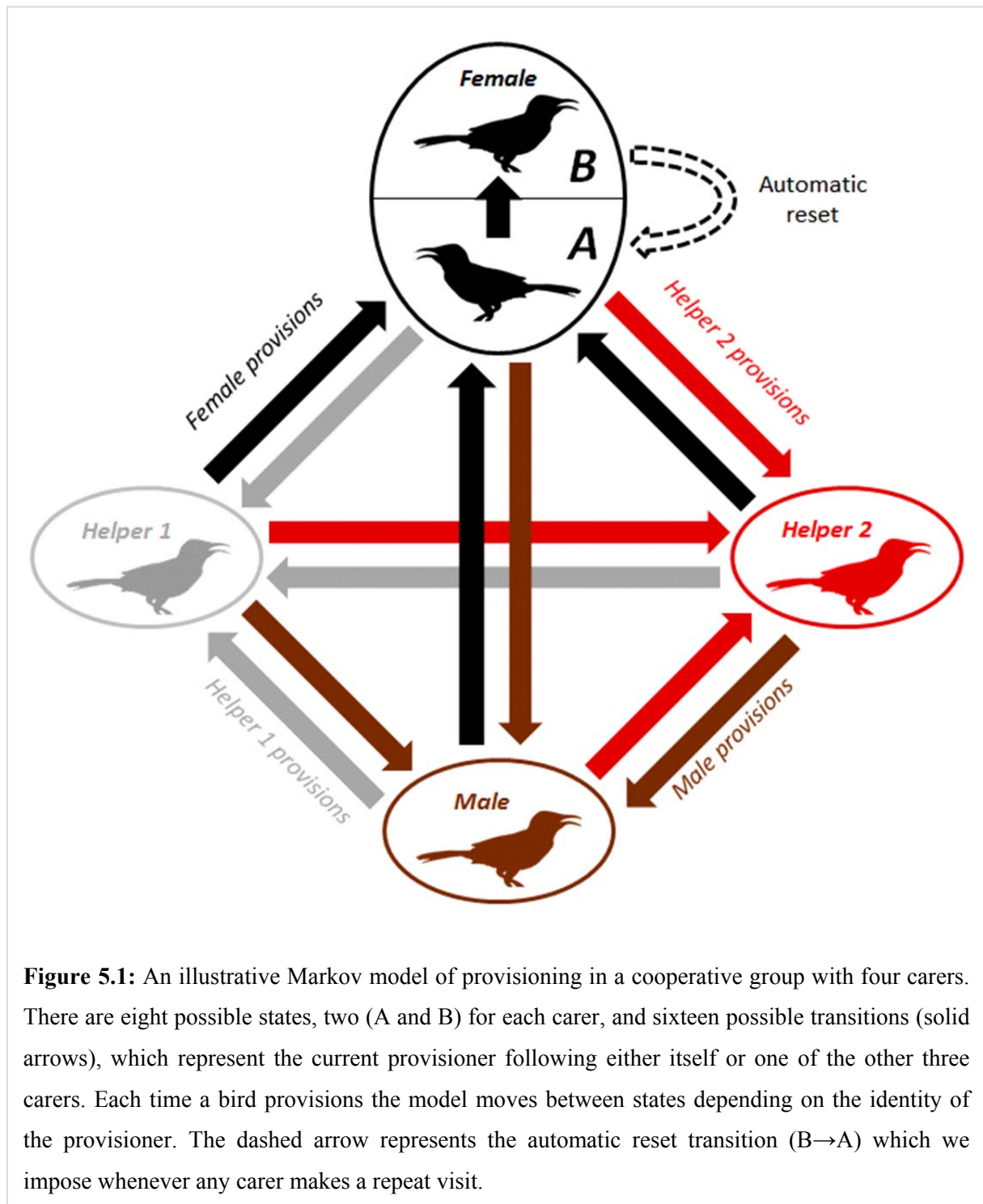
Methods

Data collection

Provisioning data were collected between July and November of 2007 and 2008 at Fowlers Gap Arid Zone Research Station, NSW, Australia (Lat. -31.1, Long. 141.7). Adults were caught using mist-nets, ringed, tagged with Passive Integrated Transponder (PIT) tags (2x12mm, Trovan Ltd.), and had a small (<100µl) blood sample taken from the ulnar vein. Chicks were similarly blood-sampled, ringed and PIT-tagged at around 15 days old. Chestnut-crowned babblers are sexually monomorphic, so identification of parentage and sex was primarily obtained through molecular analysis (Holleley et al. 2009; Rollins et al. 2012). Group composition was determined through repeated group counts and colour-ring sightings before and after group capture, and only groups known to have all individuals PIT-tagged were used for the current analysis. Chestnut-crowned babblers build large enclosed stick nests with a single entrance, around which we fitted a coil antenna connected to a data-logger (LID650, Dorset ID b.v.) at the base of the nest tree; this allowed us to capture all of the nest visits of PIT-tagged individuals. For further details of the system and techniques used to collect nest visit data see Young et al. (2013).

Babbler groups used for this analysis were known from observation and capture to have all members PIT-tagged, to remove any ambiguity arising from provisioning by extra birds invisible to the data-logger. For our analysis, we restricted ourselves to nest visit data from broods above ten days in age to avoid confusing female brooding behaviour with provisioning, and also removed any partial days of visit data in which each significant carer (see below) visited fewer than ten times. We also discounted data from the last day in the nest prior to the fledging date, and any data from periods of disturbance (such as periodic measuring of chicks or changing of data-loggers). Any group with at least one complete day of provisioning data was then used in the analysis. To determine independent nest visits, we grouped multiple

triggers by the same individual into a single visit when they occurred within two minutes, an approach validated by direct nest observations and nest camera data showing that repeat visits by the same individual within two-minute intervals do not generally represent additional food delivered to offspring (Young et al. 2013).



Classification of carers

In chestnut-crowned babblers some individuals in a group do not visit the nest to assist with chick provisioning, or visit infrequently; these individuals are usually immigrants or juveniles (Browning et al. 2012b). In addition, birds from other breeding groups will occasionally visit a nest, usually when they are members of the same, larger social group. For our purposes we are interested only in significant carers not the total group size, as individuals that contribute only rarely to offspring care have little opportunity to respond to the investment of others. Furthermore, attempting to fit individuals with very few visits into our model is problematic because some possible model transitions may never appear in the data (e.g. if two rare visitors are included they are likely to never follow one another), making it impossible to estimate some theoretically viable transition rates. To determine the number of significant carers, individuals in a group were first ranked in order of total visit number. The individual with the lowest number of visits was excluded if its total visits failed to exceed 20% of the mean total visits of the rest of the group. If excluded, the process was repeated with the next-lowest visiting individual until all remaining individuals exceeded 20% of the group mean. When important, helpers are differentiated from each other by their visit rate, with the highest-rate helper referred to as the primary helper.

Applying the above process to all groups with complete visit rate data available over several days resulted in 4 groups with two (significant) carers, 6 with three carers, 5 with four carers, 3 with five carers, and 2 with six carers; between zero and five individuals in each group were excluded for failing to classify as a significant carer (mean = 1.1). The amount of data required to fit our model grows rapidly as group size increases, because the number of transitions to be estimated is equal to the square of the carer number. This need for disproportionate amounts of data at large group sizes meant that two groups with good visit rate data were excluded from the final analysis because they contained too many significant carers (8 and 9) for the data available. Among the groups used, brood size ranged from 1-5 chicks (mean 3.3), and initial chick age from 10-19 days old. Previous work suggests that babbler provisioning rate increases only slightly between day 10 and day 20 (Browning et al. 2012b). Differences in provisioning rates between different classes of carer, and effects of nestling age have previously been described for this system in detail and with higher sample sizes (Browning et al. 2012a, 2012b), so we did not pursue any further analyses of the relative levels of contribution provided by different carers.

Markov analysis

For each breeding attempt ($n = 20$, one breeding group represented twice) we fitted a continuous-time Markov Chain model to the nest visits by the group, using the R package MSM (Jackson 2011). Each visit was treated as a discrete event, and the model ‘state’ was defined by the identity of the last individual to visit the nest. This formulation violates the assumptions of MSM, because some of the events, specifically repeat visits by the same bird, do not change the state of the system. To allow for this we added a second ‘dummy’ state for each bird to represent a repeat visit by the same individual. Whenever a transition to a dummy state occurred (i.e. whenever there was a repeat visit), we imposed an immediate ‘reset’ transition to return the system to the base state for that individual. With this arrangement, which we used in all of our analyses, groups with c carers featured $2c$ states and $c(c+1)$ possible transitions between those states, including resets (Fig. 5.1). The best fit model calculated by MSM specifies the rate at which each possible transition occurs (which determines how likely particular birds are to follow particular other birds). We assume that individuals may react differently to each other carer visiting the nest, and thus estimate, for each individual, as many different visit rates as there are carers (so that there are c^2 transition rates to be estimated, ignoring resets). However, because of the number of possible transitions in larger groups, it is also useful to define an individual’s mean transition rate when they follow any bird other than themselves. Following Johnstone et al. (2014), we define this transition rate (‘following another’) as λ , and the transition rate when an individual makes a repeat visit (‘following self’) as μ .

Model validation

A major problem with naïvely analysing visit data for patterns of turn-taking is that confounds can easily arise from foraging behaviour. If each individual has to spend a certain amount of time foraging and travelling to and from the offspring between successive provisioning events, then ‘passive’ turn-taking will arise simply because other individuals can visit during this interval, while the focal bird cannot. If the minimum inter-visit interval of each individual is highly consistent, near-perfect turn-taking might be expected even if individuals do not monitor or respond to one another’s behaviour in any way. Passive turn-taking will be less

precise if the ‘refractory period’ is variable, but even with highly variable intervals any significant refractory period will introduce some degree of bias towards turn-taking. To distinguish between this ‘passive’ turn-taking and ‘active’ turn-taking that is a direct result of individuals responding to one another’s visits, we therefore employed a randomization test similar to that used by Johnstone et al. (2014).

To carry out the randomization test, we first removed potential ‘active’ turn-taking from the data by eliminating any relationship between the visit times of different individuals. To perform this dissociation we first calculated all of an individual’s inter-visit intervals in a given day, then randomly reordered these intervals within each individual and day. From these randomized intervals we reconstructed a new list of artificial visit times for each individual on each day. The artificial visit times for all individuals were then combined to form an artificial provisioning day, which was recoded and analysed in the same way as the original data. We re-ran the above dissociation followed by our standard analysis 1000 times on the data from each breeding attempt, to generate a distribution of expected (passive) turn-taking given the structure of nest visits. By comparing the extent of turn-taking observed in the natural data to the distribution of values obtained from the dissociated data, we can determine the degree to which turn-taking is ‘passive’, i.e. simply attributable to the lack of immediate re-visits, or ‘active’, being caused by individuals responding to one another’s behaviour.

Results

Visit rates and turn-taking ratios

Provisioning data were analysed for 20 breeding attempts by 19 different breeding groups (315-1475 nest visits per attempt, mean = 765). As an initial test for non-randomness in the patterns of individual visits, we used a runs test on the five groups with only two carers, and in all of these groups the carers visited significantly non-randomly ($p < 0.0001$). Across all carers ($n = 73$) and group sizes (2-6), individuals were more likely to visit following another bird than to visit twice in a row (total: 13096 vs. 2208 visits), with the proportion of visits

following other birds increasing with group size (0.75-0.94 for group sizes 2-6, mean proportion across all attempts: 0.85).

