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Models of conflict and voluntary cooperation between individuals in non-egalitarian social groups

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Abstract

This thesis broadly investigates the evolution of voluntary cooperative behaviour among individuals in conflict in non-egalitarian social groups. This work is partitioned into three sections.

In the first section, we study the emergence of non-egalitarian social groups by examining leader-follower relationships in the context of group dispersal. We construct an inclusive fitness model to demonstrate that group dispersal is more likely to emerge when followers are given a greater share of resources. relatedness among individuals is higher, and costs of dispersal diminish rapidly for larger dispersal groups. Our results provide evidence for the fact that non-egalitarian groups may emerge even when individuals do not differ in immediate condition.

In the second section, we study several scenarios in which genetically related individuals with unequal control over resources cooperate despite being in conflict. Two chapters are dedicated to research on the evolution of offspring signals and parent-offspring conflict over provisioning. First, we create an evolutionary game to show that environmental conditions can influence whether signals convey offspring need or quality. Next, we propose and substantiate using a simple theoretical model that sex differences in begging observed in several bird species could be the consequence of sex differences in parental care provided by these species. In the third chapter of this section, we create a full life-cycle model to clearly demonstrate that, in agreement with recent empirical data but in contrast to previous theory, the emergence of cooperative breeding may either increase or decrease a species average clutch size, depending on several ecological and social conditions.

In the last section, we investigate cooperative behaviours between unrelated individuals in conflict by modelling the evolution of coalitionary behaviour. We create an evolutionary model to explain how certain social and ecological conditions, particularly a species coalition solicitation pattern and the specific resources being contested by the coalition, can influence the

relative frequencies of various forms of coalitionary behaviour observed in the animal kingdom. Results also suggests concessions granted by dominant individuals rarely evolve and are only used to make the recipient a more attractive target of coalitionary behaviour.

Keywords: Evolutionary biology, behavioural ecology, conflict, cooperation, social behaviour, life-history

Co-Authorship Statement

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Chapter 1

Introduction

Behaviour is considered social if it influences both the actor and other conspecifics — the recipients [1]. The effect of social behaviour on the actor and recipient is often measured in terms of how the behaviour influences an individual's inclusive fitness, a metric describing the success of an individual in contributing their genes to the gene pool of the population (see Mathematical tools and concepts) [2, 3, 4]. Social behaviour is described as cooperative if it increases the recipient's fitness [5]. Cooperative behaviour can occur when certain interests of individuals overlap in an evolutionary sense, such as when individuals are genetically related. Many animals frequently live in social groups, allowing for increased frequencies of cooperative behaviour. However, whenever the genetic material between individuals differs, their evolutionary interests do not completely overlap, and this can result in conflict [3]. Conflict between individuals arises due to competition over mating opportunities and limited resources, and ultimately results in a decrease in fitness for one or more individuals. Despite sometimes frequent conflict between individuals, many animal species voluntarily form social groups. Some animals such as various primates even form extensive and permanent social groups with non-relatives, despite the apparent scope for conflict [3].

The outcome of conflict in social groups varies from an even distribution of resources

among all individuals (i.e. low skew, egalitarian groups) to complete monopolization of resources by a few dominant individuals (i.e. high skew, despotic groups) [6, 7]. Non-egalitarian groups may form when certain individuals are physically or socially dominant and use their dominance to secure a disproportionate amount of resources. In some animals, dominance and resource skew is determined by the outcome of frequent fights, such as lethal engagements common among female meerkats (*Suricata suricatta*) [8], or expensive displays of physical dominance, such as the roaring of red stags (*Cervus elaphus*) [9]. In other species, dominance hierarchies are established without fighting, forming static social roles that change only occasionally when subordinates challenge dominant individuals [10, 11]. The dominance hierarchies of white-crowned sparrows (*Zonotrichia leucophrys gambelii*) are determined strictly by the colour of their plumage: individuals with greater proportions of white feathers consistently enjoy higher social statuses [12]. While conflict often increases resource skew, cooperation frequently leads to more egalitarian outcomes. In altricial species, for example, newly born or hatched offspring are unable to secure sufficient amounts resources by themselves and rely on the cooperation of adults to share resources with them [13]. Cooperation among members of non-egalitarian social groups, particularly between those in different social roles, can be difficult to explain from an evolutionary perspective since it is not always clear how both parties benefit. For example, parental care — the simplest example of cooperation in non-egalitarian social groups whereby parents sacrifice their own resources for their offspring — was observed in various animal species for many centuries but was not rigorously explained until Fisher's formal mathematical treatment of kin selection in 1930 [14], and was not thoroughly understood until Hamilton's mathematical framework in 1964 [2]. Such cooperative behaviours commonly emerge between members with unequal control over resources even when individuals are in direct conflict over resources; these cooperative behaviours often influence the outcome of the conflict to favour one party more significantly than the other.

Why should subordinates voluntarily engage in cooperative behaviour when only the dom-

inant party appears to benefit? Why are voluntary leader-follower relationships so common even though it often seems only one party benefits from the association? Why in cooperatively breeding species do subordinates aid dominant breeders, often lengthening the breeder's tenure as monopolisers of breeding opportunities, even though a primary incentive for helping is thought to be territory inheritance?

Why do dominant individuals so frequently cooperate with their subordinates even when they are able to monopolize resources? Why do parents allow the begging of their offspring to manipulate their resource allocation strategy? In species where offspring begging dictates parental provisioning rates, why do females often resign to begging at lower rates than males even though they can gain more resources if they chose to beg louder? Why would dominant individuals in social hierarchies of unrelated individuals concede resources to low-ranking members?

In this thesis, we address some of these questions by examining how the evolution of cooperative behaviours exhibited between members with different social roles in non-egalitarian groups can influence the outcome of conflict in these social groups. The thesis is divided into three sections. In section 1, we analyze the very formation of egalitarian and non-egalitarian groups. Chapter 2 demonstrates that cooperation itself can motivate the emergence of different social roles and that the formation of social hierarchies of various skew can be established even in the absence of any physical differences between individuals. In section 2, we dedicate three chapters to exploring cooperative behaviours in non-egalitarian groups of kin. In Chapters 3 and 4, we study how parent-offspring conflict over resource allocation may be influenced by offspring signalling their condition to help guide parents' provisioning and allocation strategies. In Chapter 5, we analyze how subordinate offspring may resolve conflict over territories by helping dominant breeders survive and raise offspring. In the final section, we explore cooperation arising from conflict existing in non-egalitarian social groups of non-relatives. Chapter

6 is dedicated to understanding how cooperation in the form of coalitions can influence and resolve conflicts in triads.

The remainder of the introduction initiates the reader into the basic theory behind the four widespread cooperative behaviours exhibited in non-egalitarian groups explored in the thesis: leader-follower relationships (Chapter 2), offspring signalling (Chapters 3 and 4), cooperative breeding (Chapter 5), and coalitionary behaviour (Chapter 6). Explanations of the core mathematical tools used in the thesis will be provided in this exposition, often supplemented with summaries of previous models constructed to explain the aforementioned cooperative behaviours.

1.1 Mathematical tools and concepts

Here, I briefly outline the primary mathematical tools and concepts used in this thesis.

1.1.1 Inclusive fitness

Evolutionary success is frequently measured in terms of inclusive fitness. An individual's inclusive fitness is the sum of an individual's fitness gained through personal reproduction (direct fitness) and the fitness produced by helping non-descendant kin (indirect fitness). Inclusive fitness is sometimes defined as a measure of an individual's total contribution to the gene pool of the next generation [3], while other sources state it measures an individual's genetic contribution to the population in the very distant future [4]. Many empirical studies frequently equate fitness with offspring quantity, though this metric may not correlate completely with genetic contributions to the population in the distant future when there is nonrandom variation in offspring quality [15]. Regardless, the concept of inclusive fitness is most often used as a tool which helps us compare the evolutionary consequences of traits and, for many models, the relative fitness consequences of any two traits does not depend on whether it is measured in the

next generation or in the distant future.

An common example of the application of inclusive fitness is its role in explaining altruistic behaviour, whereby an individual endures a cost to itself in terms of direct fitness in order to aid relatives, thereby increasing the individual's indirect fitness. For an altruistic trait to evolve, the inclusive fitness of an altruistic individual needs to be greater than the fitness of an individual that does not engage in the altruistic behaviour. Hamilton derived a now famous mathematical condition describing when altruism should be expected to spread: $c < rb$, where c can be described by the cost to the altruist in terms of direct fitness, b denotes the reproductive benefit experienced by the recipient of the altruistic behaviour, and r measures the degree of relatedness between actor and recipient.

1.1.2 Nash equilibria

Game theory was first introduced to study strategic interactions among rational individuals. Games are essentially situations involving two or more players, in which each player has a number of strategies, the set of actions from which the player chooses in any given situation. Each strategy is associated with some expected payoff, which may be influenced by the strategies used by other players in the game. The basic tenant of game theory is that all players are rational and will therefore seek to maximize their own payoffs. The structure of the game and the payoffs of each player for any given outcome is knowledge common to all players, and, as such, players can predict the actions of their opponents [16].

The solution concept of evolutionary game theory is that of the Nash equilibrium, defined as an equilibrium where no player can fare better by unilaterally changing strategies. Suppose each individual in a population uses strategy X. If one player in this population decides to adopt strategy Y instead, then strategy X is considered a Nash equilibrium whenever $E(X, X) \geq E(J, I)$, for any strategy Y, where $E(i, j)$ is the expected payoff for using strategy i against

strategy j. If a Nash equilibrium is strict, any player that unilaterally changes strategies receives a lower payoff; that is, $E(X, X) > E(Y, X)$. In this sense, in a strict Nash equilibrium, every player is choosing the 'optimal' given that the strategy of every other players is constant [16].

1.1.3 Evolutionarily stable strategies

In the models presented here, we will generally seek to identify possible endpoints of evolution. The primary distinction between early game theory and evolutionary game theory is that players are no longer assumed to be aware of the structure of their game, nor can consciously predict the actions of their opponents via rational foresight. In evolutionary game theory, strategies are genetically determined and heritable and payoffs are measured in terms of inclusive fitness. Essential for this is the concept of an evolutionarily stable strategy (ESS), defined as any strategy which, once adopted by a population, cannot be invaded by any initially rare alternative strategy. An ESS is a Nash equilibrium, but not all Nash equilibria are ESSes [16]. For a strategy to be an ESS, it must be a strict Nash equilibrium or, if the Nash equilibrium is not strict, the Nash equilibrium strategy must fare better in a population that uses any alternative strategy that is neutral with respect to the Nash equilibrium strategy than the neutral strategy itself, thereby ensuring some advantage for continuing to play the Nash equilibrium strategy. That is, for X to be an ESS, we require that either $E(X, X) > E(Y, X)$ or, if $E(X, X) = E(Y, X)$, then $E(X, Y) > E(Y, Y)$ [16].

For example, consider a very simple game involving two players — the parent and the offspring. The parent can decide between feeding at a normal rate and feeding at an elevated rate. The offspring will decide between signalling and not signalling. If both players choose between their options simultaneously (i.e. without knowledge what the other player has chosen but with the knowledge of the payoffs of both players for any given outcome), we can represent the game in the payoff matrix given in Table 1.1. The values in the matrix represent the inclusive fitness of each player in each of the game's possible outcomes. Identifying the

Table 1.1: Example payoff matrix

		Offspring	
		Signals	Does not signal
Parent	Normal parental care	5, 2	6, 4
	Elevated parental care	2, 3	4, 5

ESS in this scenario is simple: the offspring always fares better by not signalling, regardless of which option the parent chooses, while the parent always receives a higher payoff by choosing to provide normal levels of parental care to the offspring, regardless of whether the offspring signals. Thus, the ESS — a strict Nash equilibrium — will always be the outcome in which the offspring does not signal and the parent provides normal levels of care.

1.1.4 Evolutionarily stable states

Following the proof outlined in Taylor & Jonker, we next study dynamic games wherein the frequencies of strategies may change over time [17]. Consider now a population of individuals, each able to choose one of n pure strategies. Let s_i and $s = (s_1, s_2, ..., s_n)$ denote the proportion of individuals using strategy i and the population's state vector, respectively. The payoff, equivalent to the fitness, of any individual using strategy i at any given time is denoted by $F(i|s)$. Strategies yielding a higher payoff are more likely to be used in the future, whether this is due to the fact that those employing more fit strategies have more offspring or others observe the success of the strategy and replicate it. Let $p = \sum p_i = 1$, $p_i \geq 0$ denote a state of the population. For any state q, we define $F(q|p) = \sum q_i F(i|p)$.State p is an ESS if for any alternative state $q \neq p$, setting $\bar{p} = (1 - \epsilon)p + \epsilon q$, then $F(q|\bar{p}) < F(p|\bar{p})$ for any sufficiently small $\epsilon > 0$. That is, p is considered stable if the system, once disturbed, returns to p [17].

We will now discuss the notion of stability in these dynamic games. Suppose there are n_i i-strategists in a total population of $N = \sum n_i$ individuals. Let $\dot{n}_i = r_i n_i$ represent the growth rate of strategy i. Suppose the fitness $F(i|s)$ is an estimate of the growth rate of an individual

using strategy i, r_i. In the time δt, each individual produces $F(i|s)\delta t$ additional individuals. Our replicator equation is thus

$$\dot{s}_i = s_i(F(i|s) - F(s|s)). \tag{1.1}$$

Suppose we are dealing with discrete generations. If an individual using strategy i produces no offspring and simply dies, then $r_i = -1$. The number of i in the next generation is given by $\hat{n}_i = n_i(r_i + 1)$. Ensuring the population size remains constant, the proportion of the population employing strategy i in the next generation is $\hat{s}_i = \frac{s_i(r_i+1)}{\bar{r}+1}$, where $\bar{r}$ represents the average growth rate of the population. Equivalently,

$$\hat{s}_i = s_i \frac{F(i|s) + 1}{F(s|s) + 1}. \tag{1.2}$$

State p is stable if every trajectory near p converges to p. We can examine the local stability of a model with continuous dynamics by linearizing (6). Given state s, let $x = s - p$. It follows that $\dot{x}_i = \dot{s}_i$, thus from (2) we have $\dot{x}_i = (x_i + p_i)(F(i|x + p) - F(x + p|x + p))$. Collecting terms on the right side that are first-order with respect to x gives the system $\dot{x} = Bx$. p is strictly stable with respect to perturbations in $\sum s_i = 1$ if the eigenvalues of the matrix B have strictly negative real parts. Similar treatment can be applied to (7), giving linearization $\hat{x} = Cx$. Here, p is strictly stable with respect to perturbations in $\sum s_i = 1$ if the eigenvalues of C have modulus less than one. Taylor & Jonker [17] demonstrate that if p is an ESS, then it is locally asymptotically stable with respect to the dynamics in (6).

1.1.5 Evolutionary invasion analysis

We now consider analysis involving continuous state variables. The goal of invasion analysis is to model the long-term evolution of phenotypes in a population. To analyze social evolution using a mathematical framework, traits are represented by continuous variables [18]. To begin, we make two assumptions: first, that the wildtype population is in dynamical equilibrium, and

second, that the long-term success of the mutant is equivalent to its initial growth rate upon invasion [19]. Suppose we seek to model the evolution of a continuous trait, x. This resident population is monomorphic exhibiting trait value x when a mutant — the focal individual — invades and exhibits trait value y. Since we are modelling the evolution of social behaviour, the fitness of the focal individual, $f(y, x)$, depends both on the strategy set it employs, y, and the strategy set of those with whom the individual interactions, x. This measure of fitness, sometimes referred to as invasion fitness, represents the expected number of offspring produced by or growth rate of a rare mutant y in a resident population that is monomorphic for trait x [20].

With small mutations, the local selection gradient is defined as $D(x) = f_y(y, x)|_{y=x}$. If the gradient is positive (resp. negative) mutants with slightly higher (resp. lower) phenotypic values may successfully invade the resident population [18]. Evolutionary singular strategies are phenotypic values x^* at which $D(x^*) = 0$, which is where the selection gradient vanishes. In the absence of evolutionary singular strategies, the trait x uniformly increases (resp. decreases) if $D(x^*) > 0$. (resp. $D(x^*) < 0$), unless boundary conditions are present [18]. If an evolutionary singular strategy is also a local maximum, then it is also an evolutionary stable strategy (ESS); that is, if $D_y|_{y=x^*} < 0$, then the strategy, once established, cannot be invaded by nearby mutants because no phenotypic value sufficiently close to the singular point has a higher growth rate than the singular trait value itself. Evolutionary singular points are thus referred to as candidates ESSes.

A singular strategy is locally convergence stable if the system returns to the singular point after any sufficiently small perturbation [18]. If x^* is convergence stable, then If both x and y are close to x^*, but y is close to x^*, y will yield a higher fitness than x; that is, the local fitness gradient leads toward x^*. More precisely, if a singular point, x^*, is convergence stable, then $D(x)$ decreases locally around x^*, and thus $\frac{dD(x)}{dx} = \frac{\partial f(y,x)}{\partial x \partial y} + \frac{\partial^2 f(y,x)}{\partial y^2} < 0$. Since whenever $y = x$, $f(x, y) = f(y, x)$, we note that the directional derivative along the line is

thus $2\frac{\partial f(y,x)}{\partial x \partial y} + \frac{\partial^2 f(y,x)}{\partial x^2} + \frac{\partial^2 f(y,x)}{\partial y^2} = 0$, and so the condition for convergence stability simplifies to $\frac{\partial^2 f(y,x)}{\partial x^2} > \frac{\partial^2 f(y,x)}{\partial y^2}$ [18].

As described, the conditions for convergence stability and evolutionary stability are, in general, different. Thus, an ESS is a possible endpoint to evolution, but only if an ESS is also convergence stable is it likely to be the end point of evolution. Points that are both evolutionary and convergence stable are continuously stable strategies (CSSes), and they represent terminal points of evolutionary dynamics. If a singular point x^* is convergent but evolutionary stable, evolution will favour selection toward x^*, but as nearby mutants can invade, evolution may subsequently diverge away from the singular point in two coexisting clusters, forming an evolutionary stable dimorphism. If a singular point x^* is an evolutionary but not convergence stable, no mutant population can invade the resident population, but if the resident population begins at a different point, it will never reach x^* [20, 18, 19].

1.1.6 Numerical approximations of ESSs

In this thesis, there were cases where explicit evolutionary stable solutions could not be derived analytically from the invasion analysis, and so numerical approximations were used. The approximations emulate replicator dynamics by first assigning a random strategy x_i to the resident population. The strategy used by the next generation, x_{i+1}, was determined by calculating the selection gradient at this point, D_i and evolution occurred at some rate k, along this gradient such that $x_{i+1} = x_i + kD_i$. Evolutionary endpoints were said to have been reached when $x_{i+1} - x_i$ was sufficiently small. Note that this condition is not equivalent to $D_i \to 0$, as boundaries were imposed on the traits (e.g. dispersal rates could never exceed 1 or fall below 0) such that a strategy was evolutionary stable if the trait was at a maximum (resp. minimum) value and selection favoured yet further increases (resp. decreases) in the trait value. To ensure the existence of a single CSS, multiple initial strategy values employed by the resident population, x_0, were used through use of a mesh. Individual-based simulations were used to illustrate and

verify predictions derived from numerical analyses.

1.2 Leader-follower relationships and the formation of social groups

We begin our exploration of behaviours between members of non-egalitarian social groups by first investigating the emergence of non-egalitarian social groups. One of the most basic forms of non-egalitarian social groups are leader-follower groups. Leader-follower groups are a common subset of social relationships in which certain individuals initiate or coordinate group activity (leaders) and others follow (subordinates) [21]. Some leader-follower groups are formed and are stabilized through coercion; that is, certain individuals are so physically or socially dominant that they can aggressively punish subordinate individuals attempting to leave the leader-follower group [22]. Explaining the emergence of these leader-follower groups is often trivial from an evolutionary perspective: even if the relationship is ultimately costly to subordinates, punishment incurred from dominants may be costlier. However, many leader-follower groups are seemingly formed from the voluntary participation of both leader and follower, and the incentives for these relationships are often less apparent [23]. Understanding of how selection may favour sociality and cooperation among competitors in conflict, particularly when subordination is voluntary, yet subordinates seem to gain little from sociality, is lacking.

Theoretically, leader-follower relationships can evolve if the reproductive success of both leaders and followers is, on average, greater than that of individuals who are not in leader-follower groups[3]; equivalently, the benefits of being in leader-follower relationships rather than being solitary must be, on average, less than the costs. Empirical studies have shown that the benefits of social living can be considerable. Compared to solitary individuals, groups have greater defense against predators and outside competitors via the dilution effect and mutual defense [24]. Further, groups have improved foraging via information flow and collaboration

[25], and assistance from others when dealing with pathogens [3]. Within groups, there is also greater opportunity to sabotage competitors' reproduction. However, the costs of sociality can also be substantial: relative to solitary individuals, groups have higher rates of disease due to greater transmission rates [26], greater competition for limited resources, and more reproductive interference [27, 3].

Where high skew exists, the cost-to-benefit ratio of participating in leader-follower relationships varies greatly between subordinate and dominant individuals [28]. For example, it is common for social species to expend energy in pursuit of not only resources but social status. Those that fail to occupy dominant or leadership positions frequently obtain a lower share of reproductively relevant resources [3]. Further, in some cases, subordinates must expend energy merely to demonstrate their submissive nature to remain in the group. The emergence of these voluntary and often high skew leader-follower groups is an evolutionary puzzle because it requires both dominant and subordinate individuals, to accrue, on average, a higher fitness than those attempting to become solitary individuals [22].

Despite extensive empirical studies on the emergence and maintenance of leader-follower relationships, some theoretical work on the evolution of leadership and followership relies on unrealistic or unjustified assumptions. First, previous literature tends to focus only on understanding the conditions in which leadership emerges, and therefore neglects the evolution of followership, despite it being central to evolutionary analysis [29, 30, 22]. Theoretical work instead needs to identify conditions under which the formation of leader-follower relationships is favourable to both leader and follower.

Secondly, studies on the emergence of leader-follower relations often suggest or assume that leaders will emerge only if they receive direct fitness benefits, and thus presupposes a certain degree of skew [31]. Yet, in nature, animal groups vary from despotic to com-

pletely egalitarian. Further, many, if not most, leader-follower groups are formed among kin [22, 32, 33, 34, 35, 36, 37, 38, 39, 40]. Thus, leaders can still benefit from an increase in inclusive fitness by forming leader-follower relationships even when subordinates experience the majority of reproductive success. Proper accounting of the inclusive fitness of leaders and followers is crucial to understanding this type of dominant-subordinate relationship. This includes the creation of models that explicitly account for population dynamics, which is often required for accurate and realistic results [41].

Lastly, leaders are commonly thought to be socially or physically dominant, in possession of specialized knowledge, or in exceptional need of particular resources [23, 42, 43, 44]. Many previous models have used the assumption of pre-existing differences in state to explain the emergence of leader-follower behaviour [45, 42], including the idea that leaders have direct control over the behaviour of their followers. These models assume some degree of reproductive skew. This assumption can hinder understanding of the emergence of leader-follower relationships and the evolution of reproductive skew in animal groups. While it is common for leaders to be physically or social dominant [22, 45], and leaders often demonstrate the ability to manipulate the behaviour of followers, both of these may, at least in some cases, be the products rather than the causes of leader-follower relationships. The assumption is valid for models exploring the consequences of leader-follower relationships, but more theoretical work needs to be dedicated to examining the emergence of leadership and followership in homogeneous populations.

In Chapter 2, I construct a model for the evolution of natal dispersal — the movement of individuals from their birth site to their breeding sites — when certain individuals (leaders) initiate dispersal and others (followers) disperse with these leaders. This inclusive fitness model uses explicit population dynamics to generate an accurate mathematical description of the evolutionary incentives for leading and following in dispersal groups. In addition to describing

how certain social and ecological factors can promote the emergence of group dispersal, the model is used to identify how leader-follower relationships affect population dynamics, including the evolutionarily stable levels of natal dispersal. I also describe how leader-follower relationships in the context of dispersal affect altruistic behaviour.

1.3 Parent-offspring conflict and offspring signals

Next, we investigate the evolution of cooperative behaviours emerging from conflict among kin in non-egalitarian groups.

Parent-offspring conflict and conflict among offspring for parental investment is influenced by offspring signals. Parental investment describes any allocation of resources expended by the parent to increase the fitness of their offspring [3]. The investment behaviours of the parent, which constitute its parental care strategy, are made at the expense of other components of the parent's fitness, such as their survival and future reproductive success. Higher degrees of parental care mean greater resource investment into a relatively smaller number of offspring. Parental care increases the direct fitness of the offspring, thereby increasing the indirect fitness of the parent, and thus, since both parties benefit, parental care can be defined as cooperative [3]. However, parent and offspring are not genetically identical in most species of animal, meaning that the evolutionary interests of the two parties do not completely align. This has led to significant parent-offspring conflict over parental investment. Consequently, parental care can be considered both a cooperative behaviour and a key source of conflict between parent and offspring.

Offspring signalling or soliciting for parental care is thought to significantly influence the outcome of parent-offspring conflict. Solicitation for parental care, exhibited in birds, mammals, insects, and even plants, is both taxonomically widespread and common [46]. This be-

haviour, often referred to as offspring begging, occurs in a variety of forms, including auditory, visual, and chemical signals [47]. Parental responses to begging behaviour via adjustments in resource provisioning and allocation are also complex and diverse in nature. The ubiquity and diversity of begging behaviour and parental responses has motivated decades of extensive theoretical and empirical research, with literature often focusing on the ultimate function of begging. Although it is often argued that begging behaviour is used to guide the feeding behaviour of parents by indicating levels of need — and is thus cooperative — debate over the function of begging is on-going, and recent empirical data has demonstrated that current theory is unable to explain and predict observed begging and provisioning behaviours.

1.3.1 Begging as blackmail

Offspring signals have been demonstrated to be metabolically taxing [48, 49, 50, 51] and to increase predation rates [52, 53, 54, 55, 56, 57], even though less expensive forms of communication between offspring and parent could seemingly evolve. For these reasons, early theory on offspring signalling focussed on the notion that offspring may evolve to effectively handicap themselves by signalling to shift the outcome of parent-offspring conflict over provisioning closer to the offspring's optimal provisioning rates [58, 59, 60]. Offspring begging reduces offspring fitness, but parents can reduce or prevent these expensive soliciting behaviours by providing greater care for the offspring than would be optimal for the parent in the absence of begging behaviours. This central idea will henceforth be referred to as the blackmail hypothesis. A series of models have determined that this blackmailing behaviour can be evolutionarily stable in a wide variety of situations [61, 62, 63, 64, 65, 60, 66].

The blackmail hypothesis was initially criticized because models supporting the hypothesis assumed the behaviour of parents and offspring were fixed rather than dynamic [67]. Johnstone later proved that the blackmail hypothesis is robust even when parent and offspring responses could evolve [66], but by then, several hypotheses, discussed below, had become more widely

accepted. The blackmail hypothesis has also been criticized because there have been several empirical studies that did not find any fitness costs associated with signalling [68]. Further, signalling can be shown to be stable even in the absence of signalling costs, and thus the blackmail hypothesis may be less parsimonious than other hypotheses.

1.3.2 Signal of quality

Grafen was the first to formalize that signalling behaviour can be stable only when they are generally honest so that the receiver may benefit on average by responding to the signal; otherwise, the receiver would ignore the signal and the signal would not evolve [69]. He extended the idea of honest signals to propose that offspring may be honestly signalling to their parents their quality by begging when their quality would otherwise be unknown to the parent. The parents may benefit by distributing resources in accordance to these signals by provisioning for the best growing chicks to avoid wasting resources on the sick or weak. The principal assumption for this hypothesis is that higher-quality offspring can 'afford' to beg more aggressively — and thus the signal is honest — whereas begging results in relatively greater harm for smaller offspring. A second important assumption is that parents are to some degree limited in the resources they can provide their offspring, otherwise they could provide all offspring with an abundance of resources [69]. This reasoning formed the signal of quality (SoQ) hypothesis.

Although Godfray broadly defined quality as being equal to the current condition or reproductive value of the offspring, the definition of 'quality' was neither very precise nor consistent among authors [69] — a primary reason the theory generally fell out of favour among theorists. The SoQ hypothesis has been suggested to be limited due to the assumption that the costs of signalling are less for higher-quality individuals [67]. Verification of this theory has remained elusive because measuring an offspring's current or potential reproductive value is required, yet there is no agreed upon metric for this value. Body size has been proposed to be a proxy closely related to potential fitness, but such cues are easily assessed by parents, meaning

signals should not be required for parents to evaluate offspring quality.

1.3.3 Signal of need

The theory that offspring with the greatest need — as defined by the marginal fitness benefits of increased provisioning — beg loudest and receive the most resources from parents is by far the most widely studied and recognized hypothesis that seeks to explain begging and provisioning behaviours. The signal of need (SoN) hypothesis was first formally proposed by Godfray (1991), and hinges on the idea that offspring condition cannot be perceived by the parent in the absence of these honest signals [67]. A SoN system benefits both parent and offspring as it guides the parent to distribute resources more optimally. Unfortunately, for mathematical convenience, the model constructed by Godfray tacitly assumed for mathematical convenience that quality and need were antonyms, where offspring with higher levels of fitness necessarily had lower levels of need. This assumption, embedded in functions that represent how offspring fitness changes with parental provisioning levels, was repeated in several models extended from Godfray's original [70, 71, 72, 73].

Like SoQ, SoN has not received strong empirical support due to the difficult in assessing the current and potential reproductive of offspring. Several hunger experiments that have ostensibly provided support for the SoN hypothesis — and criticism for the SoQ hypothesis — have now been criticized, as hunger does not necessarily correlate to potential marginal fitness gains [46], conflating proximate and ultimate explanations for begging behaviour. Further, models [70] often assume that the intention of the parent is to always raise all offspring and ignore the importance and prevalence of brood-reduction behaviour that is widespread in the animal kingdom [46]. It has been argued that when resources are scarce, parents should instead allocate resources only to the few offspring which they can successful raise, an argument that is in line with SoQ [46]. More recent experiments on species that regularly use brood reduction tactics have shown parents skew resources toward larger offspring, and that there is a corre-

lation between total resources allocated to offspring and the size of fledging. Indeed, while several studies have been viewed as champions for the SoN hypothesis, there are a considerable number of studies, particularly those focusing populations with very limited food, that are in opposition of SoN and in support of SoQ [74, 75, 76, 77]. Although these two hypotheses have frequently been compared, they need not be mutual exclusive, with SoN being used whenever there is enough resources to reliably raise all offspring, and SoQ employed whenever there are a shortage of resources [46].

1.3.4 Signal of hunger

Both SoN and SoQ hypotheses assume that the offspring is more aware than the parents of its own potential reproductive value, an assumption that has not yet been carefully examined for plausibility. The SoN and SoQ hypotheses also somewhat fail to account for the information conveyed by body cues (e.g. size, weight) which, regardless of begging levels, are very often readily available to parents and could influence provisioning and allocation tactics. Mock [46] argues that these weaknesses are addressed by his signal of hunger (SoH) hypothesis, which stipulates that signals are merely proximate indications of fullness. This is precisely what hunger experiments are, in fact, assessing (as opposed to need), with the general finding that, as predicted by SoH, offspring beg less intensely after a large meal. Parents can either choose to respond to signal intensity (complying with SoN) or body cues (inline with SoQ), depending on resource availability.

This theory, like the SoN and SoQ hypotheses but unlike the blackmail hypothesis, suffers in part because it is unable to explain why conspicuous signals, such as exuberant vocal begging, are used instead of more subtle cues that are less metabolically taxing and are less likely to attract predators. While Mock champions SoH for its parsimony, it does have an additional assumption compared to SoN and SoQ: parents must be able to reliably and efficiently assess body cues. In species that build nests in tree cavities, the assessment of visual cues may not

be very efficient. Body cue assessment may also be unreliable: inherent sex differences in the size of offspring, for example, could make ineffective parental provisioning and offspring begging behaviours that are based solely on offspring size; the consequences of this oversight are addressed in Chapter 4. Most importantly, however, this theory applies more to the proximate rather than the ultimate causes for begging behaviour.

1.3.5 Begging for efficiency

A final hypothesis that has yet to be concretely formalized posits that offspring begging may comprise a system that is not entirely necessary but is simply a more efficient method for offspring to convey information to parents. Referring again to the many species that lay eggs in tree hollows, it may cost parents less time or energy to assess offspring signals instead of body cues, and these resources could instead be redirected toward greater overall provisioning levels. If offspring signals are more easily assessed, they could benefit both parent and offspring, increasing either or both direct or indirect fitness. The wide prevalence of exuberant vocal cries may also be explained with this through by recognizing that parents often need to leave the nests to gather resources. Auditory cues provide parents with a means of leaving nests while also being able to monitor the status of their offspring.

Note that none of the above hypotheses are mutually exclusive. However, the offspring blackmail and begging for efficiency hypotheses are more closely related to the provisioning levels — the total amount of resources given to all offspring — whereas signals of need, quality and hunger may significantly influence both parental provisioning and allocation behaviour – the way parents distribute resources among offspring.

1.3.6 The mathematics of signalling theory

Signalling theory has been investigated using a diverse set of mathematical models and tools. Generally, these models involve a single parent and one or two offspring, with the goal of find-

ing the begging intensity of the offspring and either the provisioning or the allocation behaviour of the parent at equilibrium. This section will review the basic mathematical framework used in previous signalling models while also addressing the limitations of these models.

Godfray model

Box #1: *Mathematical framework of Godfray's (1991) one-offspring model* [67]

Godfray was the first to concretely and mathematically formulate the SoN hypothesis [67]. His models had two players: the parent and the offspring. The fitness function of an offspring, $f(c, x, y)$, depends on its initial or baseline condition, level of solicitation, and the amount of resources the offspring receives, denoted by c, x, and y, respectively. Signalling is assumed to be costly, and thus offspring fitness decreases with increasing x. The parent's residual fitness, $g(y)$, decreases as it provides more resources to its current offspring. The amount of resources provided to the offspring is some unknown function of the offspring's begging intensity, $y = S(x)$, which will be identified by finding the evolutionarily stable level of solicitation, x^*, and the level of parental provisioning, y^*, as functions of offspring condition, c. At equilibrium, small increases in begging intensity will not produce a change in the offspring's net inclusive fitness. Mathematically, this condition corresponds to

$$S'(x^*)f_y(y^*, x^*, c) + S'(x^*)rg_y(y^*) + f_x(y^*, x^*, c) = 0, \tag{1.3}$$

where the first term represents the increase in the offspring's direct fitness as provisioning increases, the second term represents the decrease in the parent's residual fitness due to increased provisioning, weighted by the relatedness between parent and offspring, r, and the third term represents the decrease in the offspring's direct fitness due to the cost of increasing begging behaviour. Similarly, at evolutionary equilibrium, small increases in provisioning should yield

no change in the parent's net inclusive fitness; that is,

$$f_y(y^*, x^*, c) + g_y(y^*) = 0, \tag{1.4}$$

where the first term represents the increase in the reproductive value of the offspring as it receives more resources while the second term denotes the decrease in residual fitness the parent experiences due to increased provisioning rates. To identify x^* and y^*, an initial condition is required. It is assumed that offspring of maximal fitness, c_{max}, do not solicit as they do not need provisioning, so we have the initial condition $(y, x, c) = (y^*, 0, c_{max})$.

We begin by revisiting the construction and implications of Godfray's model [67]. First, while the general construction of Godfray's model (see Box #1) assumes neither SoN nor SoQ (no explicit relation between begging intensity, provisioning, and condition is required), it should be made clear that Godfray's model does not provide evidence for SoN. Instead, after building the general model, Godfray analyzes it under the assumption that SoN is true: he defines an offspring's need as the marginal fitness gain it experiences by obtaining more resources, and assumes that parents will provide more resources to young in "poor condition" (low reproductive value) [67, 46] (mathematically, he assumes f_y is greater for offspring with lower c). Note that nothing in the framework given in Box #1 prohibits the converse assumption that parents will provide more resources to young in good condition, such that parents feed according to which offspring has better intrinsic fitness. He then explicitly states that offspring fitness increases monotonically with respect to greater resources (mathematically $f_x > 0$), and adds a further restriction — that this increase occurs at a uniformly decelerating rate. While the former assumption is altogether reasonable, no justification is provided for the latter assumption, even though there is good evidence that fitness as a function of resources obtained is typically of a very different form compared to what he proposes, and is often instead modelled as being sigmoidal [78, 79].

Godfray chooses to illustrate his model by selecting example offspring and parent fitness functions based primarily on mathematical convenience, $f = (1 - e^{-cy}) - 0.1x$, and $g = 1 - 0.08 * y$, respectively, and solves for y^* and x^*. While there is no issue with the foundation of Godfray's model, other than perhaps its simplicity compared to the known intricacies of begging behaviour observed in nature [72, 80, 81, 82], which has been addressed elsewhere, there are several issues with the example Godfray selects. First, as Rodriguez-Girones points out in several of his papers [71, 83, 72], Godfray fails to recognize that the equilibrium he found for his example is, in fact, unstable, and that there exists a non-signalling equilibrium that is stable. Rodriguez-Girones demonstrates that sibling competition is a mechanism that could be used to stabilize the signalling equilibrium [72]. However, he did so by focusing only the specific example (and hence the specific fitness functions) that Godfray uses; even slightly modifying the fitness functions (e.g. using $f = (1 - e^{-cy}) - c_1 x$, where c_1 is a sufficiently low positive constant) is sufficient to ensure at least the local stability of the signalling equilibrium. Second, the example Godfray selects is misleading because he states that "as condition of the young deteriorates, both the level of display and the amount of parental investment increases". This is only true for a certain range of conditions; for $0 < c < 0.5$, both resources obtained and level of solicitation as a function of condition are non-monotonic, and indeed reach a peak before declining in the fashion suggested by Godfray. This is to say, these results do not indicate that this is not wholly a signal of need model, since needier offspring (lower c) do not necessarily exhibit lower levels of solicitation nor obtain more resources from parents. Another issue with the example Godfray uses is that he finds the equilibrium level of parental investment, $y^* = \frac{1}{c} \ln \frac{c}{\gamma}$, is completely independent of the offspring's solicitation level. Mathematically, this result is due to the offspring's fitness function having linear dependency on x. Because of this, parents are not explicitly modifying their allocation strategy based on the need of their offspring, despite the fact that Godfray designs the model with the intention of offspring begging intensity influencing parental provisioning (Box #1).

Despite these limitations of Godfray's model, his work suggests that SoN can be evolutionarily stable under a variety of conditions without the assumption that the cost of signalling is dependent upon the signaller's condition — an assumption that is incompatible with SoQ. SoN was thus viewed as being more parsimonious and many signalling models published since Godfray's seminal paper have SoN as a built-in assumption [70, 71, 72, 73]. However, the assumption that offspring fitness monotonically increases at a decelerating rate ensures 'need' and 'quality' are antonyms, and thus that SoQ and SoN are mutually exclusive. We take issue with how SoQ has been defined, since quality can hold many different meanings. Most theoretical work regards quality as being the opposite of need and the same as condition and reproductive value; however, in these works, offspring all had the same fitness functions (although may have differed in condition — effectively the offspring's current placement along the fitness function curve). When fitness functions differ (Figure 1.1), need as defined by the marginal change in the offspring's fitness with increased investment may no longer be the opposite of quality. Alternatively, quality could refer to the potential reproductive value that an offspring possesses, meaning that offspring with the greatest reproductive value, if resources were effectively unlimited, could be considered of highest quality. For example, certain offspring may be "late bloomers": perhaps initial investments into this offspring yield only small increases in reproductive value, but there may exist some threshold of provisioning/nutrition passed which the higher quality sibling actually possesses uniformly higher reproductive value than its siblings per degree of investment (Figure 1.1).

Box #2: *Mathematical framework of Godfray's (1995) two-offspring model* [70]

Suppose instead that a parent has two offspring, i and j, and x_i, c_i, y_i, and $f_i(x_i, y_i, c_i)$ (resp. x_j, c_j, y_j, and $f_j(x_j, y_j, c_j)$) represents the level of solicitation, condition, resources received by, and the fitness function of offspring i (resp. offspring j). Again, there is assumed to be some relationship between the begging intensity of offspring and the amount of resources it receives. Suppose the parent has a set amount of resource, Y, and distributes this amount

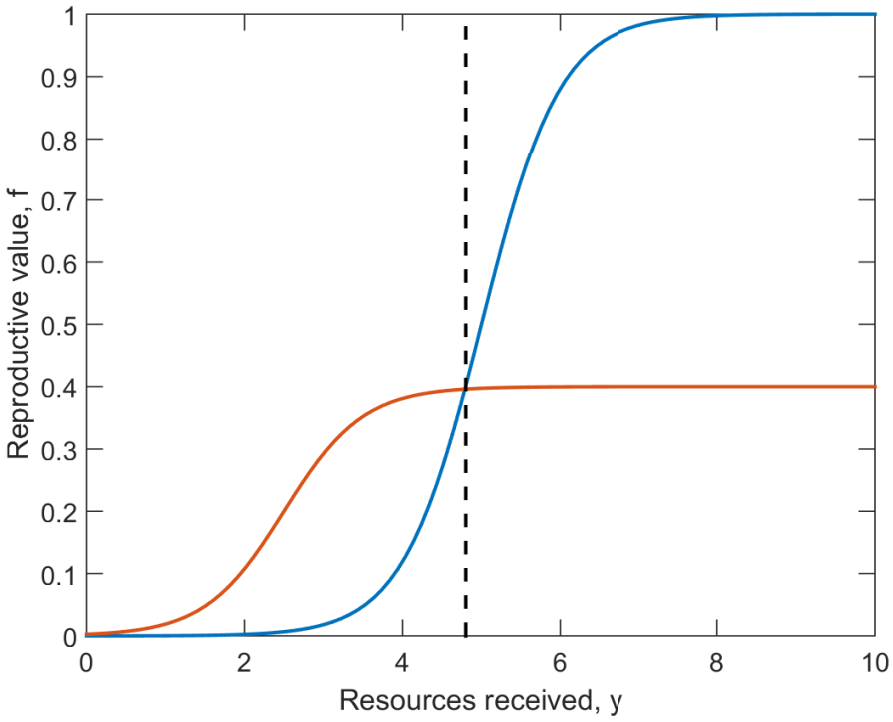

Figure 1.1: When the fitness functions of offspring differ significantly, it becomes difficult to define which offspring has greater quality. To the left of the dashed line, the fitness of offspring i (red line) is uniformly higher than the fitness of offspring j (blue line), and could be considered as being of higher quality. Conversely, to the right of the dashed line, offspring j may be considered of higher quality. Given perfect information, a parent that has only 2 units of resources would allocate all resources to offspring i. However, if the parent had 6 units of resources, it would invest all resources into offspring j.

between its offspring such that $y_i + y_j = Y$). At equilibrium, parents will allocate resources such that slight changes in resource distribution will not change the parent's net inclusive fitness; mathematically,

$$\frac{\partial f_i}{\partial y_i} = \frac{\partial f_j}{\partial y_j}. \tag{1.5}$$

At the ESS, the net change in the inclusive fitness of each offspring should zero; that is,

$$\frac{\partial f_i}{\partial x_i} + \frac{\partial y_i}{\partial x_i}\frac{\partial f_i}{\partial y_i} + r\left(\frac{\partial x_j}{\partial x_i}\frac{\partial f_j}{\partial x_j} + \frac{\partial y_j}{\partial x_i}\frac{\partial f_j}{\partial y_j}\right) = 0, \tag{1.6}$$

where r is the relatedness between the two offspring. The ESS begging and allocation strategies can be found using (3) and (4) only for specified offspring fitness functions. An alteration of this model created by Rodriguez-Girones [72] allows flexibility in the total amount of resources the parent allocates to the offspring, Y, by making allocation decisions explicitly a function of begging behaviour, $y_i = \frac{Yx_i}{x_i+x_j}$ and $y_j = \frac{Yx_j}{x_i+x_j}$; this extension, inspired by empirical data, makes the model more realistic. Due to this, the residual fitness of the parent, $g(Y)$, needs to be tracked, producing the following fitness functions, F_i, F_j, and F_p, for offspring i, j, and the parent, respectively,

$$\left.\begin{aligned} F_i &= f_i(x_i, y_i, c_i) + r_s f_j(x_j, y_j, c_j) + r_p g(Y) \\ F_i &= r_s f_i(x_i, y_i, c_i) + f_j(x_j, y_j, c_j) + r_p g(Y) \\ F_p &= f_i(x_i, y_i, c_i) + f_j(x_j, y_j, c_j) + g(Y) \end{aligned}\right\} \tag{1.7}$$

where r_p and r_s represents the relatedness between parent and offspring and the offsprings, respectively. Again, by specifying fitness functions, the evolutionary stable levels of begging, x_i^* and x_j^*, and resource allocation strategy, y_i^* and y_j^*, can be solved by numerically analyzing system (5).

To examine Godfray's model, then, it is crucial to identify the ESS levels of begging and provisioning using more realistic offspring fitness functions. This is made especially apparent by examining Godfray's two-offspring extension (see Box #2) of his 1991 model [70]. Un-

fortunately, Godfray once again chose to discuss the implications of his model by selecting specific functions (of the same general structure as the functions chosen to illustrate his one-offspring model), which does not properly represent the diversity nor complexity of begging behaviours observed in nature.

The parent's residual fitness function may also be modified to investigate phenomena observed in empirical studies. For instance, to better understand how environmental conditions influence whether parents feed offspring with the greatest need or quality [80, 84], one simply needs to modify the nature of the parent's residual fitness function, $g(Y)$: harsher environments cause the parent's residual fitness to decrease at a faster rate per unit of investment into their current brood (mathematically, harsher environments increase $\frac{\delta g(Y)}{\delta Y}$). In this way, both SoN and SoQ may be rules that dictate behaviour, but which theory better explains behaviour may be dependent on fitness functions, which in turn are influenced by environmental factors. As such, we find it prudent to divorce ourselves of the notion that a higher-quality offspring necessarily has greater reproductive value, but rather simply has the potential to be of greater reproductive value. In doing so, one nullifies one of the most common criticisms of the SoQ theory, that parental intervention of food allocation in favour of higher quality offspring pointless since offspring of higher quality should be able to out-compete their siblings anyway [85]. There are two issues with this criticism: first, it is plausible that, even if one equates quality with current reproductive value, that parental control over food allocation may better optimize food distribution — at least from the parent's prospective — than the outcome of competition among offspring for resources would. Second, there are many dimensions to quality (a chick that is better able to fight its siblings may in fact have lower reproductive value because it may fare poorly in other arenas, like sex competition). Further, an offspring that is currently of higher quality (i.e. is better able to compete against its siblings) may not necessarily be so for every given level of provisioning received (that is, the relation $f_i > f_j$ for all $y_i = y_j$ should not be required to conclude that offspring i is of higher quality than offspring j).

Wild et al. model

Wild et al. [86] use a three-player evolutionary game to explore the idea that offspring may signal to convey information to parents more efficiently than can otherwise be transmitted. Note that this is in contrast to many previous models that assume signals communicate information that parents cannot otherwise obtain. The three players are the parent, one high-quality offspring, and one low-quality offspring. The parents can distinguish between the quality of their offspring by investigating cues, but this is assumed to be less efficient than using offspring signals to distinguish between the low- and high-quality offspring.

It is assumed that the family resides in a poor-quality environment such that the parent is only able to successfully rear one offspring. Before the parent decides which of the two offspring to feed, the offspring each simultaneously and independently decide whether to signal. An offspring that uses signals reduces its own fitness by some fraction. If neither or both offspring signal, the parent is unable to use the signal to distinguish between the offspring and must instead either feed randomly or investigate offspring quality using cues. If only one offspring signals, the parent must decide between feeding the signaller and feeding the non-signaller. By responding to the signal, the parent avoids wasting time and energy investigating cues and so it can improve the fitness of the offspring that it does rear by some factor. After identifying the inclusive fitness payoff for each individual for each outcome, the conditions for the stability of Nash equilibria in which only one offspring signalled were derived.

Wild et al. assume that resources are so scarce that parents may raise only one offspring. This assumption can be removed by instead allowing the amount of resources available to the parent to vary. By investigating how this changes the conditions for the stability of Nash equilibria in which only one offspring signals, one can explore the relationship between environmental quality and the evolution of signalling behaviour.

Alternatively, the base model built by Wild et al. [86] could be modified to understand how begging behaviour influences parental conflict over provisioning. Instead of modelling two offspring with one parent, the players in the game could instead be two parents and one offspring. In this way, one could explore how paternal uncertainty can differentially manipulate maternal and paternal provisioning patterns. For example, the blackmail hypothesis has been previously investigating in very simple models involving only one parent and one offspring.