Our Markov analysis further supports the occurrence of turn-taking, as across all carers individual transition rates for visits following another bird ($\lambda = 123.7 \pm 43.4$) were much higher than those of an individual following itself ($\mu = 50.5 \pm 18.2$) (mean \pm s.d., $p < 0.0001$). One breeding attempt was excluded from further analysis due to insufficient data; for a majority (17/19) of the remaining groups, models in which individuals visit at different rates following particular other individuals were a better fit ($p < 0.05$) than models that assumed each individual had only two possible visit rates (λ and μ), and in all groups both of the above individual-specific models were better fits to the data ($p < 0.01$) than a null model assuming all individuals has the same two possible rates (λ and μ). Despite this variation, across all groups mean transition rates were not significantly different between breeding males, breeding females, and the most helpful helpers in a group (Figure 5.2a). The only significant differences among carers were between the lowest-visit-rate helper and the other carers in groups with more than one helper (Figure 5.2b).

There were no significant effects on individual transition intensity from mean visit rate of the breeding group, group size, brood size, brood age, or the number of carers per offspring ($p > 0.05$), although this is attributable to small sample sizes and our restricted window of analysis, as some of the above factors are known to influence babbler provisioning behaviour when the entire rearing period is considered (Browning et al. 2012b). There were no significant pairwise relationships between individual transition intensities, leading to the conclusion that particular birds were not more likely to follow birds that in turn were more likely to follow them (Figure 5.2c). We infer from this finding that there are no sub-group organisations within which babblers adopt turn-taking rules.

Inter-visit intervals

As indicated above, the natural data show that individual babblers tend to alternate their visits, and are less likely to visit again after they have just visited themselves. Although potentially attributable to ‘active’ turn-taking by individuals responding to others’ investment, it is also possible that turn-taking arises ‘passively’ due to constraints on the distribution of individual

inter-visit intervals, for instance because individuals require a well-defined minimum period to forage for food items and return to the nest. We found that individual inter-visit intervals are highly skewed, peaking at short (2-6 minute) intervals with very long tail of larger intervals that approximates the shape of a geometric distribution, which would be expected in the absence of a refractory period (note that no intervals below 2 minutes are present in the data due to the initial processing of the PIT data: see methods). Median intervals across different group sizes and carer categories ranged between 393 and 611 seconds (means: 522-1324 seconds). Approximately 97% of all inter-visit intervals were less than one hour, suggesting that provisioning was generally continuous by all individuals within a day: the primary difference between high-visit rate and low-visit rate carers is in the number of very long inter-visit intervals, suggesting that lower visit rate carers take more frequent ‘breaks’ from provisioning offspring rather than foraging less efficiently (Figure 5.3).

‘Passive’ or ‘active’ turn-taking?

The tendency for babbler visit data to show turn-taking ($\lambda/\mu > 1$) in all groups is far lower under our randomization test than in the natural data (Figure 5.4), suggesting that the largest component is ‘active’ turn-taking caused by individuals directly responding to each other. Of 19 groups, only one randomization test generated turn-taking rates that overlapped with those in the natural data. Nevertheless, significant ‘passive’ turn-taking is still present in a majority of groups in the randomized data (12/19 groups exclude $\lambda/\mu=1$ from the minimum possible value on 1000 randomized data runs), suggesting that individual inter-visit intervals generate some degree of visit structure (Figure 5.4).

Discussion

We found strong evidence that chestnut-crowned babblers use information about when other carers visit to modify their own personal visit rate (‘active’ turn-taking), however part of the turn-taking observed in the natural data is attributable to the distribution of individual inter-visit intervals, and hence represents ‘passive’ turn-taking. Our findings both support and contrast with those of a previous study on great tits (Johnstone et al. 2014), as although

babblers demonstrate ‘active’ turn-taking in the same manner as great tit parents, Johnstone et al. found that great tits show little evidence of ‘passive’ turn-taking. Turn-taking was similarly prevalent across all group sizes, and helpers and breeders adopted similar rules provided that they were contributing similar amounts of care.

Our conclusion that turn-taking in our data is partly a passive by-product of individual inter-visit intervals raises the question of how this passive turn-taking arises; we argue that it can be straightforwardly explained through foraging ecology. If an individual takes some well-defined minimum period to travel to and from the foraging site, and another minimum period to find food while foraging, then its inter-visit intervals will have a well-defined minimum value. Furthermore, if an individual must regularly cease provisioning chicks to restore its personal energy reserves, a further period will be added to the minimum visit interval during continuous provisioning. In these cases, likely in many natural systems, there will always be a weak signal of turn-taking because other contributing individuals can visit during the refractory period while the focal individual cannot. In an extreme case, when foraging and travel time are highly consistent and personal needs of the carer are negligible, near-perfect turn-taking could appear in natural provisioning data without individuals deliberately responding to each other at all. For the above reason, a weak signal of passive turn-taking was inevitable in our data due to the way the raw PIT-tag data was processed: no individual inter-visit interval could be less than two minutes, as PIT readings from the same individual were grouped into a single visit if they occurred within two minutes of each other. While the choice of a two-minute grouping window has been validated using nest video data and nest-watches (Young et al. 2013), and hence we believe our results to be robust, it makes it difficult to accurately assessing the relative strengths of ‘passive’ and ‘active’ turn-taking in babblers.

Several possible reasons for babblers exhibiting both ‘active’ and ‘passive’ turn-taking are suggested by their breeding behaviour and ecology. Compared to great tits, babblers forage more distantly from the nest (Portelli et al. 2009), are not agile flyers, and appear to suffer costs associated with travelling to and from the nest (Browning et al. 2012b). These factors decrease the ability of individual babblers to deliver separate food items in quick succession, and hence bias the natural data towards passive turn-taking. Unlike great tits, babblers bring prey of similar size to the nest on each visit (Browning et al. 2012b), which supports the use of simple turn-taking rules because visit rate alone is a reasonable proxy for investment delivered (i.e. individuals cannot reduce food item size to free-ride off others’ efforts). Recent

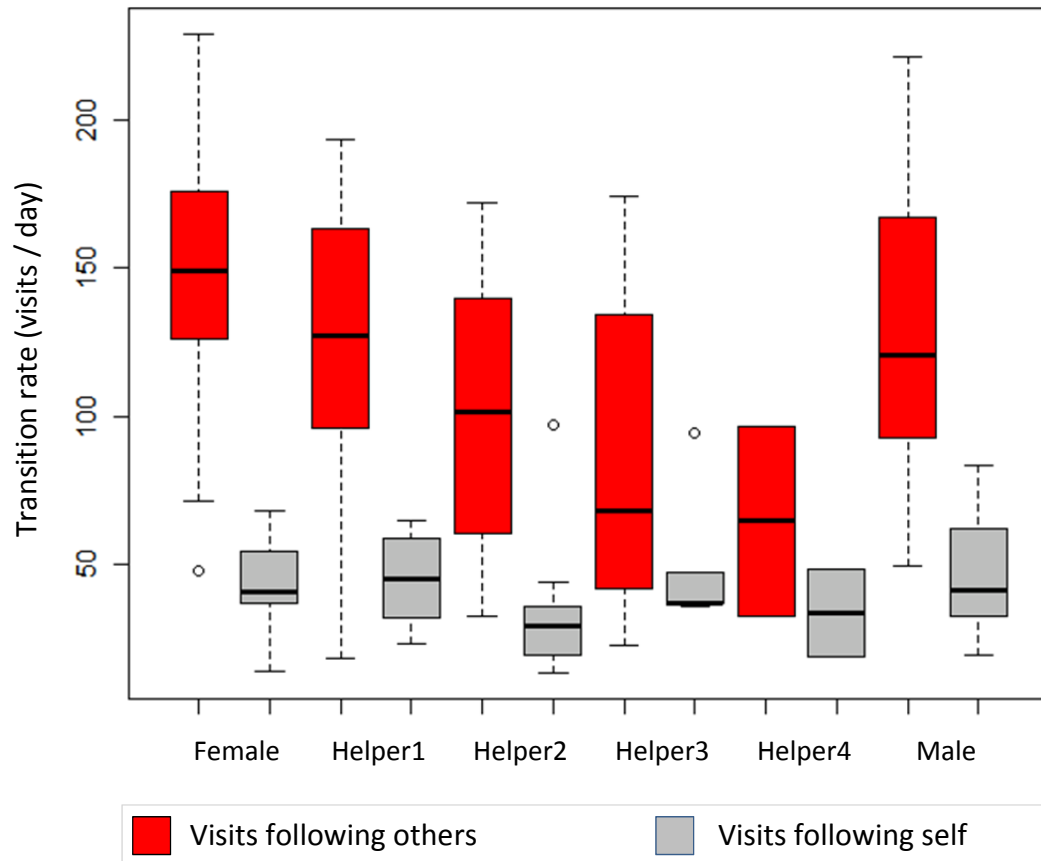
work has suggested that babbler groups often visit the nest area as a unit, irrespective of whether or not they have food to provision nestlings (Nomano et al. 2012), which potentially increases the scope for turn-taking by allowing individuals to more easily monitor the contributions of the entire group. Group visits may further contribute to the strong signal of turn-taking in babblers by increasing the refractory period (if individuals must visit the nest when they do not personally have food to provision), and by increasing the likelihood that multiple different individuals provision in quick succession (when several group members have food to deliver during a group visit).

Our results suggest that when analyses of investment in offspring are focused entirely on the nest, important influences of foraging ecology can be easily overlooked. In our study we used the distribution of inter-visit intervals and a randomization test to check whether we were observing true responsiveness to the behaviour of others, and found greater levels of turn-taking in the natural data than expected when there is no interaction between individuals. However, the randomized data still showed ‘passive’ turn-taking, and one can easily imagine a case in which turn-taking was entirely attributable to patterns of individual visits. The potential lack of robustness in our initial results underlines the importance of considering the foraging ecology of the species in question, and ensuring that individuals are actually responding to one another. Although our randomization test successfully dissociates ‘active’ from ‘passive’ turn-taking, it would be valuable to undertake a more general analysis of how different foraging paradigms and group sizes might lead to passive turn-taking in visit data, as there is still potential for passive turn-taking to confound the interpretation of future empirical results.

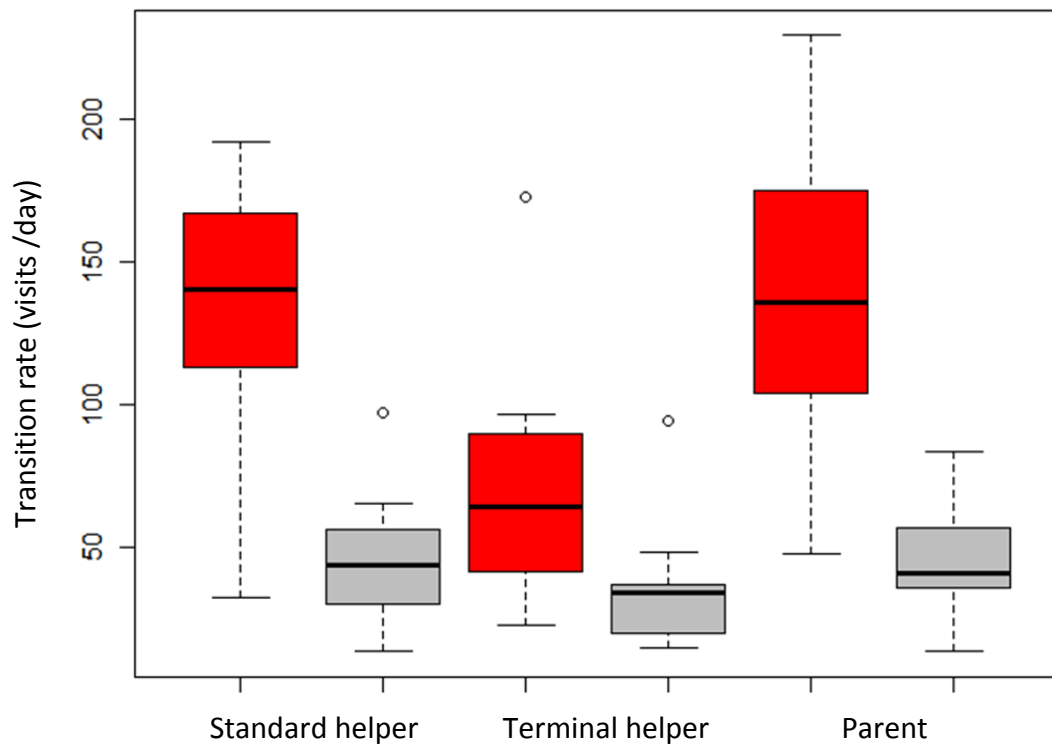
Theoretical and empirical work suggests that turn-taking is an efficient way to organize investment in a brood of young (Johnstone et al. 2014), however species will vary in their ability to adopt a provisioning rule that requires attending to the contributions of others. Whether individuals cooperating to rear young will adopt turn-taking rather than applying a strategy of ‘negotiation’ (McNamara et al. 1999, 2003; Johnstone 2011) or ‘sealed bids’ (Houston & Davies 1985) at the start of the breeding attempt seems likely to depend on the biology and feeding ecology of the species in question. If the costs of acquiring the necessary information about group investment are high, and the accuracy or benefit of obtaining such information low, an individual may do better to make investment decisions based only on its knowledge of the brood and its current personal energy reserves. However it remains feasible

that cooperative species might adopt a simple alternation rule to organize their investment in offspring when contributions to care are easily observable by the entire group. Given the potential benefits to adopting a turn-taking rule, and the greater ease in employing one if all carers visit the nest together, turn-taking might provide an additional explanation for the high visit synchrony observed in several bird species (e.g. Marzluff & Balda 1992; Doutrelant & Covas 2007), which is often found to increase breeding success (Raihani et al. 2010; Mariette & Griffith 2012). Further work is needed to determine both the prevalence of turn-taking and the degree to which its potential benefits are realized in nature.

(5.2a)



(5.2b)



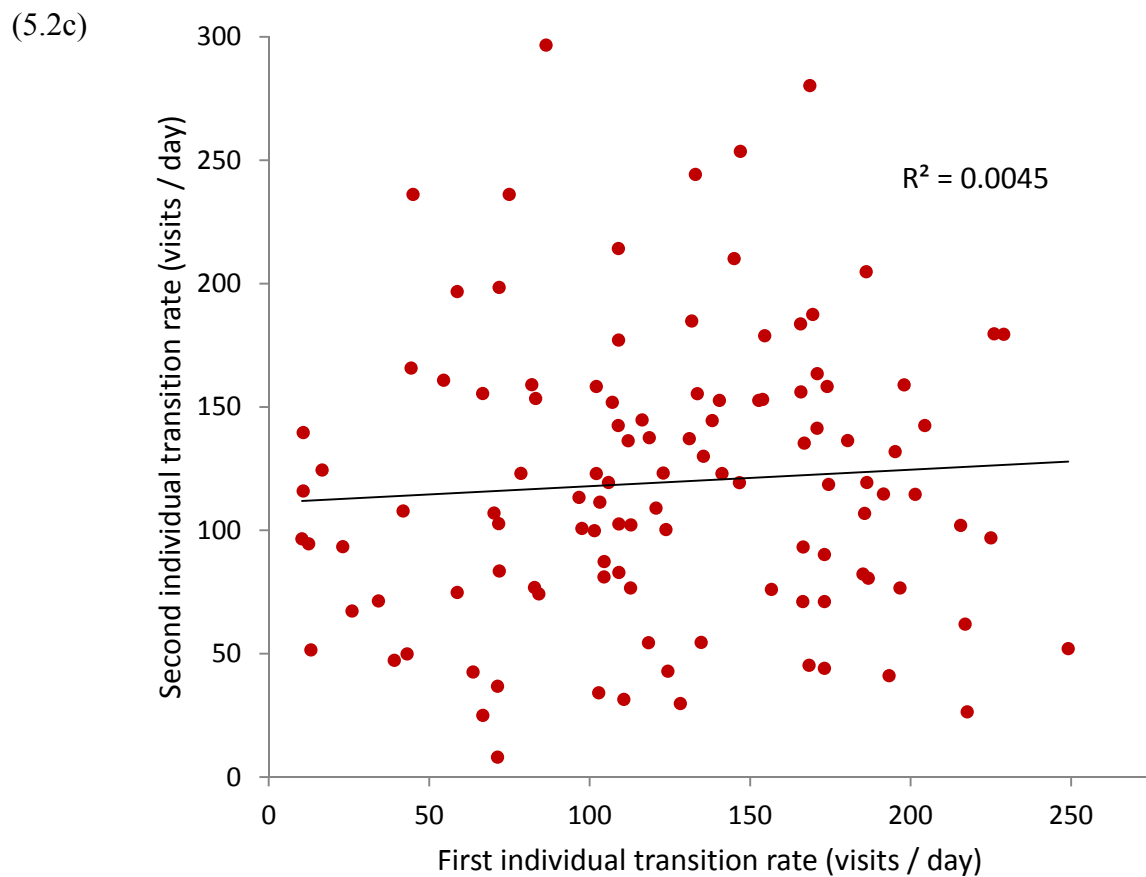
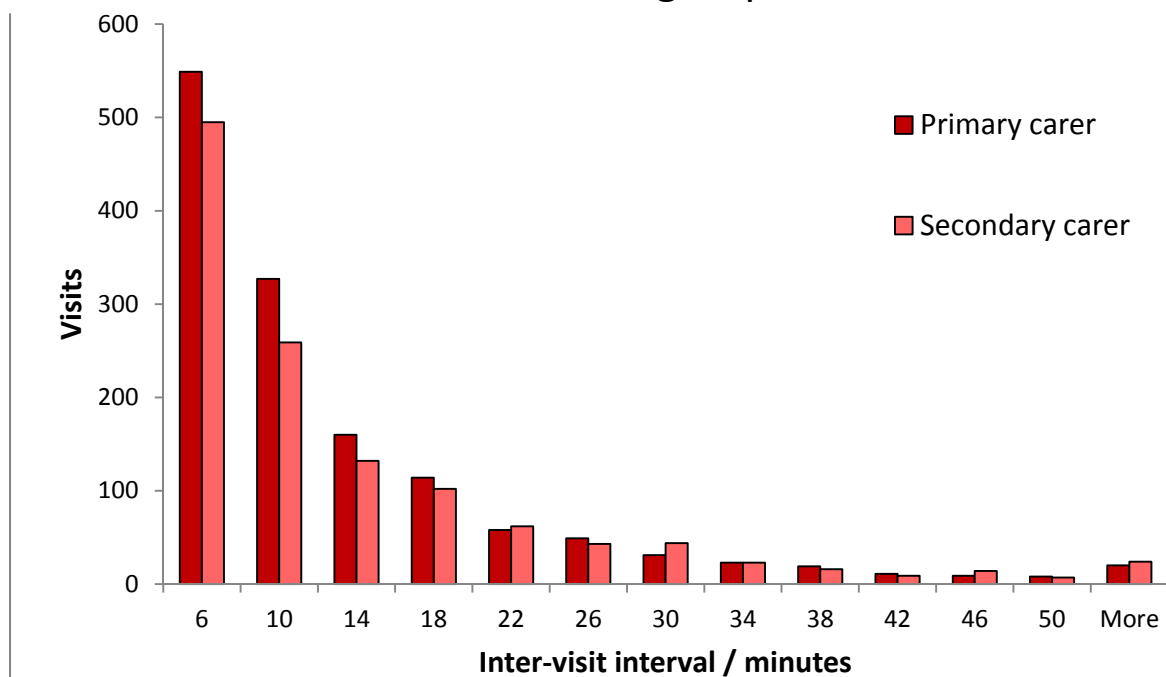


Figure 5.2: (a) Individuals are generally more likely to follow other birds than to visit the nest twice in a row, demonstrating turn-taking in the provisioning of offspring. Turn-taking is strongest for breeding males (M), females (F) and the most helpful helpers (H1), and then decreases with helper visit rate (H2-4). (b) Although all classes of carer show a tendency to alternate, differences in visit rate arise between terminal (lowest visit rate) helpers when compared to the other helpers contributing to that breeding attempt ('standard' helpers). Standard helpers and parents are similar in their visit rate and proportion of alternated visits. (c) Birds are not more likely to follow particular other birds if those birds follow them, i.e. there is no evidence that babblers employ reciprocal alternation rules to organise their investment in offspring.

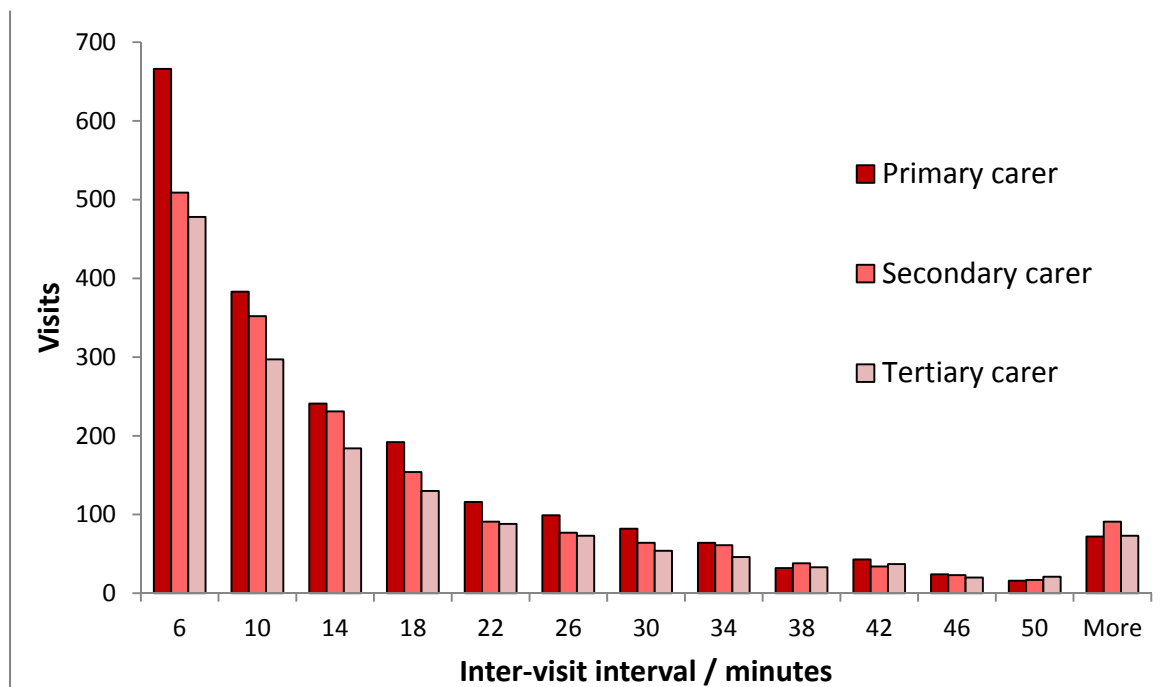
(5.3a)