A simplifying assumption common to nearly all previous signalling theory is the presence of only one parent. These models are unable to expound why numerous species exhibit sex differences in the provisioning patterns of adults and the begging behaviour of offspring [87, 88, 89, 90, 91]. While uncertain paternity is an obvious motivator for differences between male and female provisioning behaviour, it remains less clear why males are frequently found to beg more than their female nestmates [87, 88, 90]. Indeed, theoretical explanations for this phenomenon may be lacking because parent-offspring conflict over provisioning has frequently been modelled without regard to sex-specific offspring behaviours. In contrast, species-specific theories for sex differences in begging behaviour have been the subject of several empirical studies. Price et al. proposed that, since males tend to be larger than females, they are in greater need and consequently beg more intensely [87]. However, this explanation cannot explain the sex-specific begging that has been observed in species that have little sex differences in size, such as the zebra finch [90], *Taeniopygia guttata*, and the barn swallow [92], *Hirundo rustica*.

In Chapter 3, we modify Wild et al.'s work to investigate how environmental variability and quality influences the signalling and provisioning strategies of parents. Guided by recent empirical data [80, 84], we use our model to elucidate the types of information (need vs. quality) offspring evolve to convey when signalling. We also examine how the limiting assumptions of Godfray's model [67], such as simplified relationship between offspring fitness and parental

provisioning, have influenced previous models and discussion regarding the type of information signals convey. In Chapter 4, we expand beyond the one-parent models of signalling behaviour by investigating conflict between parents over provisioning can explain differences in the begging behaviours of male and female offspring observed in several species of bird.

1.4 Cooperative breeding

In cooperatively breeding species, certain individuals (auxiliaries) delay or even refrain from reproduction to help rear offspring produced by other individuals (breeders) [93]. Two prominent, complementary theories have been proposed to explain why some individuals chose to help raise offspring that are not their own. The *habitat saturation hypothesis* suggests that individuals will not disperse if it is unlikely to result in independent reproduction [94, 93]. The *benefits of philopatry hypothesis* is a related explanation which focuses on the benefits of staying rather than the costs of dispersing [93, 95]. These benefits can be divided into two categories: i) the passive advantages of remaining on the territory which include group augmentation, territory inheritance, access to mating opportunities, increased survival and access to resources from group living, and enhanced ability to form alliances and court future mates, and ii) benefits associated with actively helping breeders raise their offspring such as increased production of kin via helping behaviour, reciprocal altruism, and the acquisition of parenting skills associated with helping [96, 24].

Breeders rarely coerce auxiliaries to stay and help [97, 98]; instead, prospects for independent breeding are so poor that helpers have greater reproductive success than those attempting to disperse [24]. Thus, cooperative breeding is another type of voluntary non-egalitarian social relationship. Like the relationship between leader and follower, there is conflict between breeder and auxiliary, resulting in distribution of resources between breeder and auxiliary to vary vastly between and within species, ranging from the complete monopolization of repro-

ductive opportunities by a single breeder or breeding couple, to an even distribution of reproductive success (i.e. communally breeding species) [99, 100].

High adult survival has been proposed to be an precursor to cooperative breeding because it increases habitat saturation [101]. In highly saturated environments, the reproductive value of each offspring is thought to diminish rapidly as more offspring are produced since offspring may compete amongst each other for limited breeding opportunities. Since there is an inherent trade-off between survival and fecundity, it has been suggested that cooperative breeders residing in these saturated environments should reduce their reproductive output, and thus should tend to have smaller clutch sizes than non-cooperative breeders [94]. Although comparative analysis has provided support for the association between longevity and cooperative breeding, results from these studies found no connection between clutch size and cooperative breeders [101].

An obvious explanation for the discrepancy between theoretical and empirical results is that, while small brood sizes may predispose species to breed cooperatively, cooperative breeding itself may drive an increase in clutch size. This idea has been tacitly proposed by Hardling & Kokko, who developed a simple model to conclude that cooperative breeders should have smaller clutch sizes compared to that of non-cooperative breeders [102]. However, this model does not use population dynamics, and therefore may not properly account for the inclusive fitness effects resulting from changes in clutch sizes. In this sense, the theoretical work on the association between clutch size and cooperative breeding suffers from the same assumptions as those used to model leader-follower relationships. Further, the model considers only the breeder's optimal resource distribution between fecundity and survival. It therefore neglects the potential conflict between breeder and auxiliary, which may cause selection on brood size to deviate from the breeder's optimum [103, 104].

In Chapter 5, I revisit this theory on the association between clutch size and cooperative breeding. In contrast to previous theory [102], I describe how the emergence of cooperative breeding influences clutch size by constructing a thorough inclusive fitness model using population dynamics. I also explore how the conflict between breeder and auxiliary over helping behaviour may influence clutch sizes.

1.5 Coalitionary behaviour

Coalitionary behaviour refers to the formation of temporary alliances between two or more individuals that target other individuals or alliances [11]. Coalitions have been commonly observed in a wide variety of species, including humans and primates [105]. Fundamentally, a coalition forms so that its members can obtain or retain more resources than would be possible if instead its members operated individually.

Coalitionary behaviour can be classified into three basic categories based on the members of the coalition and its target: i) 'all-up' or 'revolutionary' coalitions in which individuals direct aggression toward those of higher rank, ii) 'all-down' coalitions formed by higher-ranking individuals targeting low-ranking individuals, and iii) 'bridging' coalitions formed among at least one member ranking above and one ranking below the coalition's target. It has been observed that all-up coalitions are relatively rare compared to all-down coalitions [11]. A theory for the relatively low frequency of all-up coalitions has been proposed [11]: the threat of revolutionary coalitions may lead high-ranked individuals to concede a greater amount of resources toward lower ranked individuals, thereby deterring the formation of all-up coalitions. Whether such an intriguing verbal argument is a valid outcome of genetic and social evolution remains to be tested. The idea is highly related to other important biological theories, including the 'concede versus control' debate regarding dominant breeders of cooperatively breeding species. In many cooperatively breeding species, such as meerkats (*Suricata suricatta*), subordinate individuals

breed [28, 106]. This is often suboptimal for the dominant breeders, as their offspring have greater competition for the group's resources. It has been proposed that this occurs because breeders are not always able to prevent subordinate reproduction (control), while others posit that dominant individuals permit subordinates to occasionally breed to retain them as helpers (concede) [106]. Other theories for the rarity of revolutionary coalitions include the high cost of targeting dominant individuals, and the fact that revolutionary alliances can be countered by all-down coalitions, which often consist of more dominant individuals [11].

The type of resources which are contested by coalitions vary vastly both within and between species. Resources can be divisible (e.g. food, eating order) or indivisible (e.g. mating opportunities), which may affect the type of coalitions that form [107, 11]. For example, because it is particularly rare for mixed-sex groups to have all-up coalitions, and coalitions in such groups often compete against others for mating opportunities, indivisible resources may deter the evolution of all-up groups [11]. This verbal argument should be readily tested, especially if social factors such as reciprocity are considered.

Revolutionary coalitions essentially function as a levelling mechanism — a means to minimize the unequal division of resources in dominance hierarchies [108]. Yet, many animal species that form dominance hierarchies do not regularly form coalitions [109]. The study of coalition formation then provides a way to understand the nature of dominance hierarchies. For example, Stamatopoulos et al. propose that resource scarcity will favour the emergence of dominance hierarchies [110] — a verbal argument that requires closer examination — but why such conditions would not also favour the emergence of coalitions to counter the unequal distribution of resources is unclear. Identifying the social, ecological, and life-history conditions that select against coalition but for hierarchical groups is a clear avenue for future theoretical work.

The costs of forming coalitions are difficult to demonstrate in empirical studies. Available data suggests that the time and energy invested in coalition formation is negligible, and that injuries and deaths because of failed coalitions are very rare [111]. Regular observations of punishment and costly retaliation in response to unsuccessful coalitions have been observed only in a few species. Instead, data suggests that there may be opportunity costs (e.g. failure to achieve higher ranks, reduced mating access) associated with coalition formation, particularly if the coalition fails, and that this form of cost may depend on age, group composition, and demography [111]. It would be of use to empiricists to create a model capable of quantifying the costs of coalition formation as a function of age, sex, and other pertinent traits.

Coalitionary behaviour has been thoroughly studied using theoretical models, which has unveiled numerous key features about coalitions, particularly regarding their formation. However, a recent comprehensive comparison between these mathematical models and the vast amount of data collected by field biologists indicates an important lack of communication between theorists and empiricists [11]. In addition to suffering from unrealistic assumptions, models of coalition formation focus extensively on the effects of rank and 'resource holding potential' (RHP) on coalition formation [112]. Yet, empirical studies have routinely demonstrated that coalition partners are selected often based on features like kinship [113, 114], sex [115, 116], and age [111, 11]. Such features are ultimately functions of life-history characteristics, including dispersal patterns, interbirth intervals, and birth cohort size [11], which can be easily integrated into models of coalition formation.

A second issue with the current state of theoretical literature on coalitionary behaviour is the focus on identifying Nash equilibria in isolated scenarios using simple economic games rather than using evolutionary game theory. The standard design for most theoretical models is to initialize a population of three individuals — often alpha, beta, and gamma males — each with its own RHP, and each rank with its own payoff or reproductive value. Next, the payoffs

of each potential coalition are calculated, and from this the evolutionary stable strategies are identified. While these simple models can and have provided some information about coalition formation, there are two potential issues with this approach. First, these models do not track the consequences of coalitions through an individual's entire life cycle, instead focusing only on the immediate, direct costs of coalition formation. Second, these models assume that coalition behaviour is not a function of genetic evolution; instead, actions are based solely on the current social dynamics. It is unclear how much coalition behaviour is influenced by genetics, although the fact that coalitions are often formed even when there are no (apparent) resources to contest [108] suggests it may play an important role.

For example, the relative rarity of all-up coalitions may be because as all-up coalitions become more common (or more successful), they may reduce the value associated with being in higher rank, causing a negative feedback loop. In contrast, a positive feedback loop is likely to develop for all-down coalitions, since they effectively secure the positions of highly ranked individuals, which provides greater reason to secure such positions. In these simple triadic interactions, the probability with which each coalition forms and succeeds should ultimately affect the reproductive value associated with each rank. The coevolution between coalition formation strategies and other essential factors, such as the reproductive value associated with each rank, has thus far been neglected by previous theoretical studies.

Chapter 6 is dedicated to amending these weaknesses in the theoretical literature on coalitionary behaviour. We create a set of life-history models to determine how the nature of coalitionary behavior that emerges at evolutionary equilibrium is influenced by the types of costs, in terms of survival, fecundity, and social rank, afflicted upon members of failed coalitions. We test the theory that the relative rarity of all-up coalitions can be explained by dominant individuals preventing their formation by granting concessions to subordinates; this is accomplished by modelling the coevolution between coalitionary behavior and concessions. We then con-

trast our results to empirical data to provide an evolutionary context for commonly observed coalitionary behaviors.

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Chapter 2

The evolution of group dispersal with leaders and followers

Koykka, C. & Wild, G. (2014) Group dispersal with leaders and followers. *J. Theo. Biol*. 371: 117-126.

Abstract

In many species, individuals disperse in groups. While there are empirical studies that explore the proximate incentives for group dispersal, theoretical research has primarily examined the consequences rather than the evolution of this phenomenon. We design a simple model to study the origin and evolution of group dispersal. We assume that like many other group activities associated with collective movement, group dispersal in our model is initiated by leaders. We use the theory of inclusive fitness to examine the incentives for leading and following in this context. High relatedness, significant reductions in the cost of dispersal due to dispersing in groups, and reproductive skew in favour of followers facilitates the emergence of group dispersal. In contrast to some previous theoretical work, which has either concluded that that leadership uniformly altruistic or that it is uniformly selfish, we find that at evolutionary equilibrium the incentives for leading can be either selfish or altruistic, depending on ecological and social conditions such as the cost of dispersal and the relatedness between leaders and followers. Our model demonstrates

that kin selection is sufficient and that individual differences in condition and ability are not necessary to promote the emergence and maintenance of leader-follower relationships.

2.1 Introduction

Leadership is not a uniquely human trait. Dominant male baboons initiate foraging activities [1], alpha-male chimpanzees resolve conflicts by eliminating aggressive behaviour [2], certain species of ants use tandem running to direct movement toward resources [3], dominant females of the dwarf mongoose determine the location of resting sites [4], and in the free-ranging dogs, *Canis lupus familiaris*, pack leaders organize group defense [4]. While there are many forms of leadership, leader-follower social structures are frequently used to coordinate group movement such as foraging and migration [5]. Despite this, little is known theoretically about the evolution of natal dispersal — dispersal from birth place to breeding sites — involving leader-follower relationships. It is standard in mathematical models to assume that dispersal occurs independently, but in many species dispersal occurs in groups of individuals that are often but not always related, and group dispersal is frequently initiated by a subset of individuals [6, 7, 8, 9, 10, 11, 12, 13]. The few models that incorporate the concept of group dispersal do not examine the emergence or maintenance of this biological phenomenon, nor do they assume the presence of leader-follower relationships [14, 15, 16].

While the impact of group dispersal on the evolution of social behaviour has been previously explored [14, 15], theoretical knowledge of the origin and maintenance of group dispersal is lacking. Additionally, the current body of literature on leadership and followership often suggests or assumes that leaders will emerge only if they receive direct fitness benefits [17], but this is seemingly in conflict with the widely-accepted theory that dispersal is an act of altruism [18]. Thus, careful analysis is required to understand the evolutionary incentives for group dispersal.

In this paper, we build a simple model for the evolution of natal dispersal with the goal of understanding how group dispersal can emerge and be maintained when certain individuals (leaders) initiate dispersal and others (followers) disperse with these leaders. Our aim is to generate a mathematical description of the evolutionary incentives for leading and following in dispersal groups. We show how certain social and ecological factors can promote the emergence of group dispersal. We identify how leader-follower relationships can affect population dynamics, including the evolutionarily stable levels of natal dispersal. We also describe how leader-follower relationships in the context of dispersal affect altruistic behaviour.

2.2 The Model

We develop an infinite-island model of an infinitely large population with non-overlapping generations based on Taylor's model for the dispersal of offspring [18]. Every island contains N breeding territories, each of which is inhabited by exactly one haploid asexual breeder that produces a very large number of offspring. The only potential difference between individuals is their dispersal strategy, which is controlled by three independent loci. The first locus dictates the probability with which a given individual will become a leader. Leaders are individuals who always disperse from their natal island. Dispersers leave their natal island and disperse toward an island chosen uniformly at random from the set of all islands. The second locus describes at what probability an individual will follow given that they are not a leader. Followers also always disperse, but will only do so only in the presence of a leader; this allows for the creation of both lone dispersers and dispersal groups of variable size. Every individual in a given dispersal group is born on the same island and will disperse together toward the same island chosen at random. The presence of followers therefore ensures that the dispersal of individuals no longer occurs independently. The third locus influences the competitive ability of leaders relative to that of followers, and is discussed in greater detail below.

Fix attention on a given island - the focal island - then fix attention on an individual on that island - the focal individual - immediately following its birth. The leadership phenotype of the focal individual is denoted by $d_\bullet \in (0, 1)$ and it expresses the probability that the focal individual will lead. Similarly, $d'_\bullet \in (0, 1)$ represents the followership phenotype, which corresponds to the probability that the focal individual will be willing to follow. Since individuals can follow only if they do not lead, $(1 - d_\bullet)d'_\bullet$ represents the probability that the focal individual is a follower. It is also possible, with probability $(1 - d_\bullet)(1 - d'_\bullet)$, that the focal individual neither leads nor follows, in which case it stays on its natal island.

Dispersal is a costly endeavour, but may be less costly when it is attempted in larger groups [19]. Let $c_k = c_0\alpha^k$ represent the cost of dispersal, where c_0 represents the cost experienced by individuals who disperse alone, $\alpha \in [0, 1]$ controls the rate at which the cost of dispersal decreases as group sizes increases and k represent the number of followers other than the focal individual that are in the dispersal group. Every individual in a particular dispersal group experiences the same cost of dispersal. If dispersers successfully arrive at their destination, they will then compete against other dispersers as well as non-dispersing natives for each of the N available breeding positions. We assume that in addition to lower dispersal costs, larger groups are better able to compete for breeding territories. Thus we define u_k may be an increasing function that describes the relative competitive advantage that groups with k followers have over lone individuals (we assume $u_0 = 1$); u_k can be viewed as a function denoting the benefits of group augmentation. We further assume that non-dispersers do not form groups and compete for each breeding site as individuals; this is done to contrast the benefits of leadership with the decision to not join groups.

For each of the N breeding territories on a particular island, a winning group or individual is selected with probability proportional to their relative competitive ability (equal to 1

for non-dispersers) multiplied by the probability that they survived dispersal (equal to 1 for non-dispersers). Should a group win the rights to a particular territory, group members then compete with each other for the sole breeding position. Followers are guaranteed to have both themselves and a leader in their dispersal group, but leaders run the risk of dispersing by themselves. Therefore we give leaders a competition advantage over followers to compensate for this risk. Let $s_{\bullet k}$ represent the probability that the focal individual, should he be a leader, successfully competes against his k followers for the right to breed on the territory that the dispersal group has won; a given follower wins with probability $\frac{1-s_{\bullet k}}{k}$. All results in this paper were generated under the assumption that $s_{\bullet k} = \frac{\beta}{\beta+k}$, where $\beta \geq 1$ can be viewed as the relative competitive ability or competitiveness of leaders compared to that of its followers. All sampling is done with replacement so that any group may win the rights to multiple breeding territories and any individual may become the breeder on multiple territories. In order to have non-overlapping generations, any individual who fails to become a breeder will die, leaving each of the N breeding territories occupied by exactly one breeder.

To calculate the expected fitness [20] of a focal individual on a focal island, some additional notation is required. Let $\bar{d}$, $\bar{d}'$, and $\bar{s}_k$ denote the focal island's average leadership, followership and competitive ability phenotypic values, respectively; similarly, d, d', and s_k represent the global-average leadership, followership, and competitive ability phenotypic values, respectively. We assume that the number of offspring produced on each breeding territory, K, is very large. In doing so, we are able to use the Poisson distribution with mean equal to the expected number of followers in a given dispersal group, $\frac{NK(1-\bar{d})\bar{d}'}{NK\bar{d}} = \frac{(1-\bar{d})\bar{d}'}{\bar{d}}$, to calculate the probability that a given dispersal group on the focal island contains k followers (see Supplementary Data). To justify all assumptions and to confirm the accuracy of our model, a stochastic simulation was created, the results of which agree with our analytic model (see Supplementary Data).

We use the direct fitness formulation from Taylor & Frank to calculate the neighbour-

modulated fitness [21] of a focal individual on a focal island (Appendix A)

$$W = \overbrace{\frac{(1-d_\bullet)(1-d'_\bullet)}{(1-\bar{d})(1-\bar{d}') + d\sum_{j=0}^{\infty} P_j u_j (1-c_j)}}^{\text{Not dispersing}} + d_\bullet \overbrace{\frac{\sum_{k=0}^{\infty} Q_k (1-c_k) u_k s_{\bullet k}}{(1-d)(1-d') + d\sum_{j=0}^{\infty} P_j u_j (1-c_j)}}^{\text{Leading}} + (1-d_\bullet) d'_\bullet \overbrace{\frac{\sum_{k=0}^{\infty} Q_k (1-c_{k+1}) u_{k+1} \frac{1-\bar{s}_{k+1}}{k+1}}{(1-d)(1-d') + d\sum_{j=0}^{\infty} P_j u_j (1-c_j)}}^{\text{Following}} \tag{2.1}$$

where P and Q represent Poisson distributions about the global mean dispersal group size, $\lambda = \frac{(1-d)d'}{d}$, and the mean dispersal group size of the focal island, $\bar{\lambda} = \frac{(1-\bar{d})\bar{d}'}{\bar{d}}$, respectively. At equilibrium, $d = \bar{d}, d' = \bar{d}'$, and so $Q_j = P_j$. This fitness expression (2.1) can be divided into three main components: the neighbour-modulated fitness gained from leading, following, and doing neither.

2.3 Results

2.3.1 Emergence of Leader-Follower Behaviour

To investigate the emergence of leader-follower behaviour in our model, suppose no individual in the population exhibits any willingness to follow (i.e $d' = 0$). In this case, our model becomes exactly equivalent to Taylor's, with the cost of dispersal uniformly equal to c_0. Assume we have a population of only leaders dispersing at Taylor's predicted evolutionarily stable strategy (i.e. $d = \frac{H+1-2Nc}{H+1-2Nc^2}$, where $H = \sqrt{1+4N(N-1)c^2}$, but see Appendix D for greater detail). Now fix attention on a mutant individual. This mutant has not dispersed; it instead exhibits deviant behaviour by following another disperser. This leader-follower pair will disperse together toward an island selected uniformly at random from the set of all islands. The change in the inclusive fitness of the focal individual as a result of its deviant behaviour can be described

by

$$\begin{aligned} \Delta W_F = &- 1 + u_1(1 - c_1)(1 - s_1) && \text{I} \\ &+ c_0 && \text{II} \\ &+ R((u_1(1 - c_1)s_1 - (1 - c_0))) && \text{III} \end{aligned} \tag{2.2}$$

where R is the expected coefficient of relatedness between the mutant and a random individual on its natal island (Appendix C), c_0 and c_1 are the cost of dispersing singly (i.e. with zero followers) and in pairs (i.e. a leader and its follower), respectively, u_1 represents the competitive advantage that dispersing pairs have over lone individuals when competing for breeding territories, and s_1 describes the probability that the leader will outcompete its follower for breeding opportunities. Equation (2.2) shows that the inclusive fitness effects of following are given by three components:

(I) The direct fitness effect of following. This term represents the difference between the focal individual's expected fitness should it have not dispersed and the expected direct fitness of the focal individual given that it is a follower. Since the population is at equilibrium, it can be assumed without loss of generality that by following and sacrificing the opportunity to breed on its natal island, the mutant forgoes a reproductive value of one [22]. The pair survives dispersal with probability $1 - c_1$ and is $u_1 \geq 1$ times as likely as a given lone individual to win a breeding territory. The mutant outcompetes its leader for breeding opportunities with probability (1-s_1). Thus the mutant has an expected direct fitness of $u_1(1 - c_1)(1 - s_1)$.

(II) The decrease in local competition due to the focal individual's increased tendency to disperse. By dispersing, any breeding opportunities that the focal individual would have won by remaining on the natal island is instead granted to another individual who, after dispersal, is present on the island. Thus this term is equal to the probability, h, that a randomly selected individual on an island after dispersal is native to that island multi-

plied by the average relatedness, R, between individuals born on the same island [18]. In a polymorphic population at equilibrium, the inclusive fitness of each strategy must be equal [23], and so the loss in direct fitness experienced by dispersers must be compensated by an increase in indirect fitness. Therefore, by dispersing and decreasing kin competition, the mutant gains $Rh = c_0$ units of indirect fitness.

(III) The change in inclusive fitness produced by the change in the direct fitness of the leader that the focal individual follows. If the leader dispersed alone, it would have an expected direct fitness of $1 - c_0$. By dispersing with a follower, the leader now has an expected direct fitness of $u_1(1 - c_1)s_1$. Then by following, the mutant changes the expected direct fitness of the leader by $u_1(1-c_1)s_1-(1-c_0)$, and given that the coefficient of relatedness between the mutant and a random individual on its natal island is R (Appendix C), this means the mutant's indirect fitness changes by $R(u_1(1 - c_1)s_1 - (1 - c_0))$.

Followership will now emerge in the population whenever following increases one's inclusive fitness [20, 21]; equivalently, leader-follower behaviour emerges if and only if $\Delta W_F > 0$. A wide range of biologically relevant parameter conditions satisfy $\Delta W_F > 0$ (Figure 2.1), demonstrating that leader-follower patterns can emerge in a population that is homogeneous apart from differences in individual propensities to lead and to follow. Followership and hence group dispersal is more likely to emerge when: (i) the cost of dispersing alone is high relative to the expected costs associated with dispersing in groups, (ii) relatedness between individuals born on the same island is high (equivalently, when N is low and c_0 is high, but see Appendix C and Figure 2.1), and (iii) followers are given a greater share of reproductive opportunities.

2.3.2 Altruism in Leader-Follower Relationships

Analytic Solutions

We now describe how leader-follower relationships affect altruistic behaviour in the population. We will continue to use Taylor & Frank's [20] direct fitness formulation to determine

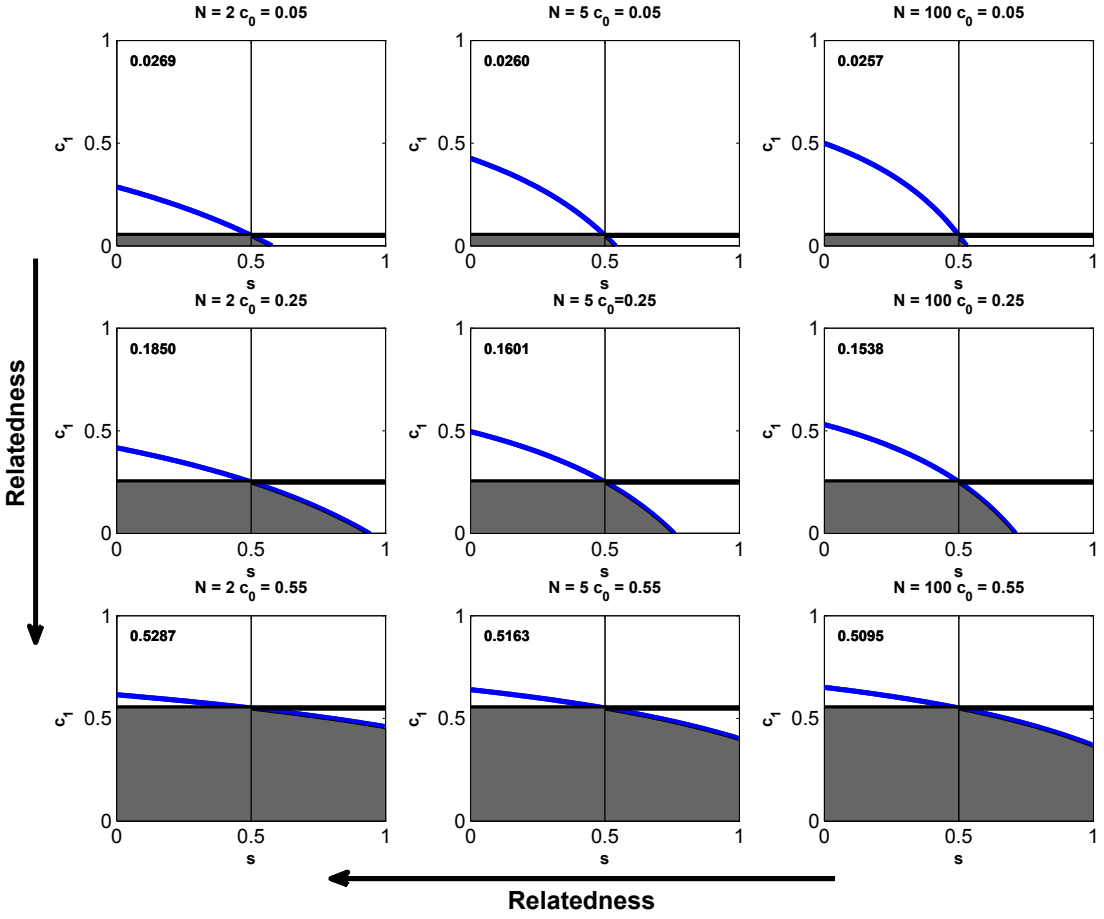

Figure 2.1: Leader-follower relationships in our model emerges under a wide variety of biologically reasonable conditions. Any point that lies below the blue lines represents parameter conditions under which followership emerges. Points below the horizontal black lines represent parameter conditions under which the assumption $c_0 > c_1$ is satisfied. Thus any values of s and c_1 that lie in the grey region (the area of which is given in the top left corner of each graph) constitute a set of reasonable social and ecological conditions that can support the emergence of leader-follower behaviour. Values of s lying to the right of the vertical black line represent situations in which leaders take a disproportionate large amount of resources. Note that as relatedness increases, so too does the parameter space under which followership emerges. All else being equal, individuals are less likely to disperse when dispersal costs are higher, and thus relatedness between individuals on the same island increases as c_0 increases. Similarly, as the number of breeding territories per island decreases, it becomes more likely that any given two individuals were produced by the same breeder, and thus relatedness increases as N decreases (Appendix C). Results were generated using $u_k = k + 1$.

evolutionarily stable levels of leadership and followership in the population. This requires the assumption of weak selection, which our stochastic simulation will demonstrate is valid. Dispersal strategies evolves until each parameter arrives at a biologically imposed boundary or a local maximum, defined below as

$$\begin{aligned}
\left(\frac{\partial W}{\partial d_\bullet} + R\frac{\partial W}{\partial \bar{d}}\right)\Bigg|_{d_\bullet=\bar{d}=d, d'_\bullet=\bar{d}'=d', s_\bullet=\bar{s}=s} &= 0, \\
\left(\frac{\partial W}{\partial d'_\bullet} + R\frac{\partial W}{\partial \bar{d}'}\right)\Bigg|_{d_\bullet=\bar{d}=d, d'_\bullet=\bar{d}'=d', s_\bullet=\bar{s}=s} &= 0, \\
\left(\frac{\partial W}{\partial s_\bullet} + R\frac{\partial W}{\partial \bar{s}}\right)\Bigg|_{d_\bullet=\bar{d}=d, d'_\bullet=\bar{d}'=d', s_\bullet=\bar{s}=s.} &= 0
\end{aligned} \tag{2.3}$$

Each expression in (2.3) has a clear biological interpretation. To illustrate this, consider a mutant individual who has some increased propensity to lead. The change in inclusive fitness due to this deviant behaviour, $\left(\frac{\partial W}{\partial d_\bullet} + R\frac{\partial W}{\partial \bar{d}}\right)\Big|_{d_\bullet=\bar{d}=d}$, is proportional to

$$\begin{aligned}
\Delta W_L = &- (1 - d') && \text{I} \\
&+ \sum_{k=0}^{\infty} Q_k u_k (1 - c_k) s_k && \text{II} \\
&- d' \sum_{k=0}^{\infty} Q_k u_{k+1} (1 - c_{k+1}) \frac{1 - s_{k+1}}{k+1} && \text{III} \\
&+ R(1 - d')h && \text{IV} \\
&+ d \sum_{k=0}^{\infty} \delta Q_k u_k (1 - c_k) s_k && \text{V} \\
&+ (1 - d) d' \sum_{k=0}^{\infty} \delta Q_k u_{k+1} (1 - c_{k+1}) \frac{1 - s_{k+1}}{k+1} && \text{VI}
\end{aligned} \tag{2.4}$$

where δQ_k is the change in the distribution of the dispersal group sizes that form on the focal individual's natal patch as a result of its increasing propensity to lead.

The sign of ΔW_L corresponds to the direction of selection: if $\Delta W_L > 0$, selection will favour a greater disposition to lead, whereas if $\Delta W_L < 0$, selection will favour lower propensities to

lead. We will explain the biological interpretation of each term in ΔW_L:

(I) The loss of direct fitness due to the decreased propensity to not disperse. Conditioned on the event that the focal individual would not have been a follower (probability $(1 - d')$), he gives up the opportunity to breed on his natal patch. Since we assume without loss of generality that that non-dispersers have a reproductive value of 1, by increasing the probability that the focal individual leads, he loses a reproductive value of $-(1 - d')$.

(II) The gain in direct fitness due to the increased propensity to lead. The focal individual is now more likely to become a leader. As with the wild-type leaders, he attracts followers and forms a dispersal group the size of which is modelled by the Poisson distribution P_k, where k represents the number of followers. The group survives dispersal with probability $1 - c_k$, and is u_k times as likely as a lone individual to win a breeding position. With probability s_k, the focal individual successfully competes against his followers for breeding opportunities. Overall then, the direct fitness of the focal individual increases by $\sum_{k=0}^{\infty} P_k u_k (1 - c_k) s_k$.

(III) The loss of direct fitness due to the decreased propensity to not follow. By becoming a leader, the mutant relinquishes his opportunity to become a follower. He would have become a follower with probability d', and in doing so would have with probability Q_k joined a group with k other followers. This group would have had $k + 2$ individuals, would have survived dispersal with probability $1 - c_{k+1}$, and would have been u_{k+1} as likely as lone individuals to have won the rights to each available breeding territory. The focal individual would have won within-group competition for breeding opportunities with probability $\frac{1-s_{k+1}}{k+1}$. This explains the loss in direct fitness represented by the third term, $d' \sum_{k=0}^{\infty} Q_k u_{k+1} (1 - c_{k+1}) \frac{1-s_{k+1}}{k+1}$.

(IV) The decrease in local competition resulting from the focal individual's increased propensity to disperse. Had he not been a leader, the focal individual would have stayed to compete on its natal patch with probability $(1 - d')$, and so the reduction in competi-

tion is valued at $1 \times (1 - d')$. This benefit is awarded to another random individual who competes on the natal island; this individual is native to the island with probability h, in which case it is related to the focal individual by R. Thus the focal individual's inclusive fitness increases by $(1 - d')hR$ through the reduction of kin competition.

(V) By modifying his tendency to become a leader, the focal individual changes the distribution of dispersal group sizes that form on its natal patch. This will change the direct fitness of a random individual born on the same island as the focal individual. In the event that this random individual becomes a leader, it has a reproductive value of $d\sum_{k=0}^{\infty}(Q_k + \delta Q_k)u_k(1 - c_k)s_k$. The relatedness between this random individual and the focal individual is R, and so it contributes $Rd\sum_{k=0}^{\infty}(Q_k + \delta Q_k)u_k(1 - c_k)s_k$ to the focal individual's inclusive fitness. It follows that the change in inclusive fitness of the focal individual is $d\sum_{k=0}^{\infty}\delta Q_k u_k(1 - c_k)s_k$.

(VI) An argument similar to the one used in (V) can be used to show that if instead the random individual becomes a follower (probability $(1 - d)d'$), the change in the distribution of group sizes, δQ_k, would change the focal individual's inclusive fitness by $R(1 - d)d'\sum_{k=0}^{\infty}\delta Q_k u_{k+1}(1 - c_{k+1})\frac{1-s_{k+1}}{k+1}$.

A similar inclusive fitness argument can be applied to interpret the biological meaning of the remaining expressions in (2.3). The system (2.3) is, in general, difficult to solve analytically, but the convergence stable strategies [23] and many other properties can be explored numerically. Numerical analysis was carried out using Matlab, and copies of the scripts used can be found in the Supplementary Data. For convenience, unless stated otherwise we set the relative competitive ability of every leader to be equal and disallowed this trait to undergo evolution, such that $s_{\bullet k} = \bar{s}_k = s_k$. Each behavioural strategy is then influenced by only two phenotypes, and numerical results were produced by finding solutions to the set

$$\left(\frac{\partial W}{\partial d_\bullet} + R\frac{\partial W}{\partial \bar{d}}\right)\Bigg|_{d_\bullet=\bar{d}=d,d'_\bullet=\bar{d}'=d} = 0,$$
$$\left(\frac{\partial W}{\partial d'_\bullet} + R\frac{\partial W}{\partial \bar{d}'}\right)\Bigg|_{d_\bullet=\bar{d}=d,d'_\bullet=\bar{d}'=d'} = 0 \ .$$

Numerical Results

Altruistic behaviour is defined as any action that increases the fitness of others while decreasing the actor's own direct fitness [21]. In this model, an individual is described as being altruistic if it has a lower-than-average expected direct fitness as a consequence of its dispersal strategy. In Taylor's model, dispersal is always costly and is therefore always altruistic: dispersers lower their direct fitness while reducing kin competition on their natal island. We investigate how leader-follow relationships affect dispersal rates and the degree to which dispersal can be described as altruistic. Numerical analysis reveals that the effects of leader-follower relationships on dispersal rates and altruistic behaviour is primarily characterized by the function u_k. We use two simple and biologically reasonable functions to illustrate this fact: $u_k = k + 1$, which implies that if a dispersal group doubles in size, the group becomes twice as effective at competing against others for breeding territories, and $u_k = \sqrt{k+1}$, which suggests that it is more difficult to coordinate a larger group, and additional group members provide diminishing returns on the group's ability to compete. Note that if $u_k = k + 1$, groups technically no longer provide a competitive advantage over lone individuals: the expected number of breeding opportunities k individuals will successfully compete for is equal to the number of breeding opportunities a group of k individuals will win; the advantage of group dispersal is strictly in reducing the cost of dispersal. We could additionally allow $u_k = (k + 1)^2$, but this would place non-dispersers at a severe disadvantage because we have assumed they cannot form groups.

Results from our model show that the emergence of leader-follower behaviour increases (resp. decreases) dispersal rates if $u_k = k + 1$ (resp. $u_k = \sqrt{k+1}$). That dispersal rates differ

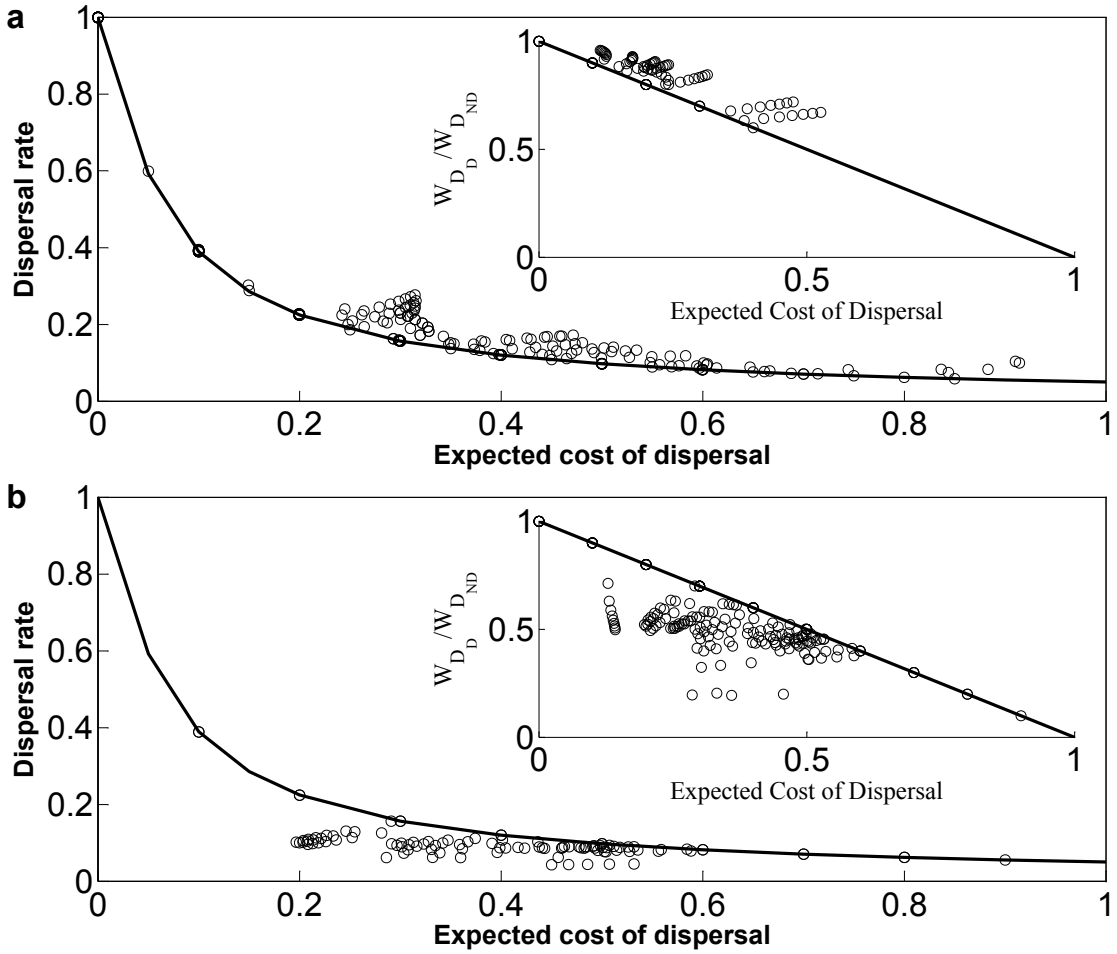

Figure 2.2: The effects of leader-follower relationship on the degree to which dispersal is altruistic. The black lines are results generated by Taylor's model (i.e. in the absence of followership relationships). The scatterplots represent results obtained after the emergence of leader-follower behaviour. If $u_k = k + 1$, the introduction of leader-follower behaviour either increases or does not affect both dispersal rates and the expected direct fitness of dispersers, W_{D_D}, compared to non-dispersers, $W_{D_{ND}}$ (a). If $u_k = \sqrt{k+1}$, the emergence of leader-follower relationships either decreases or does not affect both dispersal rates and the expected direct fitness of dispersers compared to non-dispersers (b). Recall that the cost of dispersal for a group with k followers is $c_0\alpha^k$. The expected cost of dispersal is the weighted average cost for all dispersal groups, which in Taylor's model is simply the cost of lone dispersal, c_0. Results were generated by numerical simulation using $N = 10$ and various values for c_0, α, and s.

once leader-follower behaviour emerges is not simply a consequence of the fact that dispersing in groups is less costly than dispersing individually: convergent stable levels of dispersal in the model with leader-follower behaviour do not necessarily equal the convergent stable dispersal rates in a model without leader-follower behaviour, even when the expected dispersal costs are equal (Figure 2.2). To explain this finding, note that although the costs of dispersal in Taylor's model are the same regardless of the proportion of individuals who disperse, there are diminishing returns on the reduction of local kin competition as a greater proportion of individuals disperse [18]. Consequently, for each cost of dispersal there is a distinct dispersal rate that maximizes the difference between the indirect fitness gained by reducing kin competition and the costs of dispersal. In our model, the cost of dispersal can be significantly influenced by dispersal strategies: whenever the cost of dispersing singly is high, followers provide a way for leaders to significantly reduce dispersal costs. Thus the expected inclusive fitness of individuals on an island is no longer simply maximal at a particular dispersal rate; instead, the proportion of leaders and followers (and hence the expected size of dispersal groups), in addition to the values of α and c_0, influences the expected cost of dispersal, and therefore influences the convergence stable dispersal rates.

Whenever $u_k = k + 1$ (resp. $u_k = \sqrt{k+1}$), the emergence of leader-follower behaviour increases (resp. decreases) the expected direct fitness of dispersers compared to that of non-dispersers, thus we conclude that the emergence of leader-follower relationships make dispersal as a whole a less (resp. more) altruistic act (Figure 2.2). We therefore demonstrate that leader-follower relationships influence both the prevalence of altruistic acts and the degree to which these acts can be described as altruistic.

We can further investigate how altruism is affected by the emergence of leader-follower relationships by delineating the direct and indirect fitness incentives for leaders and followers. We show in Appendix E that the direct fitness of followers is less than or equal to that of

non-followers. Numerical analysis reveals that the direct fitness of leaders is always greater than or equal to that of followers (Figures 2.3a, 2.3b), but can be greater or less than that of non-leaders (i.e. followers and non-dispersers), depending on social and ecological factors, namely s_k, c_k, u_k, and N (Figures 2.3c, 2.3d). Thus, while the act of following in our model is always more altruistic than leading, under some circumstances leaders, too, can be viewed as altruistic whenever leaders have lower direct fitness than non-dispersers. Even in conditions in which leading is the dispersal strategy that yields the highest direct fitness, followers may be sufficiently altruistic such that the presence of leader-follower relationships increases the direct fitness of those who neither lead nor follow. This implies that under certain conditions (namely when dispersal is extremely costly for all but very large groups) where leaders are not altruistic, leader-follower groups are altogether altruistic.

Finally, when the competitiveness of leaders, s_k, is allowed to evolve, we find that selection favours leaders that are neither completely selfish nor completely egalitarian. Individuals in this model have the ability to not participate in leader-follower relationships by choosing not to disperse. By allowing non-participation as a strategy in which there are no pre-existing differences in states, followership is voluntary and cannot be imposed by leaders via coercion. Leaders must instead strike a balance: if their competitiveness is too low they gain little direct fitness from dispersing because their followers out-compete them for breeding opportunities, but if their competitiveness is too, high fewer individuals will be willing to follow, thereby increasing the cost of dispersal and lowering the leader's direct fitness. Leaders evolve as if to optimize their inclusive fitness, an action which in this and all other inclusive-fitness models is not necessarily equivalent to optimizing their direct fitness.

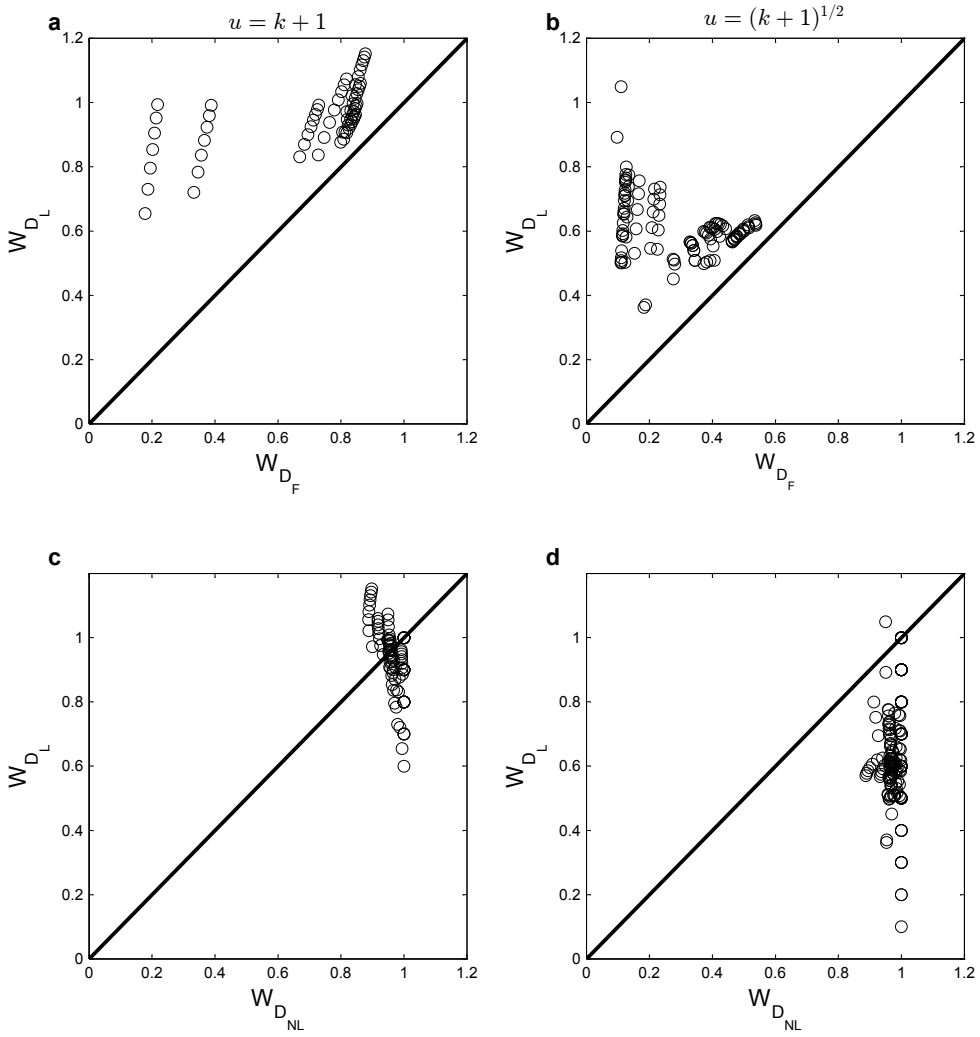

Figure 2.3: The degree to which leadership is altruistic depends on social and ecological factors. For any values the social and ecological parameters - $s \geq 1$, N, and c_k - the direct fitness of leaders is greater than that of followers for both $u = k + 1$ (a) and $u = \sqrt{k+1}$ (b). These factors also determine whether or not leaders have a greater direct fitness than non-leaders for both $u = k + 1$ (c) and $u = \sqrt{k+1}$ (d).

2.4 Discussion

2.4.1 A Comparison to Previous Models

Both empirical and theoretical research has led to conflicting conclusions regarding whether leaders coordinate group activities for selfish or selfless reasons. On one hand, animal leaders are known to manipulate group activities in order to gain a disproportionately large personal advantage [24]. On the other hand, leaders can bear a disproportionately large share of costs associated with enforcing group cohesion and cooperation [24, 25, 26]. To make matters more complicated, recent theoretical work shows that even the seemingly altruistic acts of leaders may simply be done to increase direct fitness gains [27]. The lack of clear definitions for altruistic and selfish leadership is a common issue in previous models, and it has compounded the difficulty in identifying the incentives for the emergence of leader-follower relationships. We use the theory of inclusive fitness to define and measure the incentives for leadership and followership. Leader-follower behaviour in our model emerges under a wider range of social and ecological conditions when followers act selfishly by taking a greater share of resources than leaders (Figure 2.1). In contrast to some previous models [17], and in agreement with Hooper et al., we demonstrate that leaders need no advantage - and thus need not be selfish - for leader-follower relationships to emerge in homogeneous populations. It is only after the emergence of followership that leaders necessarily evolve to acquire a disproportionately large share of breeding opportunities compared to followers. Unlike Hooper et al., we further show that leaders do not need greater direct benefits than that of non-leaders (followers and non-dispersers) for the maintenance of leader-follower behaviour.