Two-carer groups



(5.3b)

Three-carer groups



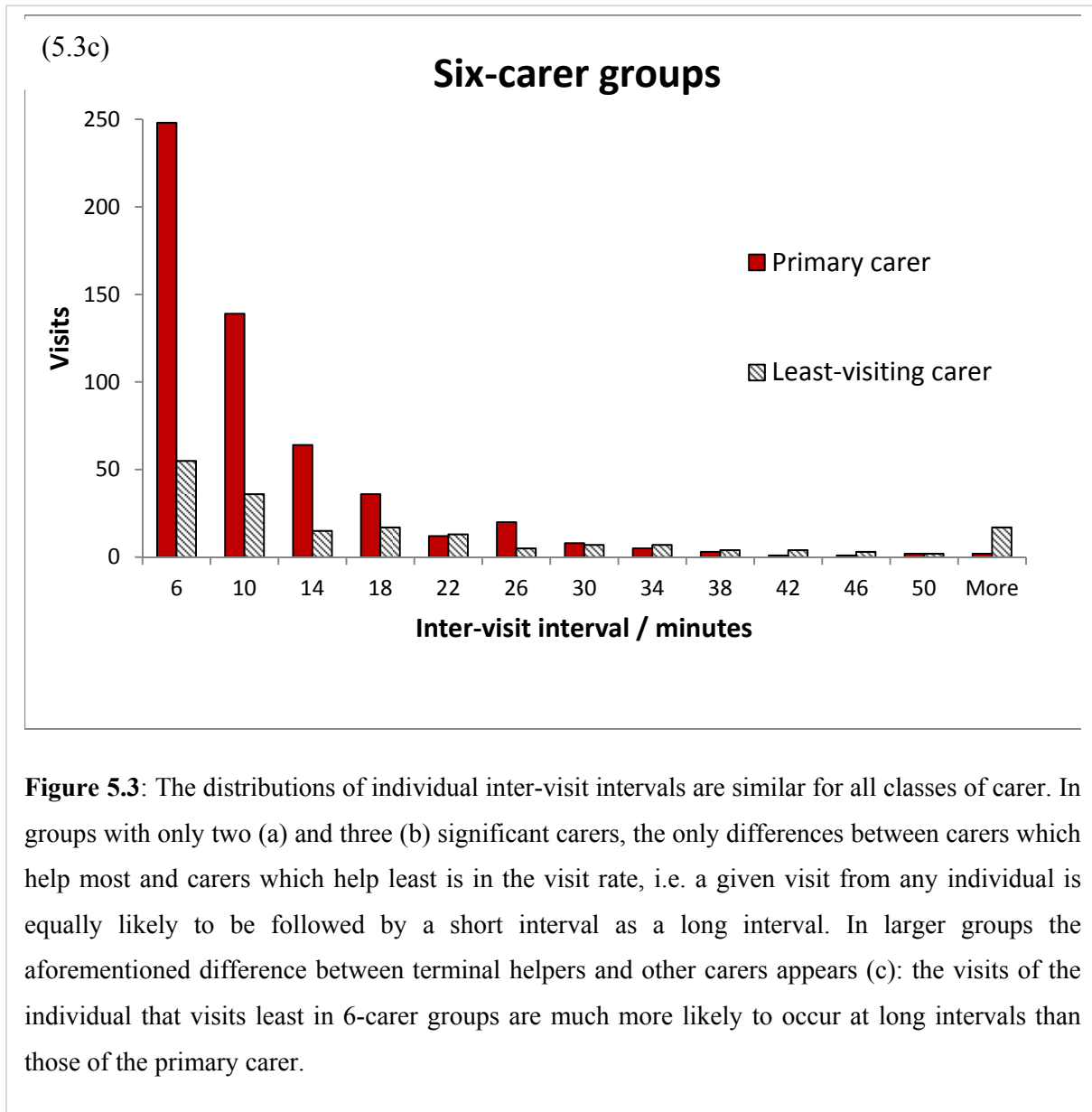
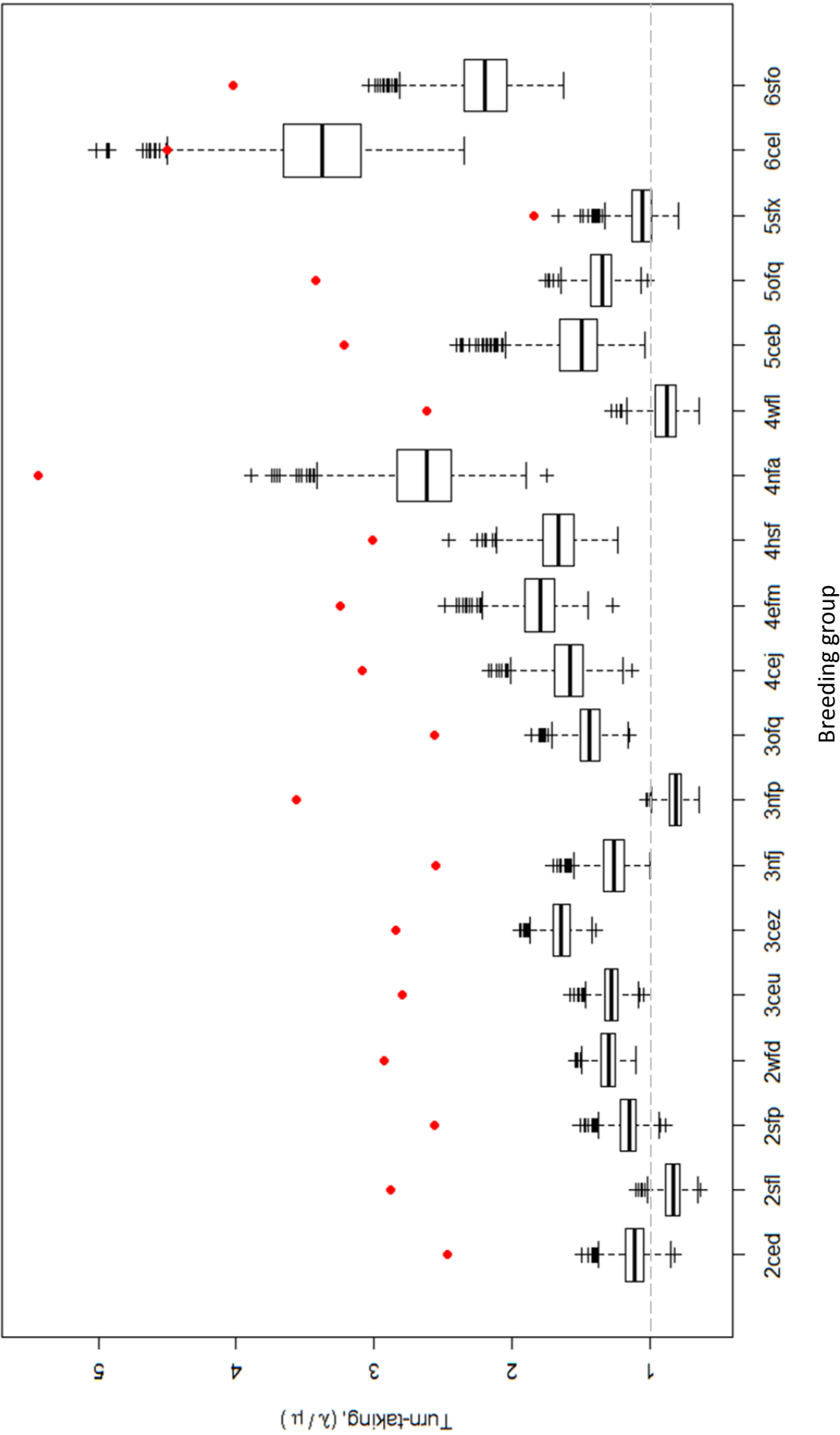


Figure 5.4 (next page): In all babbler groups analysed, the observed mean transition rate following other birds (λ) was greater than the rate of repeat visits (μ); the λ/μ ratio did not change across group sizes (red dots). Box-and-whisker plots show the distributions of λ/μ ratio for 1000 sets of randomised inter-visit intervals, analysed using the same method as the natural data. For all groups, the natural data showed significantly greater turn-taking than the randomized data. Individual groups are plotted on the x-axis, with the prefix indicating the number of significant carers.



6: The influence of maternal costs on helping behaviour in cooperative birds



Abstract

While biparental species commonly exhibit incomplete compensation in response to the presence of their partner, much greater variation in provisioning rules is observed in cooperative breeders as group size changes. In birds, females pay the majority of the pre-hatching costs of producing eggs and caring for them until they hatch, whereupon all carers can contribute similarly. As a result, the costs incurred by breeding females are biased towards the start of the breeding attempt when compared to breeding males and helpers. Recent theoretical work suggests that diverse responses to different levels of available care should be expected based on whether breeding females can respond by changing the number or size of offspring before other carers can contribute. We use data from existing studies to review the range of provisioning behaviour observed in 60 species of cooperatively breeding birds, and to test whether there is an association between maternal-only allocation, breeding group sizes and maternal provisioning rules. We find that females are more likely to compensate when incubation periods are relatively longer, and when their breeding group is comprised of close kin. Larger breeding group sizes are associated with smaller relative total investment in eggs, supporting the hypothesis that helpers facilitate a lowering of personal costs paid by the breeding female. Our results reinforce the importance of considering investment as a multi-stage process, and may partially explain the greater variation in provisioning rules seen in cooperative breeding when compared to biparental systems.

Introduction

Cooperative breeding, in which more than two individuals contribute to the care of offspring, is a breeding system exhibited by a significant minority of terrestrial vertebrates (Cockburn 2006; Lukas & Clutton-Brock 2012). Approximately 9% of all bird species regularly breed cooperatively (Cockburn 2006), an estimate which has steadily increased over time as the breeding behaviour of more species has been studied in detail. Among avian cooperative breeders the prevalence and intensity of care delivered by non-parents varies tremendously, from a single helper attending a small fraction of nests (as in pinyon jays, Marzluff & Balda 1992) to an average of greater than four helpers at every nest, with unhelped nests universally failing (white-winged choughs, *Corcorax melanorhamphos*, Heinsohn 1992; apostlebirds, *Struthidea cinerea*, Woxvold & Magrath 2005). The forces selecting for and maintaining cooperative breeding in birds have been the subject of much debate, with suggestions that kin selection (Hamilton 1964), group augmentation (Kokko et al. 2001), ecological constraints (Emlen 1982), aspects of life history (Rowley 1965; Arnold & Owens 1998), and maternal effects (Russell & Lummaa 2009) could all lead to individuals benefiting from helping rather than attempting to reproduce independently. In this article we focus on the relative importance of the different stages of investment across a breeding attempt as an explanatory factor in the prevalence of cooperative breeding.

Whenever care of offspring is shared between multiple individuals, each individual benefits when a greater proportion of costs are borne by the other carers (Trivers 1972). Theoretical work predicts that individuals should generally respond to changes in the investment of others with incomplete compensation, (Houston & Davies 1985; McNamara et al. 1999; Johnstone 2011), although threshold effects or asymmetric information can modify this prediction (Jones et al. 2002; McNamara et al. 2003; Johnstone & Hinde 2006). Empirical results from experiments modifying partner contribution in biparental species are largely supportive of incomplete compensation (Harrison et al. 2009), although exceptions exist. By contrast, cooperative species show far less consistency in their response to additional carers (Hatchwell 1999): across various studies, responses range from complete compensation (Brown et al. 1978; Hatchwell & Russell 1996; Russell et al. 2008), through various degrees of partial compensation (Wright 1998a; MacColl & Hatchwell 2003) to no change in investment at all

(Mumme & Koenig 1990; Emlen & Wrege 1991) or even an increase in individual investment (Valencia et al. 2006).

What causes this variation in provisioning rules, and why is it so pronounced in cooperatively breeding species? One possibility is that the observed provisioning rules depend on whether the mother can tactically manipulate investment in offspring size or number based on the amount of help she expects to receive (Savage et al. 2013a, 2013b). In this case, if the breeding female can both anticipate the number of carers and modify her investment to match, she can produce more offspring (as in Davies & Hatchwell 1992; Russell et al. 2003; Woxvold & Magrath 2005), or offspring requiring greater future investment (Russell et al. 2007) in response to greater numbers of carers. Recent theory suggests that this will lead to additive provisioning rules (by all carers) when female investment is flexible, and compensatory rules when it is not (Savage et al. 2013a), however this suggestion has yet to be tested on natural data. Regardless of the breeding female's relative ability to tactically alter investment, we should expect compensation by her to be more common than by the breeding male, due to greater costs incurred in producing offspring.

When a breeding attempt comprises multiple non-independent stages of investment it is likely that these stages will not be equally costly to individuals or the group as a whole. Carers may be restricted in their investment to particular stages, and the relative importance of these stages may also influence provisioning rules (Savage et al. 2013a). In birds, typically the nest must be built, the eggs produced and incubated, and the chicks and fledglings fed until independence, throughout which time the carers must hide and/or defend the offspring from predators. Producing and incubating eggs is costly (Monaghan et al. 1998; Visser & Lessells 2001; Reid et al. 2002; Williams 2005) and incubation is often performed exclusively by the breeding female, sometimes with supplemental feeding by other carers (Martin & Ghalambor 1999). Helpers, when present, may contribute to incubation (Heinsohn & Cockburn 1994), but will more often restrict themselves to feeding nestlings, or even only fledglings (Waite & Strickland 1997). When the breeding female suffers a large cost of reproduction before other individuals invest in offspring (e.g. large eggs and female-only incubation), later stages (e.g. provisioning nestlings) become relatively less important and fewer carers will be able to meaningfully contribute to the breeding attempt: more helpers may reduce female costs later in the breeding attempt, but these are a small fraction of the total costs incurred. This inflexibility in female costs with changes in helper number leads to inflexibility in maternal

investment tactics with changes in helper number, resulting in incomplete compensation and load-lightening as predicted by single-stage investment models (Savage et al. 2013a). The opposite case, where costs restricted to the breeding female are small and group costs large, is predicted to lead to flexibility in female investment strategy as group size changes, and little or no change in provisioning rate as the number of carers changes (Savage et al. 2013a).

We present an analysis of cooperative provisioning across 60 species whose breeding behaviour has been previously studied in detail. For each species we record the prevalence and intensity of cooperative breeding and calculate the overall contributions of the breeding female to offspring care in terms of her investment in eggs (relative to body size), whether she incubates alone, and the relative lengths of different stages within the breeding attempt. We then determine the degree to which these factors predict the observed provisioning rules and levels of cooperation in particular species.

Methods

Data collection

Data on provisioning rules, helper effects and group sizes were obtained from studies referenced in Hatchwell (1999) and Kingma et al. (2010), with further studies identified by articles citing Hatchwell (1999) and systematic searches of Scopus, Web of Knowledge, and JSTOR using the terms ‘cooperative breeding’ and ‘helpers at the nest’ (with irrelevant disciplines excluded). The key measures of helping behaviour used were ‘proportion of nests helped’ and ‘mean breeding group size’, two parameters that together broadly describe the prevalence and intensity of cooperative breeding and which were either directly available or easily calculable from all studies used in the analysis. Where data were available for contributions to care over multiple stages, or multiple dimensions of helping behaviour (such as nest defence in addition to provisioning), we focused exclusively on provisioning during the nestling stage due to sparse data from other stages and the potential difficulties in comparing the relative costliness of different modes of investment. Following Hatchwell (1999), we recorded whether males and females compensated for the presence of helpers by reducing their provisioning effort, and whether total care delivered to the brood increased

when helpers were present. Where the response to additional helpers changed with group size, we recorded the response to the first helper (in facultatively cooperative species) or the response at small group sizes (in obligate or ubiquitous cooperative species). We also recorded whether helpers had a positive effect on reproductive success or not, and whether the proposed mechanism of the effect was reduced offspring starvation, reduced nest predation rate, or some other benefit (such as an increased probability of immediately re-breeding).

In species for which provisioning and group size data were available, supplementary data on mean egg and clutch sizes, life-history traits, body masses, and kin-structure of groups were then collected from the literature. These data were taken from publications arising from the same study population where possible, with additional data sourced from encyclopaedia sources and review articles (see Appendix B for a full reference list by species). Where body masses were available independently for both sexes the mean female mass was used, otherwise female mass was assumed to approximate the mean of all adult masses. The mean lengths of the incubation and nestling periods, and which individuals contributed to incubation were also recorded. Breeding occurred year-round or under particular weather conditions in some species, while others had a well-defined breeding period: we divided species into two simple classes on the basis of whether multiple successful attempts were possible in a given breeding period under good conditions. No data on adult survival rates were collected, as these data were only readily available for a few studies beyond those analysed in previous studies (Hatchwell 1999; Kingma et al. 2010). Species-specific data on egg shape were not generally available, so egg volumes were calculated from mean reported length (L) and width (W) measurements (in mm) using a standard formula of $(0.6057 - 0.0018 \cdot W) \cdot L W^2$ (Narushin 2005). Appendix A provides further details of the inclusion and exclusion criteria for species used in this study.

Statistical analysis

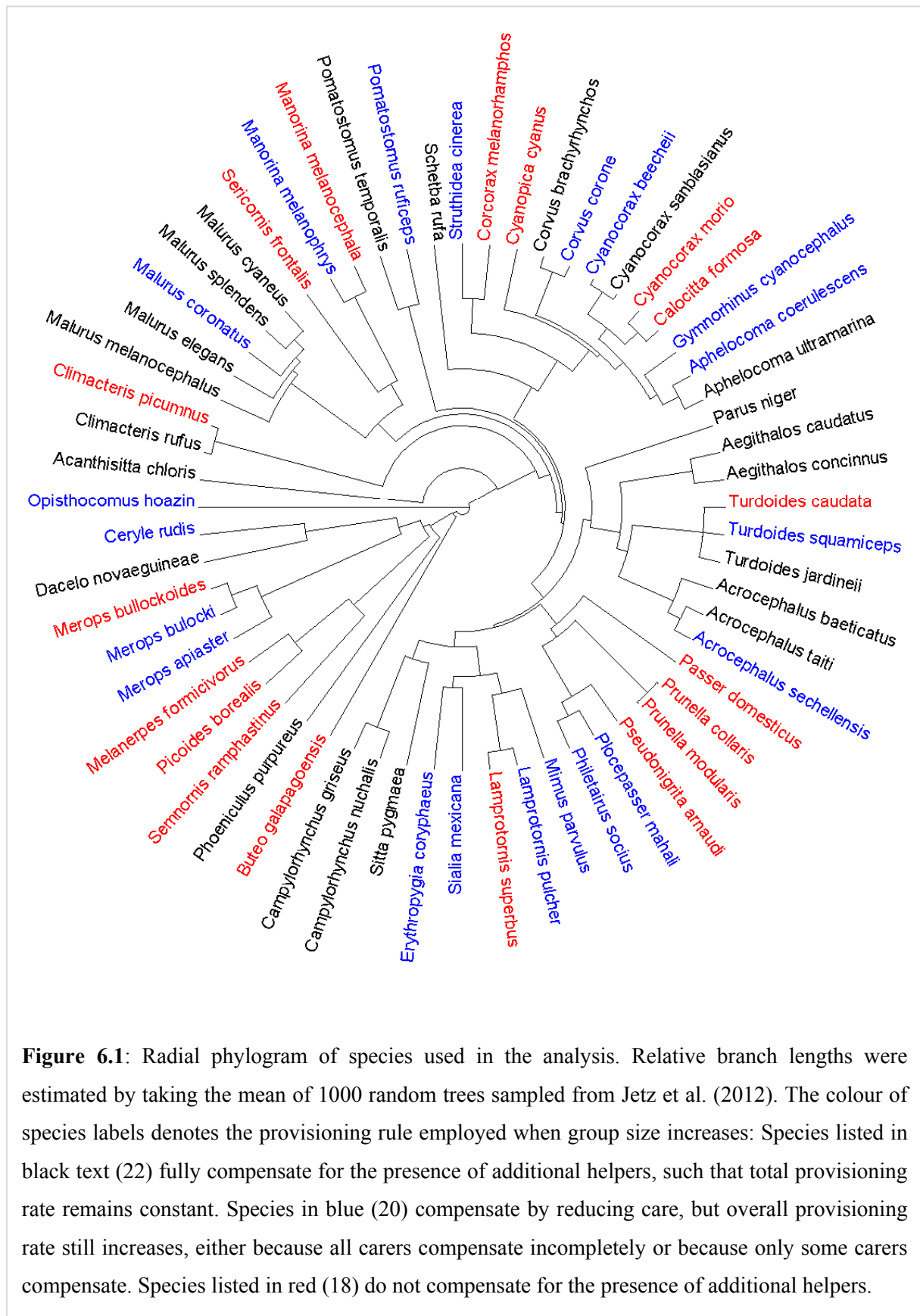
The primary aim of this study was to determine whether there is a general relationship between relative maternal investment levels and group size or observed provisioning rules in cooperative breeders. Life-history traits are variable but highly conserved across birds, and hence controlling for the phylogenetic non-independence of species is important (Owens & Bennett 1995). Phylogenetic relationships between species in our study were obtained from

Jetz et al. (2012) (via birdtree.org), with branch length estimates generated by taking the mean of 1000 randomly sampled trees from the Hackett et al. (2008) backbone. When analysing the data, we used phylogenetic generalized least-squares (PGLS) models to control for the phylogenetic non-independence of species traits (Martins & Hansen 1997; Pagel 1999; Freckleton et al. 2002).

All statistical analyses were performed in the R programming language (version 2.12, R Development Core Team), using packages ‘ape’ (Paradis et al. 2004) and ‘caper’ (Orme et al. 2011) for tree manipulation and PGLS functions. We chose PGLS over phylogenetic independent contrast (PIC) methods (Felsenstein 1985) for convenience, as the two approaches are mathematically equivalent (Blomberg et al. 2012). Continuous input variables were centred by subtracting the mean and scaled by dividing by two standard deviations, to facilitate comparisons with binary input variables (Gelman 2008). To select and compare between models we used Akaike’s information criterion, corrected for small sample size (AICc) (Akaike 1974; Burnham & Anderson 2002). To avoid selection bias from the large number of possible models (Zucchini 2000), the number of input variables was reduced by fitting models of each input variable in isolation, then excluding those variables that failed to outperform an intercept-only model (based on AICc comparison). All retained variables were then used to construct a complete set of candidate models. Models with significant support (defined as $\Delta\text{AICc} < 3$ from the ‘best’ model) were model-averaged using Akaike weights (Burnham & Anderson 2002).