Leaders are often thought to be socially or physically dominant, in possession of specialized knowledge, or in exceptional need of particular resources [24, 28, 29, 30]. Many previous models have used the assumption of pre-existing differences in state to explain the emergence of leader-follower behaviour. For example, Rands *et al.* create a game-theoretical model to

demonstrate that leadership can emerge in foraging pairs when individuals have differing energetic reserves. Johnstone and Manica [31] developed a repeated coordination game to challenge the importance of pre-existing differences in state has, but even this model relied on differences among individuals with regard to an unspecied state variable (e.g. preferences that reflect physiological condition) to produce the emergence of leaders and followers.

Only recently have models shown that leader-follower relationships can emerge and be maintained in completely homogeneous populations. Both Hooper *et al.* and Powers & Lehmann created models of homogeneous populations to show that leader-follower behaviour can be voluntarily created by followers rather than through coercion by leaders if leadership generates a sufficiently large increase in group productivity. However, these models apply only to very specific biological systems; they were designed to investigate leadership in ancestral human populations, and as such involve several very specific assumptions, including the pre-existence of egalitarian social groups. We have created a model in which emergence of leaders and followers is motivated by kin selection, and is influenced solely by social and ecological factors, such as the cost of dispersal and the relative competitive advantage that groups have over individuals. The coordination of group movement - the form of leadership we have studied - is particularly widespread because it does not involve sophisticated cognitive processes: it only requires one individual to initiate the movement and others individuals to follow [5]. That state-dependent conditions are not required to explain the emergence of leader-follower behaviour is an idea that can thus be applied to a wide variety of animal species.

Leader-follower behaviour cannot emerge in homogeneous populations unless both leaders and followers gain from the relationship; that is, unless the relationship increases the inclusive fitness of both the leader and the follower. Ultimately then, what is required for the emergence of leader-follower behaviour in the absence of coercion is that it increases group productivity in some manner. In Hooper's model, group productivity was increased due to leadership be-

cause it allowed defectors to be more efficiently punished, and so it lowered the costs required to maintain cooperation [32]. In Powers & Lehmann's model, hierarchies evolved from egalitarian groups whenever leader-follower behaviour provided sufficient increases to resource production, such that even when leaders took a greater share of resources, followers were still better off than those who neither lead nor follow [17]. In our model, individuals are able to more efficiently decrease kin competition in the presence of leaders.

2.4.2 Limitations and Future Directions

It is important to note that our model relies on the assumption that leader-follower relationships form predominantly among kin. Indeed, kin selection is the main incentive for the emergence and maintenance of leadership and followership in our model. We do not view the assumption that individuals in leader-follower relationships are related as restrictive because genetic relatedness has been shown to help facilitate the emergence of many types of social interactions and social organizations [33, 34]. Consequently, while leader-follower relationships can occur among non-relatives, many [5, 6, 7, 8, 9, 10, 11, 12, 13, 35] (if not most) observed leader-follower behaviour has occurred between relatives. Therefore the general conclusions drawn from our model should still be applicable to a wide variety of animal species. In fact, depending on what type of leadership is being modelled, it may be important to include the assumption that leader-follower relationships are formed among kin. This is particularly true of models that study how leadership can emerge from pre-existing social groups, as genetic relatedness is thought to very frequently facilitate group living [34].

Group formation occurs randomly in our model, and so the number of individuals that will follow a given leader is random. As a result, leadership as it is modelled here is risky: if a leader attracts too few followers, the cost of dispersal is high and the expected fitness of the leader will be well below the global average, but if the leader attracts many followers, dispersal is less costly and the leader (and possibly his followers, depending on the reproductive skew)

can expect an above-average fitness. Of course, group formation in real populations is unlikely to be completely random. Instead, individuals may decide which leader they will follow based on the leader's attributes, namely the leader's selfishness. Following Hooper, our model could be extended to include this idea of a biological market [36], wherein leaders who are willing to concede a lower reproductive skew (low β) attract more followers than despotic leaders [37] (high β). The evolutionarily stable level of leader selfishness in such a biological market would depend on a number of additional social factors, such as information flow. For example, if dispersal groups are formed randomly, it would be reasonable to assume that followers may pay some cost or bear some risk in the pursuit of finding more selfless leaders to follow. If these costs are sufficiently high, even relatively selfish leaders are likely to retain followers. However, in contrast to Hooper, kin competition is present in our population, and should lower the evolutionarily stable levels of leader selfishness. It is unclear how precisely the conflict between leader and follower over resources is resolved when both the biological market and kin selection are factors.

2.4.3 Conclusions

We have established that leader-follower behaviour can emerge even when leaders and followers have no pre-existing differences in state. This provides further support for the theory that individuals may differ in their intrinsic propensity to become leaders and followers, irrespective of their immediate condition [31]. Further, our model demonstrates that, despite the assumptions commonly made in previous theoretical work, leaders need not be selfish in order for leader-follower relationships to emerge; in fact, these relationships can emerge even if followers are selfish and take a greater share of resources produced by the group than leaders. Therefore, while it is frequently assumed that certain differences in condition or ability motivate leader-follower relationships, our model shows that no such differences are necessary. It is thus possible that leaders and followers evolved to possess different traits only after leader-follower relationships had emerged in order to take advantage of their respective social

positons. For example, leaders may have evolved to become socially or physically dominant so they could more easily use their leadership position to monopolize resources for their own personal gain.

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2.5 Appendix

2.5.1 Appendix A. Fitness Calculation

To show that the Poisson distribution accurately models the probability of dispersal group sizes when the number of offspring becomes large, a stochastic simulation was created (Supplementary Data). To justify all other simplifications, a stochastic simulation was designed without implementing the aforementioned assumptions; the results of the stochastic simulation are equivalent to that of our analytic model (see Supplementary Data). We calculate the neighbour-modulated fitness of a focal individual on a focal island:

$$W = \overbrace{\frac{(1-d_\bullet)(1-d'_\bullet)}{(1-\bar{d})(1-\bar{d}') + d\sum_{j=0}^{\infty} P_j u_j (1-c_j)}}^{\text{Neither leading nor following}} + \overbrace{d_\bullet \frac{\sum_{k=0}^{\infty} Q_k (1-c_k) u_k s_{\bullet k}}{(1-d)(1-d') + d\sum_{j=0}^{\infty} P_j u_j (1-c_j)}}^{\text{Leading}} + \overbrace{(1-d_\bullet) d'_\bullet \frac{\sum_{k=0}^{\infty} Q_k (1-c_{k+1}) u_{k+1} \frac{1-\bar{s}_{k+1}}{k+1}}{(1-d)(1-d') + d\sum_{j=0}^{\infty} P_j u_j (1-c_j)}}^{\text{Following}} \tag{A1}$$

where P and Q represent Poisson distributions about $\lambda = \frac{(1-d)d'}{d}$ and $\bar{\lambda} = \frac{(1-\bar{d})\bar{d}'}{\bar{d}}$, respectively. At equilibrium, $d = \bar{d}, d' = \bar{d}'$, and so $Q_j = P_j$. This fitness expression (A1) can be divided into three main components: the neighbour-modulated fitness gained from leading, following, and doing neither. We will illustrate the derivation of the first term in the fitness expression. The probability that a non-disperser wins a breeding site is equal to one divided by the sum of the relative competitive abilities of every competitors. There are two types of competitors: other non-dispersers, of which there are $NK(1-\bar{d})(1-\bar{d}')$, and dispersers. We expect from any given island there to be NKd dispersing groups; the expected relative competitive ability of these groups is equal to the probability of each group size, multiplied by one minus the cost of dispersal of groups that size, multiplied again by the relative competitive advantage of that

group size, summed over all possible groups sizes: $\sum_{j=0}^{\infty} P_j u_{j+1} c_j$. But there are N breeding sites to be won, and should an individual win a breeding site, its fitness will be K; we thus find the neighbour-modulated fitness of a non-disperser to be $\frac{NK}{NK(1-\bar{d})(1-\bar{d'})+NKd\sum_{j=0} P_j u_j c_j}$. Cancelling the NK terms and multiplying by the probability with which the focal individual neither leads nor disperses, $(1-d'_\bullet)(1-d_\bullet)$, we obtain the first term in our fitness expression. Similar calculations can be made to derive the remaining two terms in (A1).

2.5.2 Appendix B. Evolutionarily Stable Strategies

We can use the direct fitness formulation from Taylor & Frank to describe the evolution of dispersal strategies; this requires the assumption of weak selection, which our stochastic simulation will demonstrate is valid. Dispersal strategies evolve until a local maximum is reached, defined as

$$\begin{aligned}
\left(\frac{\partial W}{\partial d_\bullet} + R\frac{\partial W}{\partial \bar{d}}\right)\Bigg|_{d_\bullet=\bar{d}=d, d'_\bullet=\bar{d'}=d', s_\bullet=\bar{s}=s} &= 0 \\
\left(\frac{\partial W}{\partial d'_\bullet} + R\frac{\partial W}{\partial \bar{d'}}\right)\Bigg|_{d_\bullet=\bar{d}=d, d'_\bullet=\bar{d'}=d', s_\bullet=\bar{s}=s} &= 0 \\
\left(\frac{\partial W}{\partial s_\bullet} + R\frac{\partial W}{\partial \bar{s}}\right)\Bigg|_{d_\bullet=\bar{d}=d, d'_\bullet=\bar{d'}=d', s_\bullet=\bar{s}=s} &= 0
\end{aligned} \tag{B1}$$

where R is the expected relatedness between the focal individual and a random individual on its natal island. Taking the partial derivatives, we find

$$\begin{aligned}
\frac{\partial W}{\partial d_\bullet}\Big|_{d_\bullet=\bar{d}=d} = &\frac{-(1-d')}{(1-d)(1-d')+d\sum_{j=0}^{\infty} P_j u_j (1-c_j)} \\
&+\frac{\sum_{k=0}^{\infty} Q_k u_k (1-c_k) s_{\bullet k}}{(1-d)(1-d')+d\sum_{j=0}^{\infty} P_j u_j (1-c_j)} \\
&-\frac{d'\sum_{k=0}^{\infty} Q_k u_{k+1}(1-c_{k+1})\frac{1-\bar{s}_{k+1}}{k+1}}{(1-d)(1-d')+d\sum_{j=0}^{\infty} P_j u_j (1-c_j)}
\end{aligned}$$

$$\left.\frac{\partial W}{\partial \bar{d}}\right|_{d_\bullet=\bar{d}=d} = \frac{(1-d)(1-d')^2}{((1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-c_j))^2} + \frac{d\sum_{k=0}^{\infty}\delta Q_k u_k(1-c_k)s_{\bullet k}}{(1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-c_j)} + \frac{(1-d)d'\sum_{k=0}^{\infty}\delta Q_k u_{k+1}(1-c_{k+1})\frac{1-\bar{s}_{k+1}}{k+1}}{(1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-cj)}$$

$$\left.\frac{\partial W}{\partial d'_\bullet}\right|_{d'_\bullet=\bar{d}'=d'} = \frac{-(1-d)}{(1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-c_j)} + \frac{(1-d)\sum_{k=0}^{\infty}Q_k u_{k+1}(1-c_{k+1})\frac{1-\bar{s}_{k+1}}{k+1}}{(1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-c_j)}$$

$$\left.\frac{\partial W}{\partial \bar{d}'}\right|_{d'_\bullet=\bar{d}'=d'} = \frac{(1-d)^2(1-d')}{((1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-c_j))^2} + \frac{d\sum_{k=0}^{\infty}\delta Q_k u_k(1-c_k)s_{\bullet k}}{(1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-c_j)} + \frac{(1-d)d'\sum_{k=0}^{\infty}\delta Q_k u_{k+1}(1-c_{k+1})\frac{1-\bar{s}_{k+1}}{k+1}}{(1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-c_j)}$$

$$\left.\frac{\partial W}{\partial s_\bullet}\right|_{s=\bar{s}=s} = d\frac{\sum_{k=0}^{\infty}Q_k u_k(1-c_k)\delta s_k}{(1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-c_j)}$$

$$\left.\frac{\partial W}{\partial \bar{s}}\right|_{s=\bar{s}=s} = -(1-d)d'\frac{\sum_{k=0}^{\infty}Q_k(1-c_{k+1})u_{k+1}\frac{\delta s_{k+1}}{k+1}}{(1-d)(1-d')+d\sum_{j=0}^{\infty}P_j u_j(1-c_j)}.$$

2.5.3 Appendix C. Relatedness Calculation

To calculate relatedness [18], we use two key assumptions. First, we assume weak selection. Second, given that there are an infinite number of islands in our model, we make the standard assumption that the relatedness between two individuals born on different islands is zero. We find that relatedness, R, is equal to

$$R = \frac{f_{yx}}{f_x}$$

where f_{yx} represents the coefficient of consanguinity, which is the probability that two random alleles, one taken from focal individual, x, and the other from a random individual born on the same patch, y, at the locus of control (i.e. the leadership and followership genes), are identical by descent. f_x is the inbreeding coefficient of x, which, for our haploid population, is equal to 1. The value of the coefficient of consanguinity for the next generation, f'_{yx}, is dependent upon that of this generation; more precisely,

$$f'_{yx} = \frac{1}{N} + \frac{N-1}{N} h^2 f_{yx}$$

where $h = \frac{(1-d)(1-d')}{(1-d)(1-d')+d\sum_{j=0}^{\infty} P_j u_j c_j}$ represents the probability that a random breeder on an island is native to that island. Setting $f'_{yx} = f_{yx}$ in order to find the coefficient of consanguinity when the population is at equilibrium, we find $R = f_{yx} = \frac{1}{N-Nh^2+h^2}$.

2.5.4 Appendix D. Emergence of Followership

By eliminating the option to follow (i.e. by setting $d' = 0$), every dispersal group is of size one, and we should recover the results of Taylor's inclusive fitness model for the dispersal of offspring. The fitness equation now becomes

$$W = \frac{1-d_\bullet}{1-\bar{d}+d(1-c_0)} + \frac{d_\bullet(1-c_0)}{1-d+d(1-c_0)}. \tag{D1}$$

We now take the partial derivatives of (D1) in order to solve system (B1)

$$\left.\frac{\partial W}{\partial d_\bullet}\right|_{d_\bullet=\bar{d}=d} = \frac{-c_0}{1-dc_0} \tag{D2}$$

$$\left.\frac{\partial W}{\partial \bar{d}}\right|_{d_\bullet=\bar{d}=d} = \frac{1-d}{(1-dc_0)^2}. \tag{D3}$$

The probability that a random breeder on an island is native to that island now becomes $h = \frac{1-d}{1-d+dc_0}$ and the expression for relatedness $R = f_{yx} = \frac{1}{N-Nh^2+h^2}$, remains the same except for the adjusted value of h. By substituting the above partial derivatives (D2) and (D3) into (B1), we find evolution will favour higher dispersal rates whenever $Rh > c_0$, which is equivalent to Taylor's result.

We are also interested in the conditions under which followership can emerge; equivalently, we seek solutions to

$$\left.\left(\frac{\partial W}{\partial d'_\bullet} + R\frac{\partial W}{\partial \bar{d}'}\right)\right|_{d'_\bullet=\bar{d}'=d'=0} > 0 \tag{D4}$$

$$-(1-d) + (1-d)u_1(1-c_1)(1-s_1) + Rh(1-d)$$

$$+R(1-d)(u_1(1-c_1)s_1 - (1-c_0)) > 0.$$

As proved by Taylor, at equilibrium $Rh = c_0$. We find that (D4) is satisfied by a wide range of biologically relevant parameter conditions. For example, it is simple to show that even in the extreme case where followers are expected to have no direct fitness ($s = 1$), $u_k = k + 1$, and $c_0 = 1, c_1 = 0$, (D4) is satisfied and so followership emerges.

2.5.5 Appendix E. Fitness Consequences of Leader-Follower Behaviour

The change in fitness of a mutant individual who has some increased propensity to lead is

$$\left(\frac{\partial W}{\partial d_\bullet} + R\frac{\partial W}{\partial \bar{d}}\right)\Bigg|_{d_\bullet=\bar{d}=d} \propto \Delta W_L$$

$$\Delta W_L = -(1-d') + \sum_{k=0}^{\infty} Q_k u_k (1-c_k) s_k - d' \sum_{k=0}^{\infty} Q_k u_{k+1}(1-c_{k+1})\frac{1-s_{k+1}}{k+1}$$

$$+R((1-d')h + d\sum_{k=0}^{\infty} \delta Q_k u_k (1-c_k) s_k + (1-d)d' \sum_{k=0}^{\infty} \delta Q_k u_{k+1}(1-c_{k+1})\frac{1-s_{k+1}}{k+1}$$

where δQ_k represents the change in the distribution of the dispersal group sizes that form on the focal individual's natal patch as a result of its increasing propensity to lead. For our analysis of the system, we are concerned only with the direction — not the magnitude — of steepest descent. By removing common factor $\frac{1}{(1-d)(1-d')+d\sum_{j=0}^{\infty} P_j u_j (1-c_j)}$ from $\left(\frac{\partial W}{\partial d_\bullet} + R\frac{\partial W}{\partial \bar{d}}\right)\Big|_{d_\bullet=\bar{d}=d}$, we derive the expression ΔW_L, the sign of which is corresponds to the direction of selection. If $\Delta W_L > 0$, selection will favour increased propensities to lead, whereas if $\Delta W_L < 0$, selection will favour lower levels of leadership.

We can use this direct fitness argument to show that it is unclear if the direct fitness of leaders will be greater than that of non-leaders. The direct fitness consequences for the increased probability to lead is given by the first three terms in ΔW_L. Consider the second term. We cannot conclude that $u_k s_k$ is uniformly less than or equal to 1. Thus whether or not the increased propensity to lead results in increased fitness depends on various parameter conditions, including s, c_k, u_k, and N.

The change in fitness of a mutant individual who has some increased propensity to follow is

$$\left(\frac{\partial W}{\partial d'_\bullet} + R\frac{\partial W}{\partial \bar{d}'}\right)\Bigg|_{d'_\bullet=\bar{d}'=d'} \propto \Delta W_F$$

$$\Delta W_F = -(1-d) + (1-d)\sum_{k=0}^{\infty} Q_k u_{k+1}(1-c_{k+1})\frac{1-s_{k+1}}{k+1}$$

$$+R((1-d)h + d\sum_{k=0}^{\infty}\delta_1 Q_k u_k(1-c_k)s_k + (1-d)d'\sum_{k=0}^{\infty}\delta_1 Q_k u_{k+1}(1-c_{k+1})\frac{1-s_{k+1}}{k+1}$$

where $\delta_1 Q_k$ represents the change in the distribution of the dispersal group sizes that form on the focal individual's natal patch as a result of its increasing propensity to follow. The direct fitness consequences for the increased probability to follow is given by the first two terms in ΔW_F. Note that $(1-c_k) \leq 1$, and recall that we assume $s_k = \frac{\beta}{\beta+k}$. Then in the cases where $u_k = k+1$ or $u_k = \sqrt{k+1}$, $\frac{u_{k+1}}{\beta+k+1} \leq 1$, and so $\sum_{k=0}^{\infty} Q_k u_{k+1}(1-c_{k+1})\frac{1-s_{k+1}}{k+1} \leq 1$. Thus under these circumstances, increasing one's propensity to follow always decreases or does not affect one's direct fitness.

We can define an action as altruistic if decreases the direct fitness of the actor but increases the direct fitness of other individuals. With this, we can conclude that followership is always altruistic but whether or not leadership is altruistic depends on social and ecological conditions.

Evolutionarily stable strategies [38] can be found by solving B1. However, this system could not be solved analytically, so it was instead assessed numerically (see Supplementary Data).

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Chapter 3

Environmental variance and the evolution of signalling behaviour

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Abstract

A recent meta-analysis has indicated that environmental quality and variability can influence whether offspring begging and parental responses to these signals are motivated by offspring need or offspring quality. We create a model to verify and apply evolutionary logic to this hypothesis. We determine the ecological and social conditions under which species signal and respond to need in favorable environments, and to quality in poor environments. The environmental conditions that favor this shift are widest when signalling costs and differences in quality between offspring are moderate. Low relatedness between siblings coupled with high signalling costs, as well as moderate relatedness between siblings coupled with low signalling costs, allow for the shift between signals of need and signals of quality to occur in more volatile environments. Further, only species whose offspring are highly dependent on parents for survival are not expected to use both signals of need and of quality. Ultimately, this shift between signalling need and signalling quality is the result of high-quality offspring benefiting more from meagre amounts of parental pro-

visioning, while low-quality offspring have most to gain when parents can contribute more substantially. We show that this differential benefit of resources depends substantially upon offspring fitness as functions of parental investments, a variable which has lacked both diversity and biological realism in previous theoretical approaches. We then use this work to reassess previous theory on signals of need and of quality.

3.1 Introduction

It is common throughout the animal kingdom for offspring to solicit resources from parents via auditory or visual signals called begging [1, 2]. Although begging behaviour has been extensively investigated, both theoretical and empirical studies have led to no consensus regarding the evolutionary purposes of signalling and the explanations for parental response strategies to begging behaviour. The two most commonly proposed theories to explain signalling behaviour are (i) the signal of need (SoN) hypothesis [3], which posits that offspring with lower reproductive value will beg more and will be preferentially fed by their parents, and (ii) the signal of quality (SoQ) hypothesis [4, 5], which proposes that offspring with higher reproductive value can better afford the costs of begging and parents will allocate more resources to these young because the survival of offspring in better condition may translate to greater reproductive value.

Both SoN and SoQ rely on the assumption that offspring are more aware of their reproductive value than their parents are in the absence of signals. It is plausible that begging instead conveys only proximate information, as outlined by the signal of hunger hypothesis proposed by Mock et al. [6]. While SoN and SoQ are neither mutually exclusive nor the only theories proposed to explain signalling behaviour, they are the most prominent and are frequently compared with little consensus reached [7, 8, 6, 9].

Most previous theoretical work either assumes or claims to validate SoN over SoQ [6], in part due to the assumption that parents are always trying to raise all their offspring to inde-

pendence [6, 2]. Yet many empirical studies seem support SoQ [10, 11, 12, 2], particularly in populations that experience frequent brood reduction. This discrepancy is exacerbated by the fact that empirical literature suggests that strategies involving begging and reactions to begging are largely species-dependent: in certain species, parents provision disproportionately large amounts of resources toward the smallest and seemingly the most needy offspring, whereas in other species the largest offspring are preferentially fed by parents, sometimes without any regard to offspring begging behaviour [2, 13]. It has been suggested [6] that neither the SoN hypothesis nor the SoQ hypothesis is alone capable of explaining and predicting the begging behaviour found in nature, and that certain species appear to beg to signal need while others beg to signal quality.

More recently, it has been demonstrated that begging behaviour and parental responses differs significantly between species [2, 13]. A thorough meta-analysis of avian species has demonstrated that, at least in some birds, the way in which parents respond to begging may actually depend on environmental conditions. In more stable environments, resources are abundant and so retention of entire broods is likely, and consequently parents feed in accordance to offspring need. Conversely, in unpredictable and poor environments, limited resources means it is frequently impossible to ensure the survival of an entire brood, and so parents fare better by feeding offspring that are in the best condition to secure the survival of the greatest number of offspring [2, 13]. However, the attractive argument that environmental variation is sufficient in explaining the between- and within-species variation of SoN and SoQ systems has not yet been rigorously tested by theory. It is further unclear how the shift between SoN and SoQ can be influenced by ecological factors, such as the cost of begging, and social factors, including relatedness between offspring.

Here, we create a simple model to confirm that certain species may employ either SoN and SoQ depending on environmental conditions. We then identify the environmental conditions

which favor the shift between SoN and SoQ, and examine how certain social and ecological factors can influence this shift. We then discuss the implications of our findings on the debate between the SoN and SoQ hypotheses.

3.2 Methods

Our primary goal is to create the simplest model capable of analyzing possible shifts between SoN and SoQ caused by environmental variation. To do so, we construct a modified version of the three-player evolutionary game found in Wild et al. [14]. Consider a parent that has one high-quality offspring and one low-quality offspring in each generation. Any differences in quality could be the result of asynchronous hatching, which can heavily influence egg size, among other factors proven to influence growth [15]. Offspring quality is cryptic, meaning parents are unable to differentiate the need and quality of their offspring in the absence of any signals (see Appendix 3.5.2 for an extension of this model that relaxes this assumption). .

Suppose that at the end of each generation the parent has collected a divisible resource (see Appendix 3.5.3 for a version of the model with indivisible resources) which it must distribute between the two offspring. Since parents are unable to distinguish between the quality of offspring, they do not know how much of the resource they should allocate to each offspring. However, offspring may use signals that indicate their quality, and this can be used to guide the parent's provisioning strategy. It is assumed that parents distribute resources in a manner that is optimal for their own inclusive fitness; the parent is better able to do this if they can identify the quality difference between offspring. It is assumed that signals may be costly to produce, as is standard in theoretical models [5, 16] and evidenced by several empirical studies [17, 18, 19, 20, 21, 22, 23, 24] .