Results

In total, we found 60 cooperative species that met the criteria for inclusion, of which 55 had available data on egg size; this is a substantially larger number than previous reviews of cooperative care behaviour (e.g. Hatchwell 1999, Kingma et al. 2010). Figure 6.1 presents a radial phylogram of all species used in this study, with scientific names colour-coded according to the most broadly defined classes of cooperative provisioning rule: Full compensation of helper contributions by the breeders (black), partial compensation (blue), and no compensation (i.e. fully additive care; red).



Variation in cooperative care

No provisioning rule could be identified as the standard across the cooperative species we reviewed, contrasting with the generally supported ‘incomplete compensation’ rule found for biparental species (Harrison et al. 2009). Compensatory reduction of feeding rate in the presence of an additional helper was found for at least one sex in 42/60 reviewed species (70%), however among those that compensated, incomplete compensation (20/42, 48%) was similarly frequent to complete compensation (22/42, 52%). In compensating species the female more often compensated than the male (♀: 39/42, 93%; ♂: 27/42, 64%), and in species where only one sex compensated, this was generally the female (15/18, 83%). Two studies reported non-significant changes in both total and individual provisioning rates when helpers were present, and hence could not be assigned to a particular rule. In the remaining species (16/42, 38%), neither sex compensated for the presence of a helper, and hence provisioning rate increased with group size: included in this category is a single case of ‘superadditive care’, in which breeders increased investment in response to the presence of a helper (Valencia et al. 2006). Superadditive care was by far the rarest of the observed provisioning rules, however an excluded study also showed a non-significant trend towards the same rule (Jing et al. 2009). Table 6.1 fully separates out all of the possible provisioning rules, and presents the number of species exhibiting each rule.

Other aspects of breeding biology were also variable across the species reviewed, suggesting potentially great variation in maternal costs of care. Helpers increased reproductive success in 67% of species (40/60), and where a mechanism for this benefit was identified (38/40), the most common were reduced starvation (20/38, 53%) and reduced predation (13/38, 34%). Mean breeding group size ranged from just over two birds (Western bluebird, *Siala mexicana*) to ten birds (Brown Jay, *Cyanocorax morio*). Mean group size and proportion of nests helped were strongly positively correlated for species in which helpers were present at less than three-quarters of nests ($n = 41, r = 0.83$), but this relationship weakened for groups with more prevalent cooperation ($n = 19, r = 0.61$) (Figure 6.2). The duration of the incubation stage ranged from only one-quarter of the total period between laying and fledging (Toucan Barbet, *Semnornis ramphastinus*), to more than three-fifths of the total period (Hoatzin, *Opisthocomus hoazin*), and mean clutch sizes varied between 1.1 (Seychelles warbler, *Acrocephalus sechellensis*) and 9.8 eggs per nest (Long-tailed tit, *Aegithalos caudatus*).

Influence of maternal investment

Mean breeding group size was associated with variation in two maternal investment parameters: (i) relative total egg investment by the breeding female and (ii) the ability of a species to make multiple successful breeding attempts within a season (Table 6.2a). Larger group sizes were associated with lower relative total egg investment by the breeding female, and with species capable of multiple breeding attempts. Neither proportional length of incubation period, nor whether the female incubates alone had any association with breeding group size. Groups comprised of kin were the same size as those comprised of non-kin, and whether females occasionally joint-nested also had no association with group size. Three models were significantly supported ($\Delta \text{AICc} < 3$ from the ‘best’ model) and hence contributed to the average model.

Provisioning rule	Total care to offspring	Female compensation	Male compensation	Number of species
No compensation / Fully additive care	Increase	No	No	16*
Incomplete compensation (symmetric)	Increase	Yes	Yes	9
Incomplete compensation (asymmetric)	Increase	Yes / No	No / Yes	8♀, 3♂ (11)
Complete compensation (symmetric)	No change	Yes	Yes	15
Complete compensation (asymmetric)	No change	Yes / No	No / Yes	7♀ (7)
Unresolved	No change	No	No	2

Table 6.1: Provisioning rules observed in cooperatively breeding birds as group size increases. Compensating parents reduce their provisioning rate when helpers are present, which may lead to no overall change in provisioning rate (complete compensation) or merely a lower increase (incomplete compensation). Compensation is asymmetric when exhibited by one sex only. Our findings suggest asymmetric compensation is far more likely to be employed by the breeding female than by the breeding male. *Includes one example of ‘superadditive’ care (an increase in individual provisioning rate as group size increases).

Four parameters were associated with breeding female compensation: (i) the relative length of the incubation period, (i) whether breeders were generally monogamous pairs, (ii) whether females sometimes joint-nested, and (iv) whether incubation was restricted to the breeding female alone (Table 6.2b). Female compensation was associated with proportionally longer incubation periods, and with breeding by monogamous pairs. Females were less likely to compensate when joint-nesting occurred in the species, and females incubating alone were slightly less likely to compensate than those with shared incubation. No association was found between breeding female compensation and her relative total egg investment, and repeated breeding within a season was also unrelated to female compensation. Females in groups comprised of kin were equally likely to compensate for helper presence than those in groups comprised of non-kin. Nine models contributed to the average model.

We restricted our PGLS models to the 55 species for which high-quality egg size data were available. Exploratory analysis on all 60 species (omitting egg size data) revealed no differences in the retained variables or best supported models between the two datasets.

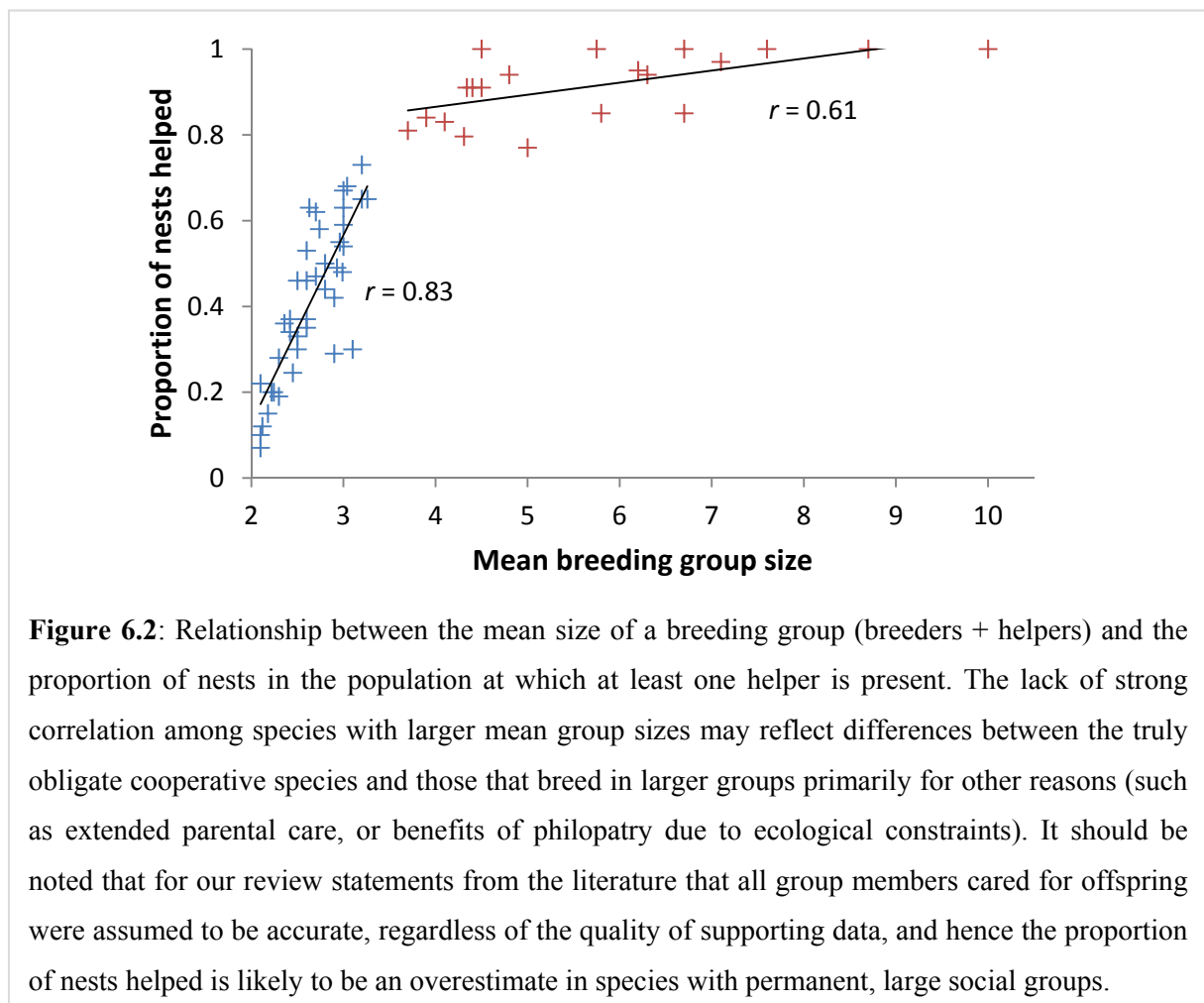


Table 6.2: The influences of maternal investment levels on (a) mean breeding group size, and (b) female provisioning rule, across 55 species of cooperatively breeding birds. The tables compare phylogenetic generalized least-square models using the Akaike Information Criterion, corrected for sample size (AICc). Log-likelihoods (log(L)), degrees of freedom (d.f.), relative AICc compared to the best candidate model (Δ AICc), and Akaike weights (Weight) are given for each model. Models with weights < 0.05 are not shown.

(6.2a): *Mean breeding group size*

Variates	log(L)	d.f.	AICc	Δ AICc	Weight
Repeat breed.	-106.98	2	218.19	0.00	0.43
Rel. tot. egg inv. + Repeat breed.	-106.18	3	218.83	0.64	0.31
Rel. tot. egg inv.	-107.47	2	219.18	0.99	0.26
Intercept only	-109.69	1	221.45	3.26	
	Repeat Breed.		Rel. tot. egg inv.		Intercept
Average model parameter estimates	0.724		-0.659		3.218

Repeat breed.: Whether groups are capable of producing multiple successful breeding attempts within a breeding season. *Rel. tot. egg inv.*: The relative total egg investment by mothers (egg size \times mean clutch size / mean female mass).

(6.2b): *Female compensation in the presence of a helper*

Variates	log(L)	d.f.	AICc	Δ AICc	Weight
Prop. inc. + Joint nest + Pair nest	-29.74	4	68.27	0.00	0.22
Prop. inc. + Pair nest	-31.19	3	68.85	0.58	0.17
Joint nest + Pair nest	-31.43	3	69.32	1.05	0.13
Prop. inc. + Joint nest	-31.59	3	69.66	1.39	0.11
Solo inc. + Prop. inc. + Pair nest	-30.69	4	70.18	1.91	0.09
Pair nest	-33.01	2	70.25	1.98	0.08
Solo inc. + Prop. inc. + Joint nest + Pair nest	-29.61	5	70.45	2.18	0.07
Solo inc. + Pair nest	-32.10	3	70.67	2.40	0.07
Solo inc. + Joint nest + Pair nest	-31.08	4	70.95	2.68	0.06
Intercept only	-36.42	1	74.92	6.65	
	Solo inc.	Prop. inc.	Joint nest	Pair nest	Intercept
Average model param. est.	-0.032	0.137	-0.193	0.277	0.290

Solo inc.: Whether the female must incubate the eggs alone. *Prop.inc.*: The proportion of the mean incubation + chick rearing period that is occupied by incubation. *Joint nest*: Whether multiple females sometimes lay in the same nest ($1 < \text{mean} < 1.3$). *Pair nest*: Whether breeding groups generally comprise monogamous pairs.

Discussion

The distribution of provisioning rules found in our review is almost identical to that reported by Hatchwell (1999), despite our inclusion of more than double the number of species. When restricting our analysis to the 58 species with resolved provisioning rules, we found that helpers were associated with compensatory responses by both parents in 24/58 species (41%), by one parent only in 18/58 (31%), and by neither parent in 16/58 (28%); the corresponding values reported by Hatchwell were 44%, 30%, and 26% respectively (using 27 species). The proportion of species in which helpers increased the reproductive success of breeders was also identical to that in Hatchwell's review, at 67% (40/60; 18/27). The striking similarities between the results of our present review and those of the Hatchwell's suggest that our observed frequencies of different provisioning rules among cooperative breeders are likely to be robust, and hence that all possible provisioning rules (aside from 'superadditive' care) appear relatively often in natural systems.

The results of our PGLS analyses underline the importance of considering maternal costs when investigating breeding behaviour in cooperative birds. Lower relative total egg investment was associated with larger group sizes, supporting the hypothesis that the presence of helpers in cooperative species allows mothers to reduce their personal costs during early stages of the breeding attempt. Species with larger group sizes were also more likely to breed multiple times within a season, potentially because helpers load-lighten (Crick 1992) the breeding female's costs enough that she retains sufficient personal resources after a breeding attempt to breed again immediately. An alternative explanation for repeated breeding is that the helpers are able to care for fledglings that still require provisioning and/or defence from predators (Heinsohn 1991), enabling the female to allocate time to the incubation of a new brood rather than extending parental care.

Our results broadly support previously predicted effects of maternal costs and group structure on female investment during offspring rearing (chapters two and three). Proportionally longer incubation periods (i.e. higher maternal-only costs) were associated with female compensation: this can be explained by mothers being more likely to reduce their effort at later stages when they have paid higher costs at earlier stages. Compensation by the breeding female was more likely with pair nesting, possibly because faithful pairs produce full-sibling helpers that contribute more, and that the breeding female is less willing to exploit. However,

contrary to predictions, mothers in kin-groups were not generally more likely to compensate for larger group size than mothers living in non-kin groups.

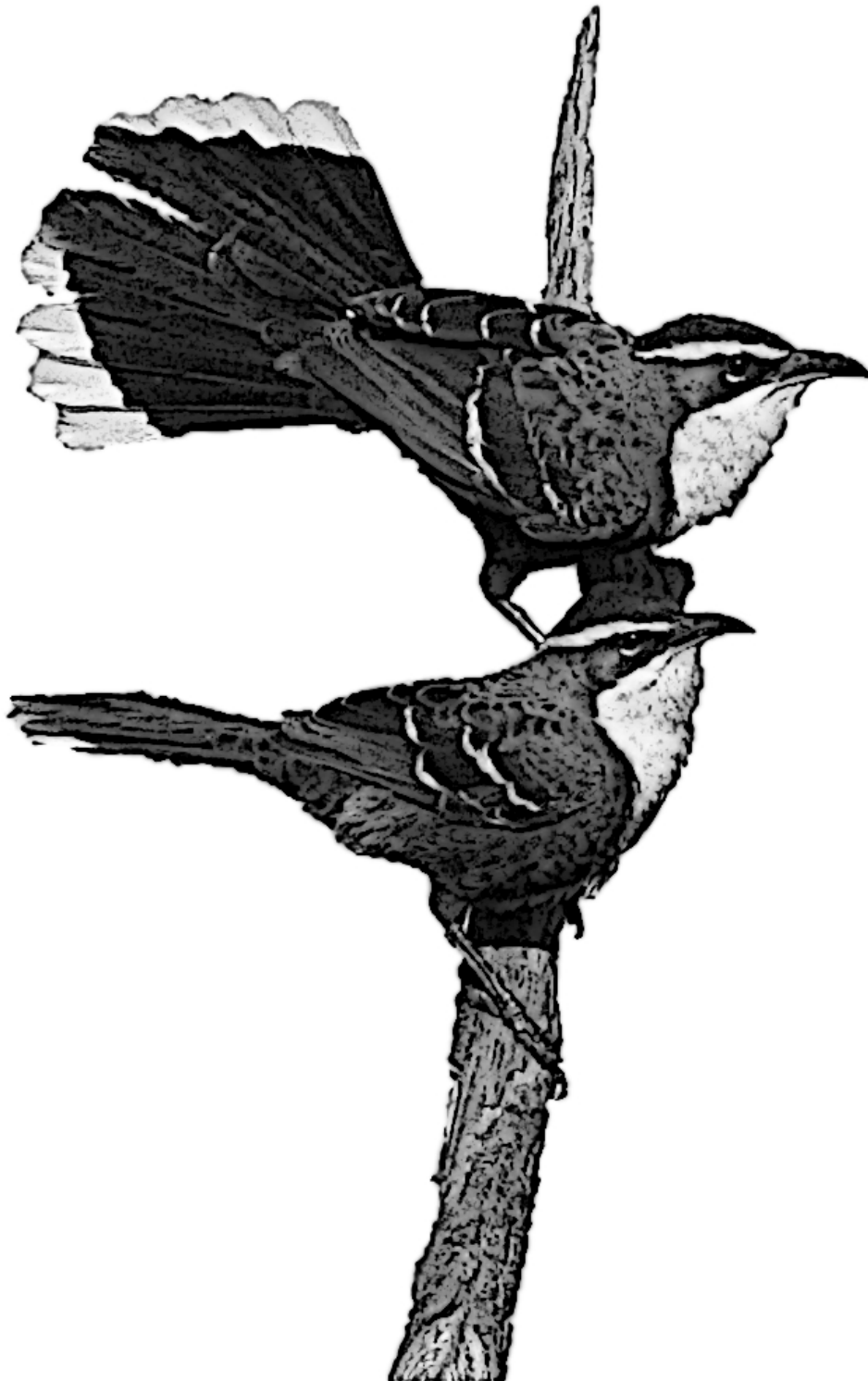
Diverse explanations have been proposed for the evolution of cooperative breeding, many of which have empirical support from multiple species (see chapter 1), including suggestions that maternal effects may be a potential contributing factor (Russell & Lummaa 2009). Our results support the influence of maternal effects on parental care behaviour and breeding groups size, and we believe these influences are currently underestimated in vertebrate systems. When mothers are able to tactically manipulate offspring size or number to match the care paradigm, all carers benefit from removing her personal costs of offspring production to facilitate the production of more offspring for the group to rear (see chapter 2), facilitating larger group sizes. Mechanisms for helpers to assist the mother at earlier stages (e.g. assisting with nest-building, sharing incubation, or feeding the incubating mother on the nest) should be expected whenever the costs of the initial stage are constraining for the mother but helpers could still benefit from the production of more offspring, as this allows more individuals to effectively contribute to the breeding attempt. Investment in offspring is a complex multi-stage process, and yet most theoretical and empirical studies have decomposed it into individual stages for the purposes of analysis, thereby missing potential influences of variation in maternal investment behaviour both within and between species.

When comparing details of breeding behaviour across a diverse clade such as birds, it is often necessary to abstract away many details about individual species. Unfortunately, specific aspects of the biology or ecology of particular species can often lead to constraints on how the species behaves during breeding, relegating general factors to lesser importance. Within birds, clutch size provides an example as it is limited not only by female costs but by the number of eggs that can be simultaneously incubated. Other than simple matters of geometry, the climate and nest type (and location) that a given species uses will also restrict breeding females to a certain maximum clutch size, regardless of their available resources. In extreme cases, where egg production costs and rearing costs are both low, breeding females might benefit from acquiring multiple mates to incubate several simultaneous or sequential clutches (Lank et al. 1985), especially if maximum clutch sizes are constrained. A full comparative analysis across a smaller clade with a mixture of cooperative and non-cooperative species would be useful to obviate some of these problems, however the relative rarity of studies on provisioning rules m

Given the large number of species for which provisioning data have been collected, more detailed meta-analytic studies of individual response rules should be possible across a substantial number of cooperative birds. Behavioural ecology would benefit enormously from greater public availability of the raw provisioning data from field studies, not only to combine existing results into comparative and meta-analytic reviews, but also to allow interested researchers to mine older data using more complex individual provisioning rules (such as those employed in chapter five to investigate turn taking). The existence of online repositories now makes the deposit and access of such data comparatively straightforward, and represents a way of adding new value to otherwise moribund field projects. Currently, much useful data for answering more complex questions about provisioning behaviour remains unavailable, and will likely be lost permanently over time (Vines et al. 2013) if better archiving practices are not employed.

In summary, our results suggest that early-stage costs borne by the breeding female influence later provisioning behaviour and group size in cooperative groups, and hence that single-stage models of investment are potentially misleading and should be treated with caution. When mothers can transfer a greater proportion the total costs of breeding to helpers, larger group sizes are possible as more helpers can effectively contribute to the breeding attempt. Consequently, maternal effects may be important contributing factor to the evolution and persistence of cooperative breeding. Further work is needed to clarify the effects of maternal costs on helping behaviour; a potential first step would be to compare maternal investment between cooperative and non-cooperative bird species across a clade in which both breeding systems are common.

7: General discussion



Summary of results

In the preceding chapters I employed field observations, comparative analysis, and theoretical modelling to examine offspring care in cooperative breeders, with particular focus on the effects of maternal tactics on investment decisions made by the rest of the group. In this short final chapter, I summarise the findings of the previous chapters and discuss how they combine into an overall picture of investment behaviour in cooperative breeders. I conclude by suggesting some possible future work that would further expand our understanding of cooperative offspring care.

In the introductory chapter I reviewed game-theoretical models of offspring care, cooperative breeding in birds, and maternal effects in relation to carer investment. I concluded that desirable extensions to current work on parental care included (i) models of care incorporating variable maternal allocation to offspring at early stages, (ii) models of cooperative care with more than a single helper, (iii) tests of the predictions of these new models, and (iv) study of how parental investment is organised on a visit-by-visit basis in cooperative breeders. The remainder of the dissertation attempted to address these topics from empirical, theoretical and comparative perspectives, beginning with a theoretical exploration of the effects of variable maternal allocation on individual investment levels.

Chapters two, three and four used a common game-theoretical framework to model how carer investment rules are influenced by variable maternal investment during initial offspring production, and generated predictions about the outcomes expected under different cost, benefit, and relatedness parameters. Each chapter uses a two-step sealed-bid model of parental care, in which all carers choose their investment levels during offspring rearing (the second step) based on the initial choice of offspring number or quality made by the breeding female in the first step. This common framework facilitates the comparison of results across chapters to generate an overall picture of cooperative investment with variable maternal allocation. When mothers' costs vary between different stages of the breeding attempt (chapter two; Savage et al. 2013a), compensatory care is more likely when costs paid entirely by the mother are relatively greater than those paid during later stages in which all group members can invest. If the costs mothers must bear alone are relatively low, mothers should adjust instead the number of offspring flexibly to helper number, resulting in little compensation during rearing. These different responses to changing group size can also arise depending on whether

helpers are closely or distantly related to offspring (chapter 3; Savage et al. 2013b), and whether they are related to offspring through the breeding female or breeding male, as females are less willing to increase the costs incurred by related carers. When mothers instead control initial offspring quality (chapter four) instead of offspring number, there are two possible outcomes depending on how initial quality influences the value of later investment. If high initial quality ‘primes’ offspring to benefit from future investment by carers, then increasing group size will lead to higher investment by offspring (i.e. a matching response to good conditions). In contrast, when initial offspring quality is additive with later investment (such that the stages can trade off against each other), mothers are expected to compensate for good conditions by reducing initial investment in offspring and hence shifting a greater proportion of the costs to the rearing period. In combination, the three chapters provide an overview of how maternal allocation strategies are likely to influence cooperative provisioning behaviour under different cost and benefit paradigms, and suggest that maternal tactics are important to generating accurate predictions.