The family resides in a volatile environment, meaning resource availability depends signifi-

cantly on environmental conditions. The parent can collect amount g_h of this divisible resource in good environmental conditions, but obtains only $g_l < g_h$ in poor environmental conditions. Here, the terms 'good' and 'poor' are strictly relative: good environments are favorable relative to poor environments, but our results will view scenarios in which even good environments have scarce resources, and others in which even poor environments have an abundance of resources. Parents can recognize the quality of environmental conditions, but not until after they lay their eggs. Consequently, the parent always lays two eggs at the beginning of each generation – many species of bird do not lay or hatch eggs in the same clutch at the same time, often hypothesized as a method of efficiently eliminating clutch sizes that are too large to maintain during poor ecological conditions [25, 26].

The two offspring can differ in terms of how their fitness changes as a function of resources provisioned to them: high-quality and low-quality offspring have fitness functions $f_h(g)$ and $f_l(g)$, respectively, where g is the amount resources provided. Since signalling may be costly for the signaller, the fitness of the signaller is subtracted by some fixed cost, c.

We assume that offspring can distinguish the quality of their environment, either by direct observation or indirectly based on the parent's behaviour. They can use this information when deciding whether to signal, a decision which is assumed to be made by offspring simultaneously. If both or neither offspring signal, it is assumed the parent is unable to distinguish between the need and quality of the offspring, and so must divide resources in a manner that maximizes the parent's own inclusive fitness without any information about offspring quality; as it turns out, the optimal strategy in these cases is for the parent to divide resources evenly between the two offspring (see Appendix 3.5.1). If only one offspring signals, the parent is assumed to be able to differentiate between the two offspring, and uses the information about offspring quality to distribute resources optimally with respect to the parent's own inclusive fitness. Note that the begging strategies of each offspring can change depending on current

environmental conditions – choices in good-quality environments may differ from choices in poor-quality environments.

For each environmental condition – good and poor – there are 4 possible outcomes for the scenario described (see Figure 3.1). There is a certain payoff for each offspring in each of the different possible outcomes. In this model, the payoff is measured in terms of the total inclusive fitness each offspring has in each outcome. The inclusive fitness payoff corresponding to each outcome and for each individual is calculated by setting the relatedness between parent and offspring and the relatedness between offspring to $1/2 < R < 1$ and $1/4 < r < R$, respectively. We are, in particular, interested in finding conditions that favor the Nash equilibrium profile under which signal of need is adopted in one environmental condition but signal of quality is employed in another. We identify the conditions in which only the low-quality offspring signals and is given a greater share of the divisible resource in good environments (SoN), and only the high-quality offspring signals and is given a greater share of resources in poor environments (SoQ). This equilibrium, which captures the outcome in which the information conveyed by signals shifts from need to quality based on environmental conditions, is henceforth referred to as the facultative outcome.

The payoffs for each individual in each outcome j, as well as the conditions in which the facultative outcome is a Nash equilibrium, are listed in Appendix 3.5.1. To examine the stability of the facultative outcome, we must first select biologically realistic fitness functions for the two offspring. Since fitness as a function of resources for many species is best modeled as sigmoidal [27, 28], we set $f = 1/(1 + e^{-t})$, where t represents the state of the offspring.

We assume that the high-quality offspring has hatched early and has thus received care from the parent for a longer period than the low-quality offspring but is otherwise identical to the low-quality offspring. That is, we will assume that the fitness functions of the two offspring

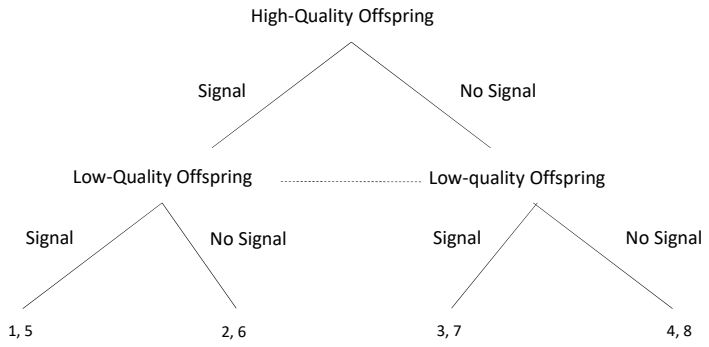

Figure 3.1: Decision tree representation of the game outlined in the main text. A separate and independent game is played in good- and poor-quality environments, although the general structure of the decision tree is the same for each environment. Note that the high-quality and low-quality offspring act simultaneously and independently. Each pair of numbers refers to the outcome name assigned to the good-quality environments and poor-quality environments, respectively.

are identical, $f_h = f_l$, but that the state of the offspring differ. Suppose in the absence of any additional resources that the low-quality offspring is in initial state $t = d$ (Figure 3.1). The high-quality offspring, having been cared for by the parent for a longer duration, is assumed to be in a better state, $t = d + a$, $a > 0$; higher values of a correspond to greater fitness advantages over the low-quality offspring. Lastly, the fitness of each offspring is influenced by the amount of resources it receives. If the high-quality offspring receives g_1 resources, it has fitness $f_h = \frac{1}{1+e^{-(d+a+g_1)}}$ (i.e. $t = d + a + g_1$), while any low-quality offspring receiving g_2 resources has fitness $f_l = \frac{1}{1+e^{-(d+g_2)}}$ (i.e. $t = d + g_2$).

Since we are primarily interested in investigating how environmental variability influences whether signals indicate need or quality, we set all other variables (r, c, a, and d) equal to constants, then numerically calculate the amount of resources available in good and poor environmental conditions, g_h and g_l respectively, for which the stability conditions of the facultative outcome are met; these values will constitute the 'region of stability'. We analyze the influence of each parameter on the region of stability; below we briefly discuss the results of this analysis for each parameter in turn.

3.3 Results

Whenever an offspring chooses to signal, there are two inclusive fitness penalties. The first is the direct cost associated with signalling and the second is the indirect cost resulting from the other offspring receiving fewer resources. This second cost is influenced by the relatedness between offspring, baseline fitness of the signaler's sibling, and the amount of resources that the two offspring are competing over. The sole benefit of signalling is that the offspring will receive a larger share of resources, which is influenced by the baseline fitness of the signaller and the amount of resources available to the parent. Note that in this model an offspring who does not stand to receive a larger share of resources by signalling simply will not beg, as begging will

only serve to alert the parent that the signaller should receive fewer resources. For the stability of the facultative outcome, the sole benefit of signalling must outweigh the two penalties for high-quality offspring (but not for low-quality offspring) in poor environments, and similarly the benefit must outweigh the cost for low-quality offspring (but not for high-quality offspring) in more favorable environments. Consequently, resource availability, relatedness, signalling costs, baseline fitness, and differences in offspring quality each affect whether SoQ in poor environments shifts to SoN in good environments.

Results for the stability of the facultative outcome are presented in terms of how relatedness, signalling costs, baseline fitness, and differences in offspring quality influence the range of environmental conditions that would lead to a shift between SoN and SoQ.

Relatedness between offspring

Generally, if signalling costs, c, are high, increasing relatedness, r, decreases the range of parameters of which the facultative outcome is stable (Figure 3.2). High signalling costs can completely offset the fitness gain produced by guiding the parental investment via signals, and so offspring are less inclined to beg. As relatedness increases, the greater share of resources that an offspring may acquire by signalling becomes less of a benefit, as the signaller is depriving its closer relative of resources. This is often particularly true when the difference between offspring quality, a, is small. The result is that, in both good and poor environments, both offspring are less likely to beg as relatedness increases. When signalling costs are large, higher relatedness between offspring translates to greater environmental volatility required for the stability of the facultative outcome (where volatility is measured by the minimum difference in resources in good versus poor environments).

If the signalling costs are low, the range of environmental conditions over which the facultative outcome is stable is instead expected to be widest at moderate relatedness levels (i.e.

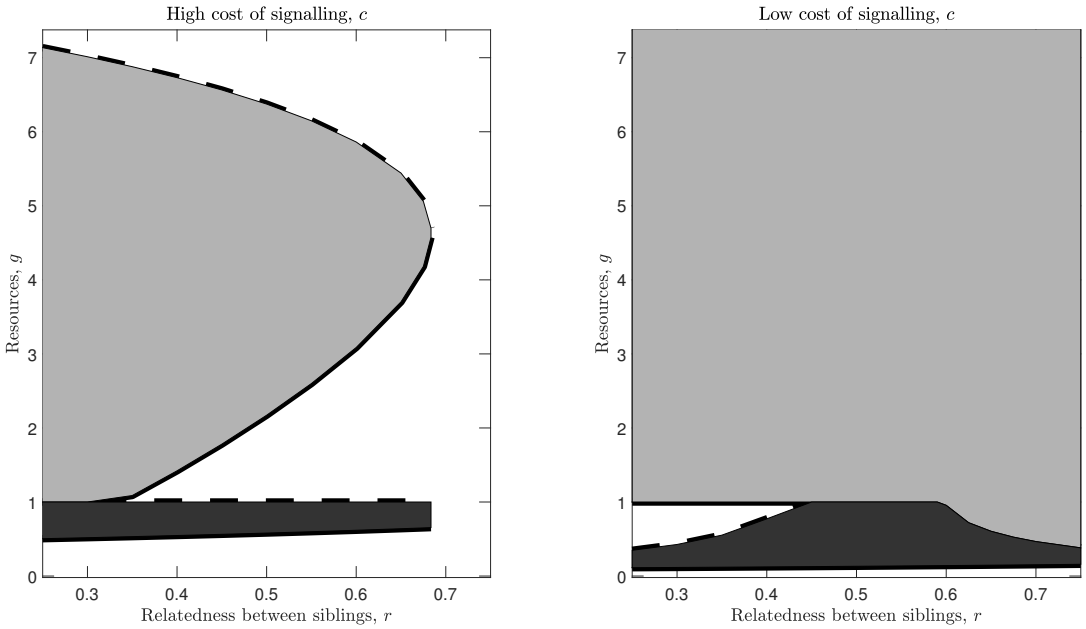

Figure 3.2: Relatedness between offspring and its effect on the amount of resources required for the facultative outcome to be stable in good environments (light grey region) and in poor environments (dark grey region). The region between the maximum amount of resources (dashed lines) and the minimum amount of resources (solid lines) constitute the amount of resources necessary for the stability of the facultative outcome. Results were generated using $c = 0.05$ in left panel and $c = 0.01$ in the right panel, $d = -2$, and $a = 1$.

with offspring that are full-siblings) compared to lower relatedness levels (i.e. with offspring of species where extra-pair copulation is more common). With lower relatedness, offspring experience a relatively greater gain in inclusive fitness by receiving a greater share of resources. As such, with low signalling costs, both offspring are more inclined to beg and the parent will distribute resources evenly (see Appendix 3.5.1). With higher-than-moderate relatedness, offspring lose more by taking a greater share of resource away from their closer sibling, and will generally opt not to signal at all, especially when the difference in offspring quality is low. When signalling costs are low, higher relatedness between offspring means lower environmental volatility (defined above) is required for the stability of the facultative outcome.

Cost of signalling

All else being equal, increasing the costs of signalling decrease the range of environmental conditions under which the facultative outcome is stable (Figure 3.3). Simply put, this occurs because the benefit of receiving increased provisioning due to signalling is more likely to be outweighed by the higher direct costs of signalling. The shift between SoN and SoQ is possible even when signalling costs are minute provided relatedness between offspring is sufficiently high, and the low-quality (resp. high-quality) offspring benefits substantially more from provisioning in good (resp. poor) environments than its sibling. If there are absolutely no direct signalling costs, $c = 0$, no strict Nash equilibrium exists because, while it may be optimal for everyone if only one offspring begs so that the parent is able to differentiate between the two offspring, offspring decide whether to signal simultaneously and as such cannot coordinate which of them should signal.

Baseline fitness

Given low to moderate baseline fitness levels, conditions for the stability of the facultative outcome can be met (Figure 3.4). All else being equal, if the baseline fitness of offspring is high, it is less likely that one offspring will gain substantially more than the other. The offspring are

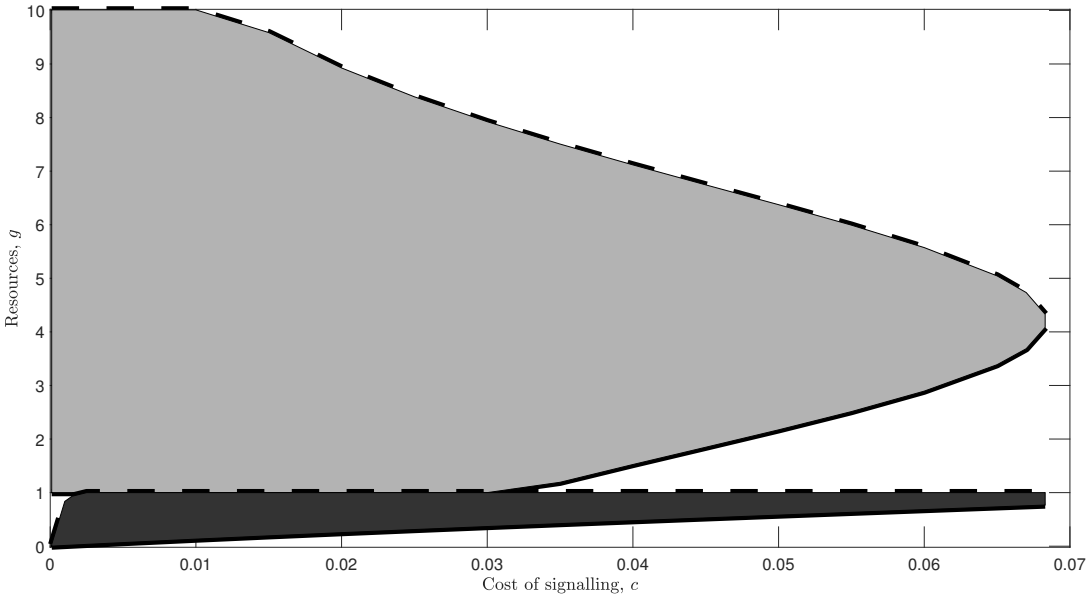

Figure 3.3: Cost of signalling and its effect on the amount of resources required for the facultative outcome to be stable in good environments (light grey region) and in poor environments (dark grey region). The region between the maximum amount of resources (dashed lines) and the minimum amount of resources (solid lines) constitute the amount of resources necessary for the stability of the facultative outcome. Results were generated using $d = -2$, $a = 1$, and $r = 0.5$.

consequently less inclined to beg since the costs of begging are less likely to outweigh the benefit of directing the parent to distribute resources more optimally, particularly when relatedness between offspring is high.

The facultative outcome is also unlikely to be stable when the baseline fitness of offspring is very low. Due to the sigmoidal nature of the fitness function, very low baseline fitness levels mean that it is unlikely for one offspring to benefit significantly more than the other by receiving a greater share of resources, particularly when the resources are very limited; the difference in quality between offspring would have to be very large. The cost of begging will then deter both offspring from begging.

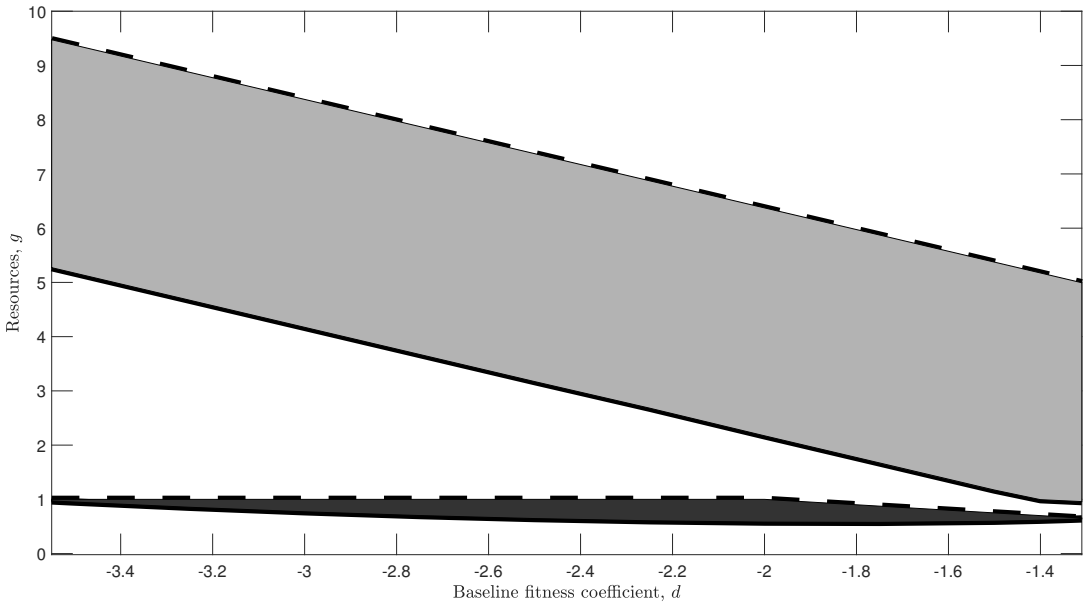

Figure 3.4: Offspring baseline fitness and its effect on the amount of resources required for the facultative outcome to be stable in good environments (light grey region) and in poor environments (dark grey region). The region between the maximum amount of resources (dashed lines) and the minimum amount of resources (solid lines) constitute the amount of resources necessary for the stability of the facultative outcome. Results were generated using $c = 0.05$, $a = 1$, and $r = 0.5$.

High-quality offspring advantage

Mathematically, both baseline fitness and high-quality offspring advantage, a, influence the offspring's conditions relative to the inflection point – where the marginal fitness benefits of increased provisioning are greatest – of the sigmoidal curve. Consequently, similar to the relationship between the stability of the facultative outcome and offspring baseline fitness, the facultative outcome is stable only when the high-quality offspring has a moderate advantage over its sibling. If the advantage is very small, it is unlikely for one offspring to gain significantly more than another from having a greater share of resources, and so bearing the cost of signalling to direct the parent's provisioning strategy is an unfavorable strategy. If the high-quality offspring advantage is sufficiently high, then the low-quality offspring will benefit more from even a small amount of resources, and so the facultative outcome will not be stable.

3.4 Discussion

We have demonstrated using evolutionary game t heory that environmental variation can influence signalling behaviour and, in particular, is sufficient to promote signals to demonstrate need in good environmental conditions and quality in poor conditions, a conclusion recently suggested by empirical data [2, 13]. Ultimately, this shift may occur only if two basic conditions are met. First, low-quality offspring must stand to benefit much more substantially from high degrees of parental investment, while high-quality offspring can benefit more when potential parental investment is limited by poor environmental conditions. Whether this condition is satisfied depends on the quality and the quality differences between offspring, and the way quality changes as a function of parental investment. The second basic condition that must be satisfied is that only one offspring begs and is preferentially fed. Whether this condition is satisfied may be influenced by the relatedness between offspring and the inherent costs of signalling.

Our work outlines some of the specific social and ecological factors that can influence how variable environments need to be for the shift between SoN and SoQ to occur. Many of these results provide testable predictions. Our results suggest there is a greater range of environmental conditions that favor the stability of the facultative outcome for species with moderate relatedness between siblings (e.g. full siblings) when the cost of signalling is low compared to low relatedness (e.g. half-siblings or less) when the cost of signalling is relatively high. If both relatedness between offspring and costs of signalling are high, it is expected that the shift between SoN and SoQ would occur only in very volatile environments, whereas when signalling costs are low and relatedness is high, this shift should be readily found in more stable environments. Given that only moderate differences between offspring quality, a, allowed for the stability of the facultative outcome, we expect to see a connection between the synchronicity of offspring hatching and whether a species shifts between SoN and SoQ depending on environmental conditions. Our results also suggest that the shift between SoN in high-quality

environments to SoQ in low-quality environments will occur only in species that depend heavily upon parents at birth (i.e. baseline fitness d small). Future empirical work should examine the degree to which young are self-sufficient soon after hatching and the probability with which environmental instability facilitates the shift between SoN and SoQ.

Many species may be able to use physical proxies (cues), such as body size, to evaluate offspring quality. Compared to simply responding to signals, investigating cues may require more energy and time, thereby making it a less efficient option. We created an extension of our model (see Appendix 3.5.2) in which the parent has the option of investigating cues. The extension demonstrates that environmental variation can still encourage SoN to be used in poor environments and SoQ to be used in favorable environments. Qualitatively, the results of the extended model are very similar to the base model, though greater efficiency associated with using cues results in increases in the minimum baseline fitness, difference in offspring quality, and relatedness between siblings, as well as a decrease in the maximum cost of signalling, necessary for the stability of the facultative outcome. For the facultative outcome to be stable, investigating cues must be more costly than feeding according to signals or at random, otherwise the parent will always use cues as they are more reliable than signals (see Appendix 3.5.4).

SoN vs. SoQ

Paramount to influencing whether a species uses signals to display need versus quality is the relationship between resources and the offspring's fitness levels. As shown by the relationship between the region of stability of the facultative outcome and the high-quality offspring advantage and baseline fitness, even translations of the same fitness function can dictate the nature of signalling systems. This importance of the nature of fitness functions has been largely neglected by previous research. Indeed, the very fact that both SoN and SoQ may be required to explain the begging behaviours of certain species, yet theoretical work almost exclusively

validates or assumes SoN [6], encourages a review of previous signalling theory.

Much of the recent theoretical literature, which frequently uses Godfray's seminal paper [3] as a basis for more elaborate models [29, 30, 31, 32], is constructed around the notion that offspring use begging to signal their need to their parents. It is therefore prudent to revisit the construction and implications of Godfray's (1991) model [3]. First, it should be made clear that Godfray's model does not provide evidence for SoN. Instead, Godfray builds the model under the assumption that SoN is true: he defines an offspring's need as the marginal fitness gain it experiences by obtaining more resources, and assumes that parents will provide more resources to young in "poor condition" – condition, here, being synonymous with reproductive value [3, 6]. He then explicitly states that offspring fitness increases monotonically with respect to greater resources, and, crucially, assumes that this increase occurs at a decelerating rate. While the former assumption is altogether reasonable, no justification is provided for the latter assumption, even though fitness functions are often modeled as being sigmoidal [27, 28]. The fitness function used by Godfray is then repeated in several extensions of his model [30, 33, 31]. The selection of specific functions which properly represent neither the diversity nor complexity of begging behaviours observed in nature has resulted in SoQ largely being neglected by previous theoretical models.

Previous research on SoN and SoQ have also been impeded by the definitions of need and quality. SoQ, as defined tacitly by Godfray [3] and explicitly elsewhere [6], effectively claims the opposite of SoN – offspring in "poor condition" will beg less and be allocated fewer resources. The largest problem with this definition is rooted in semantics, since "quality" can hold many different meanings. Most signalling theory regards quality as being the opposite of need and the same as condition and reproductive value: the greater the need of the offspring, the lower its quality, reproductive value, and condition. However, with biologically reasonable fitness functions (like the sigmoidal relationship between offspring resources and fitness used

in this study), need as defined by the marginal change in the offspring's fitness with increased investment may no longer be the opposite of quality. An offspring can reasonably have higher fitness than its siblings while also standing to gain more from additional parental investment. One may even argue that quality and need are equivalent because, from the perspective of the parent, a quality investment into an offspring should naturally mean an investment into offspring that have most to benefit most from further investment. Definitions of need and quality become even less intuitive if offspring have entirely different fitness functions, as quality could refer to the potential reproductive value that an offspring possesses given unlimited provisioning. A limitation of our work is that we use a single offspring fitness function. While this setup is sufficient to investigate the role of environmental variation in the shift between SoN and SoQ, our model lacks the predictive power that fitness functions that are modeled closely after empirical data could generate.

Our work supports Mock's [6, 13] theory that parents are not restricted to using signals to convey only need or only quality. However, rather than parents simply being able to switch between SoN and SoQ, it may be that signals (or lack thereof) evolved to roughly indicate where along the fitness curve an offspring's condition currently resides, whereas cues (such as weight) indicate to the parent the general shape of the offspring's fitness curve. That is, as suggested by Mock [6], the distinction between SoN and SoQ may be more artificial and certainly less useful than previously suggested.