Chapter five diverged from the analysis of tactical female investment to consider strategies for efficient offspring provisioning in a cooperatively breeding bird. How individuals organise joint investment in offspring is crucial to understanding care behaviour in both biparental and cooperative species, as individual interactions largely determine the ease with which individuals can free-ride on the contributions of others. The results supported recent evidence that individuals may adopt turn-taking rules to ensure equitable investment in biparental species (Johnstone et al. 2014), and demonstrated some potential pitfalls of visit-by-visit analysis by also showing evidence of ‘passive’ turn-taking caused by the distribution of inter-visit intervals. A better theoretical understanding of how foraging ecology influences the ability of individuals to assess and respond to the investment of others would facilitate general predictions about the likelihood of turn-taking being employed in particular species, and more empirical work is needed to confirm and explore turn-taking behaviour in nature.

In chapter six, I reviewed all cooperative species for which provisioning behaviour is known in detail, in order to test whether maternal costs influence the group sizes and provisioning behaviours seen in empirical studies. I found several associations between maternal costs and cooperative behaviour, most notably that species with larger breeding groups tend to invest less in their eggs, and that mothers in species that spend a larger proportion of their time incubating are more likely to take advantage of helpers by reducing care when rearing

offspring. I also found a wide range of different provisioning rules present in cooperative breeders, at strikingly similar frequencies to those reported in a prior, smaller review of cooperative provisioning behaviour (Hatchwell 1999).

Overall, my results support the importance of incorporating maternal allocation strategies into empirical and theoretical studies of cooperative investment, although more work is needed in both areas. The importance of considering offspring investment as a multi-stage process, particularly when multiple individuals are involved, is hard to overstate. Any studies that confine their analysis to a single stage will only be relevant when comparing species with identical maternal allocation strategies, and a similar ability to predict the availability of later care. The much greater variation in provisioning rules within cooperative species, when compared to biparental ones, is partly a result of cooperative species varying more widely in both of the above.

To summarise the questions addressed, and conclusions made within this dissertation:

- 1) Does maternal control of initial offspring quality and/or number influence the predicted investment levels of carers in cooperative breeding systems?

YES: maternal strategies can strongly influence how individuals are predicted to respond to changes in group size, and there are multiple possible responses to receiving additional helpers.

- 2) Is variation in costs between different stages of a breeding attempt predicted to influence investment behaviour in cooperative breeding systems?

YES: lower rearing costs are predicted to lead to load-lightening at later stages, while lower offspring production costs are predicted to lead to noncompensatory care at later stages through more flexible maternal investment during offspring production.

- 3) Do differences in intra-group relatedness influence this predicted investment behaviour?

YES: load-lightening is predicted to be more common when helpers are related to the mother, and exploitative strategies are predicted to be more common with unrelated helpers.

- 4) Does evidence from comparative analyses support maternal allocation levels as predictive of group size and/or female provisioning rules?

YES: Total investment in eggs and whether multiple breeding attempts are possible both associate with breeding group size. Maternal provisioning rules are influenced by the proportion of time spent incubating, and also by the breeding system.

- 5) What strategies can carers use to ensure that investment is equitably divided among group members?

ACTIVE TURN-TAKING is used in cooperative chestnut-crowned babblers when bringing food to offspring, although passive turn-taking also occurs.

Conclusions and future work

Cooperatively breeding species vary widely in their behaviour and ecology, making it difficult to establish universal benefits or specific conditions under which cooperative behaviours evolve and are maintained. The level of investment necessary to raise offspring, the potential sources (and stochasticity) of success and failure with and without helpers, the viability of alternative options to helping, and the possible routes to fitness through helping will all influence the benefits and costs of cooperation in a given species, and may interact in complex ways. To these factors, we must now also add the influence of tactical maternal investment on the investment rules, costs, and benefits of other carers.

Many questions remain regarding the potential influence of maternal tactics on investment behaviour in cooperative breeders. More detailed comparisons within particular species and across small clades of mixed cooperative and non-cooperative species would be helpful in removing some phylogenetic biases, and greater reporting of egg and clutch size variation in empirical studies would help to facilitate within and between species comparisons. Some questions that follow directly from the conclusions within this dissertation are:

- 1) Do non-cooperative species show consistently lower flexibility in maternal investment than cooperative species, due to lower variation in the amount of care available across breeding attempts?
- 2) How do alternative options available to helpers influence the ability of mothers to tactically manipulate the investment of other carers?
- 3) How would we expect carer investment rules and maternal tactics to differ between different types of cooperative breeders, such as those that queue for breeding positions, those that nest jointly (with one or multiple females) with all individuals breeding, and those in which helpers are juveniles that later disperse? Do future direct benefits of helping lead to different predictions than indirect benefits?

- 4) In stable cooperative groups, when should mothers invest ‘selfishly’ (by producing helpful or low-quality offspring), and when do they benefit from maximising offspring quality?

Beyond maternal tactics, it is currently unclear how widespread turn-taking strategies are in cooperatively breeding (or even biparental) species. The high efficiency and overall simplicity of turn-taking strategies suggests that they should be a relatively common solution to ensuring investment in offspring is equitable, but empirical tests are rare despite the enormous amounts of provisioning data collected by field studies investigating total contributions to care. More theoretical work is required to identify the ecological conditions under which turn-taking strategies are most easily employed, and better availability of older data would mean that only re-analysis, rather than new work, is needed to establish some estimates of the prevalence of turn-taking.

Although it seems unlikely that we will ever formulate a concise, overall explanation for cooperative breeding, incorporating maternal tactics into theoretical and empirical studies may explain some of the variance so far unaccounted for by phylogeny, life-history, or environmental factors. The conclusions of this dissertation suggest that future studies must take care to justify any assumptions made about the independence of different investment stages, or the degree to which parental care represents a symmetrical game between carers.

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Appendix A: Selection criteria for species used in comparative analysis

Criteria for inclusion

Species were used if the following data were available from published sources:

- 1) Clutch size
- 2) Body mass of female (or adults when monomorphic)
- 3) Mean group size
- 4) Proportion of nests with helpers
- 5) Whether breeders compensated for the presence of helpers
- 6) Whether offspring were fed more in the presence of helpers

Criteria for exclusion

Species were excluded from our analysis if any of the following conditions were met:

- a) Joint-nesting occurred at a large proportion of nests (mean above 1.3 laying females per nest). This was to avoid difficulties in accurately assessing individual female contributions to the breeding attempt; species with lower (but non-zero) proportions of joint-nesting were included to maximise the available data and the potential presence of multiple females coded as a binary effect.
- b) Provisioning by helpers occurred only after fledging. Post-fledging care is more difficult to quantify than care delivered to nestlings, and may not be directly comparable.
- c) Egg dimensions and at least one other important datum were unavailable (incubation behaviour, incubation period, nestling period, or the effect of helpers on reproductive success).
- d) The species was a very recently split or currently debated species with a better-studied sister species (e.g. *Aegithalos (caudatus) glaucogularis* excluded in favour of *Aegithalos caudatus*).

No minimum sample size was required for studies to be included. Species were excluded and data collection abandoned after one exclusion criterion was met, so it is not possible to determine whether particular species would have been excluded on multiple criteria.

Appendix B: References for data used in comparative analysis

General data sources

Egg dimensions:	[1]
Clutch sizes:	[2]
Female body mass:	[3]
Kin structure of groups:	[4]

Species data sources

<i>Acanthisitta chloris</i>	[5,6]
<i>Acrocephalus baeticatus</i>	[7]
<i>Acrocephalus sechellensis</i>	[8–10]; H.L. Dugdale, unpublished data
<i>Acrocephalus taiti</i>	[11]
<i>Aegithalos caudatus</i>	[12]
<i>Aegithalos concinnus</i>	[13]
<i>Aphelocoma coerulescens</i>	[14–17]
<i>Aphelocoma wollweberi</i>	[18–20]
<i>Buteo galapagoensis</i>	[21–24]
<i>Calocitta formosa</i>	[25–28]
<i>Campylorhynchus griseus</i>	[29–31]

<i>Campylorhynchus nuchalis</i>	[31,32]
<i>Cercotrichas coryphaeus</i>	[33]
<i>Ceryle rudis</i>	[34,35]
<i>Climacteris picumnus</i>	[36–38]
<i>Climacteris rufus</i>	[37–41]
<i>Corcorax melanorhamphos</i>	[42–44]
<i>Corvus brachyrhynchos</i>	[45–48]
<i>Corvus corone</i>	[49–51]
<i>Cyanocorax beecheii</i>	[52,53]
<i>Cyanocorax sanblasianus</i>	[54,55]
<i>Cyanopica cooki</i>	[56,57]
<i>Dacelo novaeguineae</i>	[58–60]
<i>Gymnorhinus cyanocephalus</i>	[61]
<i>Lamprotornis pulcher</i>	[62,63]
<i>Lamprotornis superbus</i>	[64,65]
<i>Malurus coronatus</i>	[38,66]
<i>Malurus cyaneus</i>	[38,67,68]
<i>Malurus elegans</i>	[38,69]
<i>Malurus melanocephalus</i>	[70,71]
<i>Malurus splendens</i>	[38,72,73]

Appendix B: References for data used in comparative analysis

<i>Manorina melanocephala</i>	[74,75]	<i>Pomatostomus temporalis</i>	[111–113]
<i>Manorina melanophrys</i>	[76,77]	<i>Prunella collaris</i>	[114,115]
<i>Melanerpes formicivorus</i>	[78–80]	<i>Prunella modularis</i>	[116–118]
<i>Merops apiaster</i>	[81,82]	<i>Pseudonigrita arnaudi</i>	[119,120]
<i>Merops bullockoides</i>	[83–86]	<i>Psilorhinus morio</i>	[121–123]
<i>Merops bullocki</i>	[86–88]	<i>Schetba rufa</i>	[124,125]
<i>Mimus parvulus</i>	[89,90]	<i>Semnornis ramphastinus</i>	[126,127]
<i>Opisthocomus hoazin</i>	[91,92]	<i>Sericornis frontalis</i>	[128–130]
<i>Parus niger</i>	[93]	<i>Sialia mexicana</i>	[131,132]
<i>Passer domesticus</i>	[94]	<i>Sitta pygmaea</i>	[133–135]
<i>Philetairus socius</i>	[95,96]	<i>Struthidea cinerea</i>	[136,137]
<i>Phoeniculus purpureus</i>	[97–100]	<i>Turdoides caudata</i>	[138,139]
<i>Picoides borealis</i>	[101–104]	<i>Turdoides jardineii</i>	[140–142]
<i>Plocepasser mahali</i>	[105–107]	<i>Turdoides squamiceps</i>	[143,144]
<i>Pomatostomus ruficeps</i>	[108–110]; A. F. Russell, unpublished data		

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