In our model, the cost of signalling is set to a constant which is then subtracted from the offspring's fitness. In this way, we assume that if there are any costs associated with signalling (i.e. $c > 0$), they are metabolic in nature and are not shared. However, signals can also draw predators to the nest [34, 35], and the cost of signalling is shared among its inhabitants. In this situation, the parent may be more encouraged to provide greater care for signallers to stop their signals. This situation is outlined by the blackmail hypothesis, for which there is some

empirical support [24], though it has been discussed mostly via verbal arguments [36, 37] and has not been explored particularly rigorously. One crucial exception is Johnstone [38], though his model does not consider increased predation as a cost of signalling, includes only one offspring (therefore disallowing offspring to compete via signals), and does not consider the influence of environmental variation. An alternative response to blackmail that lacks discussion since previous theory has often operated under the assumption that parents attempt to raise all offspring [6, 2] is the option for the parent to abandon the entire brood or even terminate and encourage the termination (i.e. via siblicide) of signallers. The relationship between the blackmail hypothesis and the signal SoN verses SoQ debate has remained unexplored. It is possible that begging does not necessarily signify need or quality in any scenario, but instead is simply used as a tool to skew the parent-offspring conflict over provisioning closer to the offspring's optimal outcome.

3.5 Appendix

3.5.1 Stability analysis of the divisible resource model

We begin by finding the optimal parental allocation strategy in any given situation. Suppose $g > 0$ is the total resource available to the parent and x is the amount given to the higher-quality offspring. To continue, we must assume the form of the high- and low-quality offspring's fitness functions which, as provided in the main text, are $f_h(x) = \frac{1}{1+e^{-(d+a+g)}}$ and $f_l(g-x) = \frac{1}{1+e^{-(d+g-x)}}$, respectively. When one offspring begs so that the parent is able to determine the need and quality of each offspring, and assuming the parent is equally related to the two offspring, the parent will distribute resources in a manner maximizes the combined total fitness of the two offspring,

$$f = \frac{1}{1+e^{-(d+a+x)}} + \frac{1}{1+e^{-(d+g-x)}}.$$

Solving $\frac{df}{dx} = 0$, we find $x^* = \frac{g}{2} - \frac{a}{2}$, the optimal amount to be given to the lower-quality offspring (SoN), such that the low- and high-quality offspring are equally fit. However, this maximum is only valid when $g \geq a$. Suppose instead that $0 < g < a$. Since no critical points lie on the interval $[0, g]$, the optimal strategy is either $x^* = 0$ or $x^* = g$. We therefore need to determine whether $\frac{df}{dx}$ is increasing or decreasing on the interval $[0, g]$. The function is decreasing, and therefore f is maximal at $x^* = g$ (SoQ), if $-(a+d) > g$, and since we know $a > g$, this condition is equivalent to $d < -2g$. Similarly, if $d \geq -2g$, f is maximal at $x^* = 0$ (SoN).

Now suppose that neither or both offspring beg, such that the parent is unable to differentiate the need and quality of the offspring. Then the parent must effectively guess which offspring she should receive resource amount x, with the remainder, $g - x$, going to the other offspring; it is assumed she suceeds at doing so only half the time. That is, the parent will distribute the

resources in a manner that maximizes

$$f = \frac{1}{2}\left(\frac{1}{1+e^{-(d+a+x)}} + \frac{1}{1+e^{-(d+g-x)}} + \frac{1}{1+e^{-(d+a+g-x)}} + \frac{1}{1+e^{-(d+g+x)}}\right)$$

Solving again for x^*, it follows that the parent will distribute the resources evenly between the two offspring whenever both or neither offspring signal.

Knowing how the parent will distribute resources in any given situation, we can next deter-

mine the payoff of each outcome for each player

$$
\begin{aligned}
O_{h,1} &= f_h(\frac{g}{2}) - c + r(f_l(\frac{g}{2}) - c) \\
O_{l,1} &= f_l(\frac{g}{2}) - c + r(f_g(\frac{g}{2}) - c) \\
O_{h,2} &= \begin{cases} f_h(g) - c + r f_l(0), & \text{if } 0 < g < a, d < -2g \\ f_h(0) - c + r f_l(g), & \text{if } 0 < g < a, d \geq -2g \\ f_h(\frac{g-a}{2}) - c + r f_l(\frac{g+a}{2}), & \text{if } g \geq a \end{cases} \\
O_{l,2} &= \begin{cases} f_l(0) + r(f_h(g) - c), & \text{if } 0 < g < a, d < -2g \\ f_l(g) + r(f_h(0) - c), & \text{if } 0 < g < a, d \geq -2g \\ f_l(\frac{g+a}{2}) + r(f_h(\frac{g-a}{2}) - c), & \text{if } g \geq a \end{cases} \\
O_{h,3} &= \begin{cases} f_h(g) + r(f_l(0) - c), & \text{if } 0 < g < a, d < -2g \\ f_h(0) + r(f_l(g) - c), & \text{if } 0 < g < a, d \geq -2g \\ f_h(\frac{g-a}{2}) + r(f_l(\frac{g+a}{2}) - c), & \text{if } g \geq a \end{cases} \\
O_{l,3} &= \begin{cases} f_l(g) - c + r f_h(0), & \text{if } 0 < g < a, d < -2g \\ f_l(0) - c + r f_h(g), & \text{if } 0 < g < a, d \geq -2g \\ f_l(\frac{g+a}{2}) - c + r f_h(\frac{g-a}{2}), & \text{if } g \geq a \end{cases} \\
O_{h,4} &= f_h(\frac{g}{2}) + r f_l(\frac{g}{2}) \\
O_{l,4} &= f_l(\frac{g}{2}) + r f_h(\frac{g}{2}).
\end{aligned}
$$

The above payoffs are for outcomes 1-4, with $g = g_h$, though outcomes 5-8 follow the same structure with $g = g_l$. Next, we calculate the stability conditions for the facultative outcome. Our first condition, D1, is that low-quality offspring in good environments will prefer to signal when the high-quality offspring remains silent,

$$D1 : O_{l,3} > O_{l,4}.$$

Next, the high-quality offspring in good environments prefers to remain silent, given that the low-quality offspring will beg,

$$D2 : O_{h,2} > \begin{cases} O_{h,3}, & \text{if } O_{l,3} \geq O_{l,4} \\ O_{h,4}, & \text{if } O_{l,4} > O_{l,3}. \end{cases}$$

Conversely, in poor environments, the low-quality offspring must prefer to remain silent given that the high-quality offspring begs

$$D1 : O_{l,6} > O_{l,5}.$$

Lastly, the high-quality offspring in poor environments must prefer to beg, given that the low-quality offspring will not,

$$D2 : O_{h,6} > \begin{cases} O_{h,7}, & \text{if } O_{l,7} \geq O_{l,8} \\ O_{h,8}, & \text{if } O_{l,8} > O_{l,7}. \end{cases}$$

3.5.2 Stability analysis of the divisible resource model with cues

Suppose that instead of responding optimally in the absence of useful information (i.e. when both or neither offspring signal) the parent is able to use cues to investigate the need and quality of the two offspring. Using cues may be inefficient, as the parent may have to spend a considerable amount of time and energy examining the offspring. To reflect this inefficiency, it is assumed that instead of having quantity g resources to distribute between the two offspring, the parent is only able to gather $g(1 - b)$ if the parent uses cues, where $b \geq 0$. The payoffs the

same as without cues, except for the following

$$O_{h,1} = \begin{cases} f_h(g(1-b)) - c + r(f_l(0) - c), & \text{if } 0 < g < a, d < -2g, f_h(g(1-b)) + f_l(0) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{g}{2}) - c + r(f_l(\frac{g}{2}) - c), & \text{if } 0 < g < a, d < -2g, f_h(g(1-b)) + f_l(0) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(0) - c + r(f_l(g(1-b)) - c), & \text{if } 0 < g < a, d \geq -2g, f_h(0) + f_l(g(1-b)) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{g}{2}) - c + r(f_l(\frac{g}{2}) - c), & \text{if } 0 < g < a, d \geq -2g, f_h(0) + f_l(g(1-b)) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{(1-b)(g-a)}{2}) - c + r(f_l(\frac{(1-b)(g+a)}{2}) - c), & \text{if } g \geq a, f_h(\frac{(1-b)(g-a)}{2}) + f_l(\frac{(1-b)(g+a)}{2}) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{g}{2}) - c + r(f_l(\frac{g}{2}) - c), & \text{if } g \geq a, f_h(\frac{(1-b)(g-a)}{2}) + f_l(\frac{(1-b)(g+a)}{2}) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \end{cases}$$

$$O_{l,1} = \begin{cases} r(f_h(g(1-b)) - c) + f_l(0) - c, & \text{if } 0 < g < a, d < -2g, f_h(g(1-b)) + f_l(0) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ r(f_h(\frac{g}{2}) - c) + f_l(\frac{g}{2}) - c, & \text{if } 0 < g < a, d < -2g, f_h(g(1-b)) + f_l(0) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ r(f_h(0) - c) + f_l(g(1-b)) - c, & \text{if } 0 < g < a, d \geq -2g, f_h(0) + f_l(g(1-b)) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ r(f_h(\frac{g}{2}) - c) + f_l(\frac{g}{2}) - c, & \text{if } 0 < g < a, d \geq -2g, f_h(0) + f_l(g(1-b)) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ r(f_h(\frac{(1-b)(g-a)}{2}) - c) + f_l(\frac{(1-b)(g+a)}{2}) - c, & \text{if } g \geq a, f_h(\frac{(1-b)(g-a)}{2}) + f_l(\frac{(1-b)(g+a)}{2}) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ r(f_h(\frac{g}{2}) - c) + f_l(\frac{g}{2}) - c, & \text{if } g \geq a, f_h(\frac{(1-b)(g-a)}{2}) + f_l(\frac{(1-b)(g+a)}{2}) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \end{cases}$$

$$O_{h,4} = \begin{cases} f_h(g(1-b)) + rf_l(0), & \text{if } 0 < g < a, d < -2g, f_h(g(1-b)) + f_l(0) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{g}{2}) + rf_l(\frac{g}{2}), & \text{if } 0 < g < a, d < -2g, f_h(g(1-b)) + f_l(0) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(0) + rf_l(g(1-b)), & \text{if } 0 < g < a, d \geq -2g, f_h(0) + f_l(g(1-b)) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{g}{2}) + rf_l(\frac{g}{2}), & \text{if } 0 < g < a, d \geq -2g, f_h(0) + f_l(g(1-b)) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{(1-b)(g-a)}{2}) + rf_l(\frac{(1-b)(g+a)}{2}), & \text{if } g \geq a, f_h(\frac{(1-b)(g-a)}{2}) + f_l(\frac{(1-b)(g+a)}{2}) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{g}{2}) + rf_l(\frac{g}{2}), & \text{if } g \geq a, f_h(\frac{(1-b)(g-a)}{2}) + f_l(\frac{(1-b)(g+a)}{2}) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \end{cases}$$

$$O_{l,4} = \begin{cases} rf_h(g(1-b)) + f_l(0), & \text{if } 0 < g < a, d < -2g, f_h(g(1-b)) + f_l(0) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ rf_h(\frac{g}{2}) + f_l(\frac{g}{2}), & \text{if } 0 < g < a, d < -2g, f_h(g(1-b)) + f_l(0) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ rf_h(0) + f_l(g(1-b)), & \text{if } 0 < g < a, d \geq -2g, f_h(0) + f_l(g(1-b)) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{g}{2}) + f_l(\frac{g}{2}), & \text{if } 0 < g < a, d \geq -2g, f_h(0) + f_l(g(1-b)) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{(1-b)(g-a)}{2}) + f_l(\frac{(1-b)(g+a)}{2}), & \text{if } g \geq a, f_h(\frac{(1-b)(g-a)}{2}) + f_l(\frac{(1-b)(g+a)}{2}) > f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \\ f_h(\frac{g}{2}) + f_l(\frac{g}{2}), & \text{if } g \geq a, f_h(\frac{(1-b)(g-a)}{2}) + f_l(\frac{(1-b)(g+a)}{2}) \leq f_h(\frac{g}{2}) + f_l(\frac{g}{2}) \end{cases}$$

3.5.3 Stability analysis of the indivisible resource model

To examine when the facultative outcome above is a Nash equilibrium, we first need to determine the payoffs of each strategy for each player. The payoffs for the parent in good environments are given by

$$
\begin{aligned}
O_{p,1} &= \frac{1}{2}R(f_h(g_h) + f_h(0) + f_l(g_h) + f_l(0) - 4c) \\
O_{p,2} &= R(f_h(g_h) + f_l(0) - c) \\
O_{p,3} &= R(f_h(0) + f_l(g_h) - c) \\
O_{p,4} &= R(f_l(g_h) + f_h(0) - c) \\
O_{p,5} &= R(f_h(g_h) + f_l(0) - c) \\
O_{p,6} &= \frac{1}{2}R(f_h(g_h) + f_h(0) + f_l(g_h) + f_l(0)).
\end{aligned}
$$

The payoffs for the parent in poor environmental conditions, $O_{p,7-12}$, can be found by substituting g_h for g_l in the equations above. The payoffs for the low-quality offspring are given by

$$
\begin{aligned}
O_{l,1} &= \frac{1}{2}(r(f_h(g_h) + f_h(0) - 2c) + f_l(g_h) + f_l(0) - 2c) \\
O_{l,2} &= r(f_h(g_h) - c) + f_l(0) \\
O_{l,3} &= r(f_h(0) - c) + f_l(g_h) \\
O_{l,4} &= f_l(g_h) - c + rf_h(0) \\
O_{l,5} &= rf_h(g_h)) + f_l(0) - c \\
O_{l,6} &= \frac{1}{2}((r(f_h(g_h) + f_h(0)) + f_l(g_h) + f_l(0))).
\end{aligned}
$$

The payoffs for the low-quality offspring in poor environmental conditions, $O_{l,7-12}$, can be found by substituting g_h for g_l in the equations above. Lastly, the payoffs for the high-quality

offspring are given by

$$
\begin{aligned}
O_{h,1} &= \frac{1}{2}(f_h(g_h) + f_h(0) - 2c + r(f_l(g_h) + f_l(0) - 2c)) \\
O_{h,2} &= f_h(g_h) - c + r f_l(0) \\
O_{h,3} &= f_h(0) - c + r(f_l(g_h)) \\
O_{h,4} &= r(f_l(g_h) - c) + f_h(0) \\
O_{h,5} &= f_h(g_h) + r(f_l(0) - c) \\
O_{h,6} &= \frac{1}{2} f_h(g_h) + f_h(0) + r(f_l(g_h) + f_l(0)).
\end{aligned}
$$

The payoffs for the high-quality offspring in poor environmental conditions, $O_{l,7-12}$, can be found by substituting g_h for g_l in the equations above.

Next, we calculate the stability conditions for the facultative outcome. Our first condition, D1, is that the parent prefers to feed the low-quality offspring when environmental conditions are favourable and the high-quality offspring when environmental conditions are poor; that is,

$$D1 : O_{p,4} \geq O_{p_5}, O_{p,8} \geq O_{p,9}.$$

The low-quality offspring in favourable environmental conditions prefers to signal given that the high-quality offspring does not; this condition can be separated into three cases

$$D2 : O_{l,4} \geq O_{l,6}.$$

Similarly, the high-quality offspring in favourable environmental conditions prefers not to signal

$$D3 : O_{h,4} \geq O_{h,1}.$$

Conversely, in low-quality environments the low-quality offspring does not signal

$$D4 : O_{l,8} \geq O_{l,7}.$$

Lastly, the high-quality offspring signals in poor environments

$$D5 : O_{h,8} > O_{h,12}.$$

3.5.4 Results

Results are presented in terms of how relatedness, signalling costs, baseline fitness, and differences in offspring quality influence the range of environmental conditions that would lead to a transition between SoN and SoQ.

Relatedness between offspring

Moderate levels of relatedness between offspring facilitate the stability of the transition outcome. When resources are scarce even in good environments (low g_h), one offspring will not benefit from the modest increase in resources significantly more than the other; consequently, in these environments, high relatedness between offspring encourages neither offspring to signal so that neither bears the cost of signalling (assuming there is a cost), thus leading the parent to feed randomly. If relatedness between offspring is low, there is less incentive for the offspring to work together using signals to direct the parent to feed the offspring that would receive the greatest fitness benefits. Instead, both offspring will signal and the parent is more likely to feed randomly, especially if the direct fitness benefit of one offspring is not significantly greater than the other.

As relatedness between offspring increases, so too does the degree of environmental variability which can sustain the stability of the transition outcome (that is, higher r allows for a

larger ratio between maximum g_h and maximum g_l).

Cost of signalling

Moderate signal costs facilitate the stability of the transition outcome. If the cost of signalling is too low, both offspring will signal. The exception is when relatedness is sufficiently high and one offspring will benefit significantly more from additional resources than the other. The transition between SoN and SoQ is possible even when there is no signalling cost (i.e. $c = 0$), provided relatedness between offspring is sufficiently high, and the low-quality (resp. high-quality) offspring benefits substantially more from provisioning in good (resp. poor) environments than its sibling. Very high signalling costs can outweigh the direct benefits of receiving the additional resources, and so neither offspring beg unless relatedness is high and one offspring benefits significantly more than the other; in this case, begging will ensure the parent feeds the offspring that benefits most.

Baseline fitness

Given moderate baseline fitness levels, conditions for the stability of the transition outcome can be met.

When offspring baseline fitness is low, as is the case for altricial species, the high-quality offspring will prefer to signal and have the parent feed randomly in good environments if g_h is too high. This is because, while the low-quality offspring would benefit more from the additional resources, the additional resources available would significantly benefit the high-quality offspring as well, and so it too signals. If g_h is too low, the parent will prefer to feed the non-signalling high-quality offspring rather than the low-quality offspring. This occurs because the high-quality offspring would benefit more than the low-quality offspring, so the parent ignores the beggar and feeds the high-quality offspring.

As the baseline fitness, d, increases, the maximum g_l in the region of stability decreases. If g_l is sufficiently large, the parent will not prefer to feed the higher-quality offspring should it be the only offspring to signal, and will instead feed the lower-quality offspring. Given sufficiently high d, which would be characteristic of precocial species, the low-quality offspring will always signal since it prefers that the parent feeds randomly rather than feed the higher-quality offspring, or the cost of signalling becomes so large relative to the potential benefits of additional resources that it is not worth it for either offspring to signal.

High-quality offspring advantage

Mathematically, both baseline fitness and high-quality offspring advantage, a, influence the offspring's' conditions relative to the inflection point – where the marginal fitness benefits of increased provisioning are greatest – of the sigmoidal curve. Consequently, similar to the relationship between the stability of the transition outcome and offspring baseline fitness, the transition outcome is stable only when the high-quality offspring has a moderate advantage over its sibling.

If the advantage is sufficiently small, the inclusive fitness benefit from the high-quality offspring's perspective of allowing its sibling to be fed in favourable environments does not outweigh the direct fitness advantage of being fed, even if the parent feeds randomly. Consequently, the facultative outcome is never stable since the high-quality offspring will always signal (D3 not satisfied). As the relative advantage of the high-quality offspring increases, the minimum g_h in the region of stability decreases. If the amount of resources in good environments, g_h, is sufficiently low, the parent may prefer to feed the high-quality offspring rather than the low-quality offspring (D1 not satisfied), since the fitness function of both offspring will be sufficiently far away from the domain of diminishing returns (Figure 3.5.1), and so the high-quality offspring will experience greater fitness gains for smaller levels of investment.

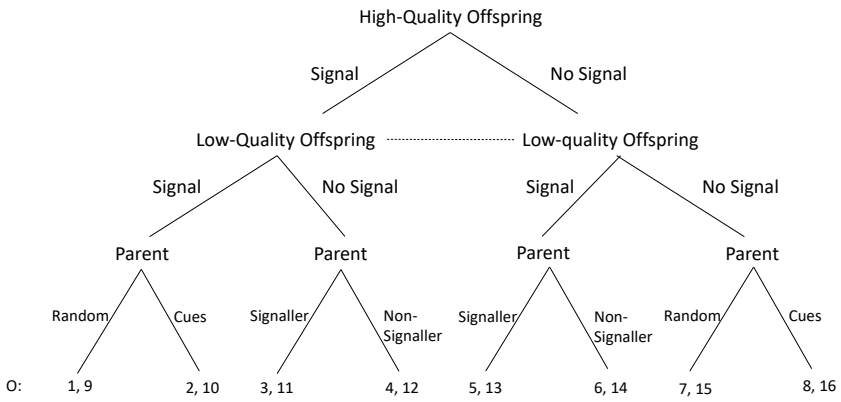

Figure 3.5.1: Offspring fitness represented by a sigmoidal (solid black line). The dashed blue lines that intersect the fitness function at t=-5, t=0, and t=5 represent the instantaneous rate of change, or marginal fitness benefits, for offspring in those three states. Note that when the offspring state is very poor, small amounts of investments do little to increase offspring fitness. Also, if the state of the offspring is $t > 0$ – the inflection point – there are diminishing returns on investment: the per-unit benefit of resource investment decreases as the offspring's state gets better.

As the advantage becomes greater, lower amounts of resources are required to push the fitness function of the high-quality offspring into the domain of diminishing returns, thereby decreasing the minimum g_h. When a increases, maximum g_h in the region of stability increases. If g_h is sufficiently large, the high-quality offspring begins to prefer that the parent feeds randomly rather than allow the low-quality offspring to signal, and thus signals (D3 not satisfied). This is because, with large g_h, the direct benefit of receiving resources, even if randomly, outweighs the inclusive fitness benefit of its low-quality sibling getting the resource, even though the resource will increase its sibling's direct fitness more than it would its own. As the advantage of high-quality offspring increases, the offspring's fitness reaches the point of diminishing returns for lower levels of investment, and as such higher levels of g_h are required for the direct fitness benefit of being fed randomly to outweigh the indirect fitness benefit of letting the low-quality offspring be fed more.

As a increases, the maximum g_l in the region of stability decreases. If g_l is sufficiently large, the low-quality offspring will signal, as it will prefer the parent to feed randomly rather than feed the high-quality offspring (D4 not satisfied). Since g_l is so large, the direct fitness benefit of being fed randomly outweighs the inclusive fitness benefit of allowing its sibling to be fed, even if the sibling would benefit more from being fed. As the fitness advantage of the high-quality offspring increases (a increases), the high-quality offspring's fitness function will be closer to the domain of diminishing returns for smaller g_l; as such, the higher-quality offspring benefits less per unit of resource, and so the low-quality offspring will signal for smaller g_l levels.

When the fitness advantage of the high-quality offspring is small, there is little difference between the marginal benefits of feeding the high-quality offspring versus the low-quality offspring for most values of g_l; the cost of signalling can easily outweigh these marginal benefits. As a increases, the fitness function of the high-quality offspring is in the domain of diminishing

returns even for very small amounts of resource investment, and so the fitness benefit of feeding one offspring over the other begins to shrink once again, and the parent is better off feeding randomly. This causes the maximum g_l in the region of stability to decrease as a increases.

3.5.5 Model with cues

Suppose parents are able to use physical proxies (cues) to evaluate offspring quality. A simple and realistic assumption is that it is more efficient for parents to use signals to guide their provisioning than it is to use physical cues (i) [14]: if the parent uses offspring signals rather than investigate cues, they have more energy or time to find more resources, and so the amount of indivisible resource obtained is increased by some factor, $b > 0$, for a total of $(1 + b)g_h$ in high-quality conditions and $(1 + b)g_l$ in low-quality conditions. If the parent uses neither signals nor cues to decide resource allocation, it is assumed to feed an offspring at random. As this is another scenario in which the parent does not expend energy investigating cues, all resources obtained are multiplied by a factor of $1 + b$ if the parent feeds randomly. If the parent uses neither signals nor cues to decide resource allocation, it is assumed to feed an offspring at random. As this is another scenario in which the parent does not expend energy investigating cues, all resources obtained are multiplied by a factor of $1 + b$ if the parent feeds randomly.
If both offspring signal, the parent can choose to either feed an offspring at random or investigate cues to decide which to feed. If only the high-quality offspring signals, the parent can choose to either feed it or feed the non-signalling low-quality offspring. Similarly, if only the low-quality offspring signals, the parent can choose to feed it or feed the non-signalling high-quality offspring. Finally, if neither offspring signals, the parent once again decides between feeding one offspring at random or investigating cues.

There are 16 possible outcomes for the scenario described (see Figure 3.5.2). To examine when the facultative outcome above is a Nash equilibrium, we first need to determine the payoffs of each strategy for each player. The payoffs for the parent in good environments are

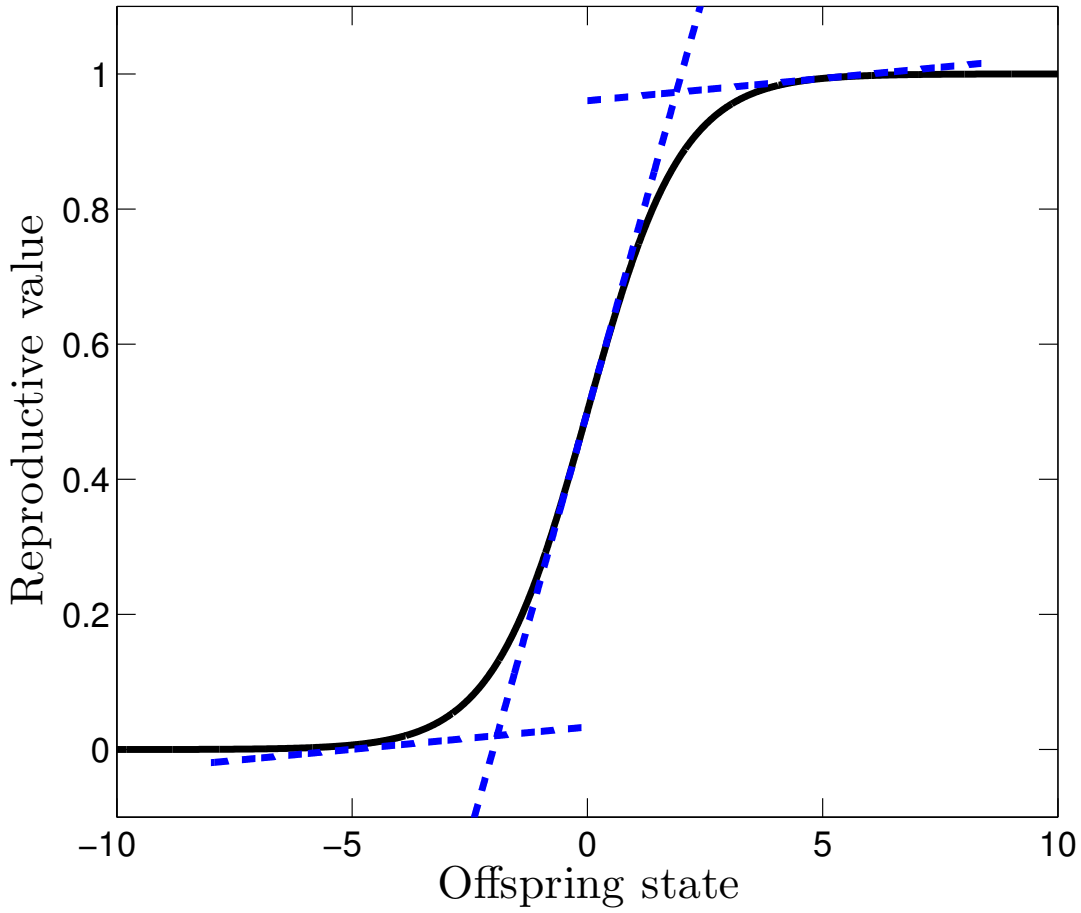

Figure 3.5.2: Decision tree representation of the game outlined in the main text. A separate and independent game is played in good- and poor-quality environments, although the general structure of the decision tree is the same for each environment. Note that the high-quality and low-quality offspring act simultaneously and independently. Each pair of numbers refers to the outcome name assigned to the good-quality environments and poor-quality environments respectively.

given by

$$O_{p,1} = \frac{1}{2}R(f_h(g_h(1+b)) + f_h(0) + f_l(g_h(1+b)) + f_l(0) - 4c)$$

$$O_{p,2} = R\max(f_h(g_h) + f_l(0) - 2c, f_l(g_h) + f_h(0) - 2c))$$

$$O_{p,3} = R(f_h(g_h(1+b)) + f_l(0) - c)$$

$$O_{p,4} = R(f_h(0) + f_l(g_h(1+b)) - c)$$

$$O_{p,5} = R(f_l((1+b)g_h) + f_h(0) - c)$$

$$O_{p,6} = R(f_h((1+b)g_h) + f_l(0) - c)$$

$$O_{p,7} = \frac{1}{2}R(f_h(g_h(1+b)) + f_h(0) + f_l(g_h(1+b)) + f_l(0))$$

$$O_{p,8} = R\max(f_h(g_h) + f_l(0), f_l(g_h) + f_h(0))).$$

The payoffs for the parent in poor environmental conditions, $O_{p,9-16}$, can be found by substituting g_h for g_l in the equations above. The payoffs for the low-quality offspring are given

by

$$O_{l,1} = \frac{1}{2}(r(f_h(g_h(1+b)) + f_h(0) - 2c) + f_l(g_h(1+b)) + f_l(0) - 2c)$$

$$O_{l,2} = \begin{cases} \text{if } f_h(g_h) + f_l(0) > f_h(0) + f_l(g_h), & r(f_h(g_h) - c) + f_l(0) - c \\ \text{if } f_h(0) + f_l(g_h) > f_h(0) + f_l(g_h), & r(f_h(0) - c) + f_l(g_h) - c \end{cases}$$

$$O_{l,3} = r(f_h(g_h(1+b)) - c) + f_l(0)$$

$$O_{l,4} = r(f_h(0) - c) + f_l(g_h(1+b))$$

$$O_{l,5} = f_l((1+b)g_h) - c + rf_h(0)$$

$$O_{l,6} = rf_h((1+b)g_h)) + f_l(0) - c$$

$$O_{l,7} = \frac{1}{2}((r(f_h(g_h(1+b)) + f_h(0)) + f_l(g_h(1+b)) + f_l(0)))$$

$$O_{l,8} = \begin{cases} \text{if } f_h(g_h) + f_l(0) > f_h(0) + f_l(g_h), & rf_h(g_h) + f_l(0) \\ \text{if } f_h(0) + f_l(g_h) > f_h(0) + f_l(g_h), & rf_h(0) + f_l(g_h). \end{cases}$$

The payoffs for the low-quality offspring in poor environmental conditions, $O_{l,9-16}$, can be found by substituting g_h for g_l in the equations above. Lastly, the payoffs for the high-quality

offspring are given by

$$O_{h,1} = \frac{1}{2}(f_h(g_h(1+b)) + f_h(0) - 2c + r(f_l(g_h(1+b)) + f_l(0) - 2c))$$

$$O_{h,2} = \begin{cases} \text{if } f_h(g_h) + f_l(0) > f_h(0) + f_l(g_h), & f_h(g_h) - c + r(f_l(0) - c) \\ \text{if } f_h(0) + f_l(g_h) > f_h(0) + f_l(g_h), & f_h(0) - c + r(f_l(g_h) - c) \end{cases}$$

$$O_{h,3} = f_h(g_h(1+b)) - c + rf_l(0)$$

$$O_{h,4} = f_h(0) - c + r(f_l(g_h(1+b)))$$

$$O_{h,5} = r(f_l((1+b)g_h) - c) + f_h(0)$$

$$O_{h,6} = f_h((1+b)g_h) + r(f_l(0) - c)$$

$$O_{h,7} = \frac{1}{2}f_h(g_h(1+b)) + f_h(0) + r(f_l(g_h(1+b)) + f_l(0))$$

$$O_{h,8} = \begin{cases} \text{if } f_h(g_h) + f_l(0) > f_h(0) + f_l(g_h), & f_h(g_h) + rf_l(0) \\ \text{if } f_h(0) + f_l(g_h) > f_h(0) + f_l(g_h), & f_h(0) + rf_l(g_h). \end{cases}$$

The payoffs for the high-quality offspring in poor environmental conditions, $O_{l,9-16}$, can be found by substituting g_h for g_l in the equations above. The remainder of the procedure to find the conditions under which the facultative outcome is stable is the same as the procedure used in the base model.

Relatedness

For sufficiently low values of relatedness, the minimum amount of resources in good environments, g_h, necessary for the stability of the facultative outcome is high (Figure 3.5.3). When siblings are mostly unrelated in good environments, there is little incentive for the high-quality offspring to remain silent it does not receive significant inclusive fitness benefits by allowing the low-quality offspring to be fed, even if the direct fitness of the low-quality offspring will benefit significantly more from receiving the resource (D3 not satisfied). But as relatedness increases, eventually the inclusive fitness benefits of allowing its low-quality offspring to be fed will outweigh the potential direct fitness benefits of being fed, and so the high-quality offspring

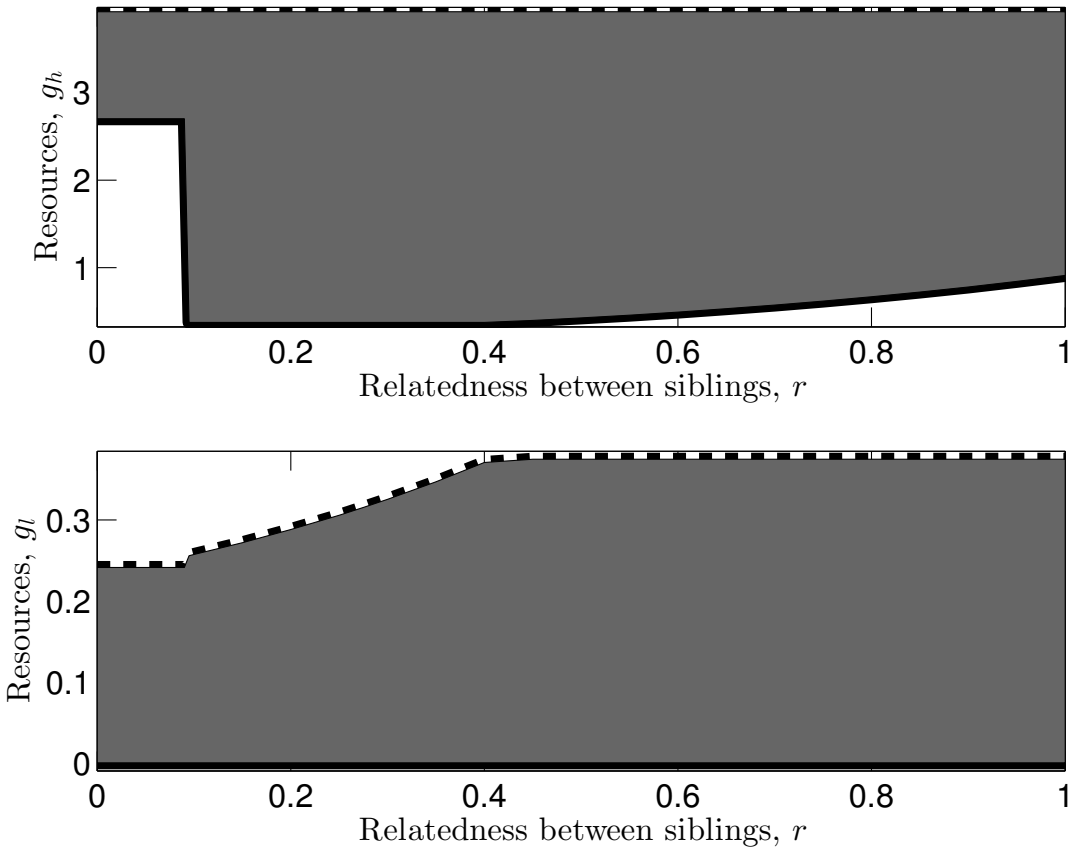

Figure 3.5.3: Relatedness between offspring and its effect on the amount of resources required for the facultative outcome to be stable in good environments (top panel) and in poor environments (bottom panel). The region between the maximum amount of resources (blue lines) and the minimum amount of resources (red lines) constitute the amount of resources necessary for the stability of the facultative outcome. Results were generated using $d = 1$, $c = \min(0.05, \frac{1}{1+e^{-t}})$, $a = 1.25$, $r = 0.5$, and $b = 1$.

will not beg. The result is a bifurcation at some threshold, the minimum g_h in the region of stability instantaneously and significantly lowers. As relatedness between siblings continues to increase, the minimum g_h of the region of stability increases: the low-quality offspring no longer prefers to signal since it benefits more from the parent feeding randomly – the marginal direct fitness benefits it obtains from being fed consistently rather than randomly does not outweigh the cost of signalling if the resource quantity is low, and this is especially true when the siblings are more closely related (D2 not satisfied).

The minimum g_l in the region of stability is very low regardless of relatedness assuming

the high-quality offspring will benefit significantly more from small amounts of additional provisioning, which occurs as long as its advantage over its sibling is not very large; the cost of signalling together with the fact that the parent can use cues to conclude that the high-quality offspring should be fed prohibits the low-quality offspring from signalling this is true regardless of the relatedness between siblings. As relatedness increases, the maximum g_l defining the region of stability increases as well, since this increases the inclusive fitness benefit of the low-quality offspring remaining silent so that the high-quality offspring will remain fed. However, this increase eventually stalls as at sufficiently high g_l values it is in the best interest of the parent to feed the lower-quality offspring, assuming they are related, because high levels of resources cause the fitness of high-quality offspring to enter the domain of diminishing returns, and thus high levels of resources benefit low-quality offspring more (D1 not satisfied).

Efficiency benefit of the signalling system

If the efficiency benefit of signalling, b, is too small, the facultative outcome will not be stable under any condition (Figure 3.5.4). In good quality environments, the high-quality offspring must remain silent, but if there is no efficiency benefit, it makes better sense for both offspring to remain silent so as to not suffer the cost of signalling (D2 not satisfied). The parent then uses cues to determine that it is better for the low-quality offspring to be fed. As the efficiency benefit increases, the minimum g_h decreases and maximum g_h increases in the region of stability, since there is a greater inclusive fitness benefit for the good-quality offspring to allow only the poor-quality offspring to beg and be fed. In contrast, as b increases, the maximum g_l defining the region of stability decreases: even small amounts of resources can benefit the low-quality offspring. This is because large efficiency benefits ensure that even small amounts of resources, g_l, make the high-quality offspring reach the domain of diminishing returns. Consequently, it is much better for the parent to allocate toward the low-quality offspring, thus incentivizing the parent to feed the low-quality offspring even though the high-quality offspring is the one signalling (D1 not satisfied). It is not advantageous for the high-quality offspring to cease

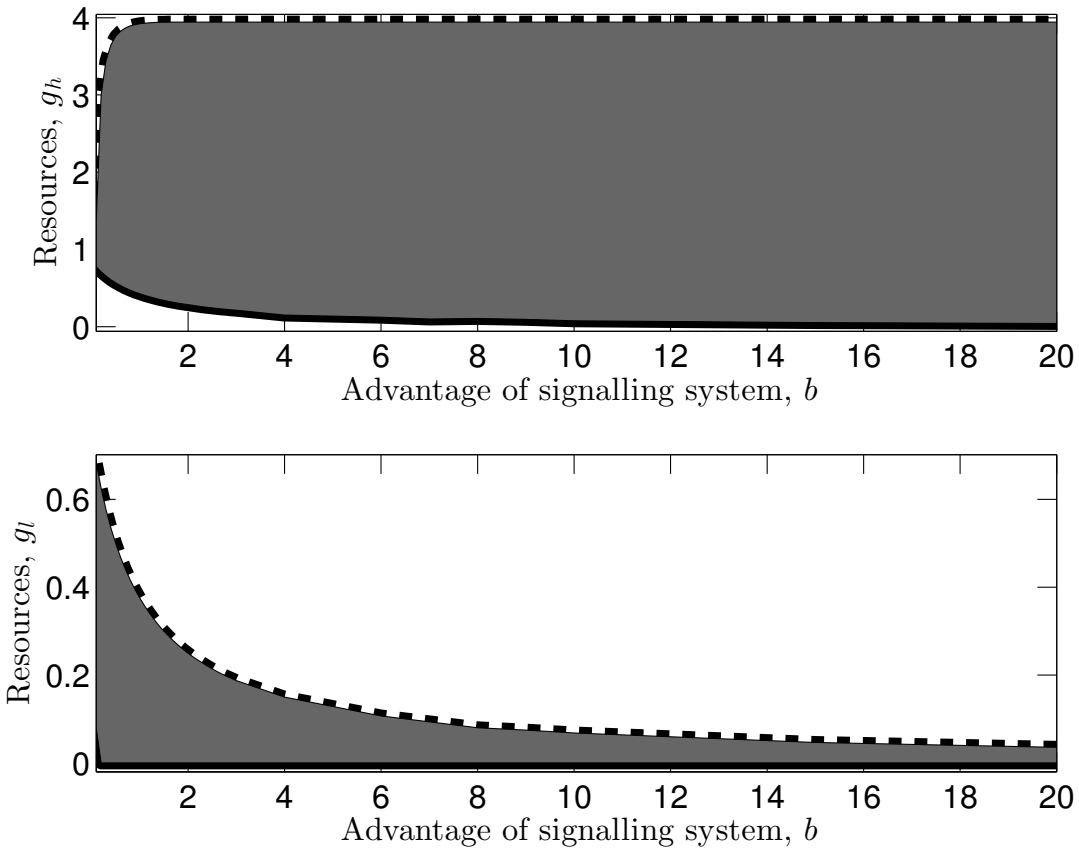

Figure 3.5.4: The efficiency benefit of not using cues and its effect on the amount of resources required for the facultative outcome to be stable in good environments (top panel) and in poor environments (bottom panel). The region between the maximum amount of resources (blue lines) and the minimum amount of resources (red lines) constitute the amount of resources necessary for the stability of the facultative outcome. Results were generated using $d = 1$, $c = \min(0.05, \frac{1}{1+e^{-t}})$, $a = 1.25$, and $R = r = 0.5$.

signalling since the system benefits everyone so significantly.

Cost of signalling

The higher the cost of signalling, the higher the minimum g_h and the lower the maximum g_h in the region of stability (Figure 3.5.5). Higher costs mean the low-quality offspring is less likely to signal, since the efficiency benefit of the signalling system no longer compensates for the cost of signalling, and as such the low-quality offspring prefers that the parent instead investigates cues to determine that it is better to feed the low-quality offspring (D2 not satisfied). Also as the cost of signalling increases, the minimum g_h required for stability increases

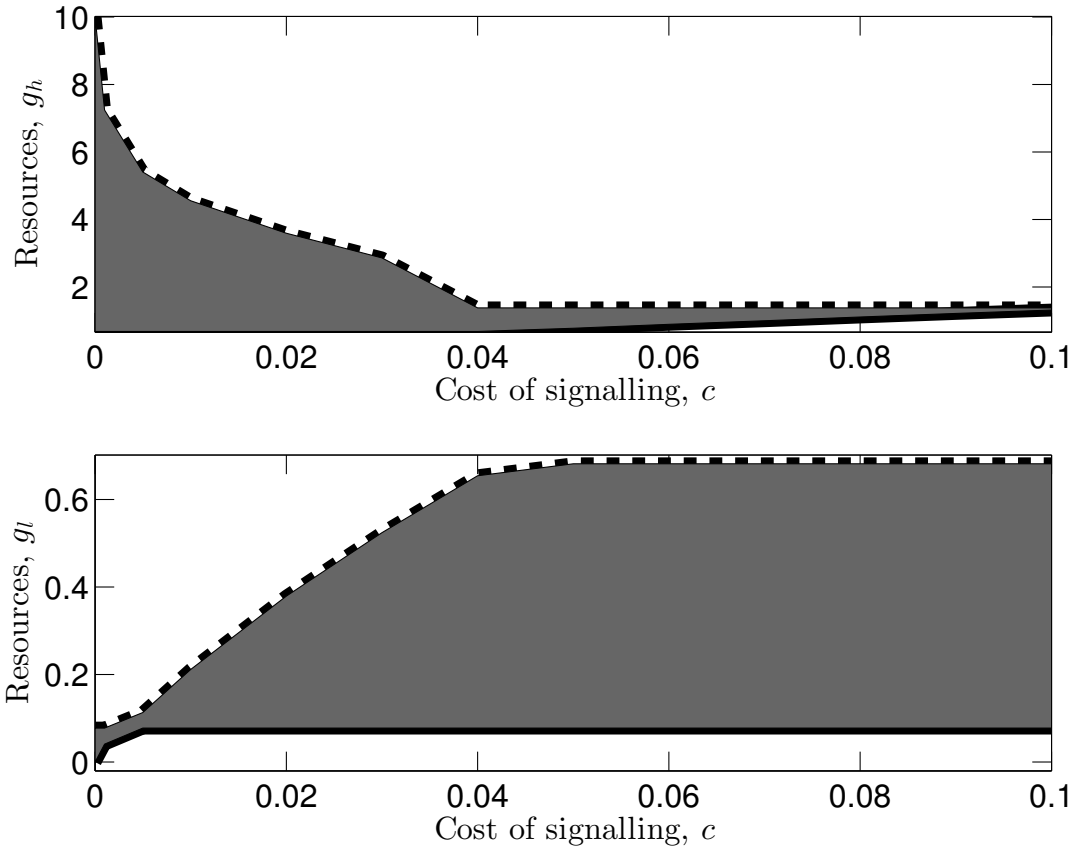

Figure 3.5.5: The cost of signalling and its effect on the amount of resources required for the facultative outcome to be stable in good environments (top panel) and in poor environments (bottom panel). The region between the maximum amount of resources (blue lines) and the minimum amount of resources (red lines) constitute the amount of resources necessary for the stability of the facultative outcome. Results were generated using $d = 1$, $a = 1.25$, $R = r = 0.5$, and $b = 0.1$.

as the low-quality offspring will begin preferring that the parent feed randomly rather than use signals since the difference in the increase of fitness does not differ much depending on which offspring gets the resource if the amount of resource is sufficiently small (D2 not satisfied).

As the cost of signalling increases in poor environments, both the minimum and maximum g_l in the region of stability increase. If g_l is too low, the high-quality offspring will prefer that the parent use cues rather than signals to confirm that it is better to feed the high-quality offspring, since the efficiency benefit of signalling means little if g_l is small anyway (D5 not satisfied). As the cost of signalling increases, this preference strengthens. On the other hand,

if g_l is too high, the low-quality offspring will signal as it prefers the parent to feed randomly rather than feed the higher-quality offspring, and since g_l is high the high-quality offspring is not better off by deciding to not signal (D4 not satisfied). As the costs of signalling increases, the preference for the low-quality offspring to signal wanes as the benefit of being fed half the time is no longer greater than the cost of signalling.

Baseline fitness

Given moderate baseline fitness levels, conditions for the stability of the facultative outcome can be met. If the baseline fitness of the offspring is too high (d sufficiently high), the parent may never prefer to feed the high-quality offspring rather than the low-quality offspring regardless of the amount of resources the poor environment offers (D1 not satisfied). Instead, any quantity of resource will always provide a greater benefit to the low-quality offspring since the sigmoidal fitness function of the high-quality offspring will always be in the domain of diminishing returns.

As the baseline fitness of offspring increases (d increases), both the minimum and maximum g_h in the domain of stability increase. If g_h is sufficiently low, low-quality offspring will not signal as they will prefer that the parent feeds randomly rather than signal and be fed (D2 not satisfied). Assuming the fitness levels of the two offspring are not already in the domain of diminishing returns (i.e. $t > 0$), additional provisioning has less of an impact on the recipient's direct fitness. Consequently, as the baseline fitness lowers, the direct fitness benefit of always being fed is less likely to outweigh both the cost of signalling and the indirect benefit of having its sibling be randomly fed if g_h is too low. If g_h is too high, the efficiency benefit has little direct consequence on offspring fitness since the fitness function is already in the domain of diminishing returns. Therefore, the low-quality offspring prefers that the parent uses cues rather than bear the cost of signalling, and so both offspring do not signal (D2 not satisfied). The maximum g_h increases with increasing d because lower baseline fitness means greater amounts

of resources are necessary to push the offspring's sigmoidal fitness function into the domain of diminishing returns and thus make the cost of signalling outweigh the efficiency benefit of the signalling system.

As d increases (i.e. baseline fitness increases), both the maximum and minimum g_l in the region of stability decrease. When g_l is sufficiently low, the parent will prefer to feed randomly rather than use cues. This is because when g_l is sufficiently small, the relative advantage of feeding one offspring over another is correspondingly small, and can be outweighed by the benefit of not wasting energy investigating cues. The result is that the high-quality offspring will not signal. The high-quality offspring prefers for the parent to use cues rather than having to bear the cost of signalling, and so it does not signal (D5 not satisfied).

As the baseline fitness decreases (d decreases), the relative advantage of feeding one offspring over the other becomes even smaller, as the rate of fitness increase per unit of resource decreases. Consequently, the minimum g_l in the region of stability increases. If g_l is sufficiently large, the parent will not prefer to feed the higher-quality offspring should it be the only offspring to signal, and will instead feed the lower-quality offspring (D1 not satisfied). This occurs because the fitness function of the higher-quality offspring more quickly enters the domain of diminishing returns, and so the parent will have greater inclusive fitness by investing in the lower-quality offspring instead. As d decreases, greater resource investment (i.e. higher g_l) is necessary for the fitness function of higher-quality offspring to reach the domain of diminishing returns, and so the maximum g_l in the region of stability increases. Eventually, given sufficiently high d, the low-quality offspring will always signal since it prefers that the parent feeds randomly rather than feed the higher-quality offspring (D4 not satisfied), or the cost of signalling becomes so large that it is not worth it for either offspring to signal (D5 not satisfied).

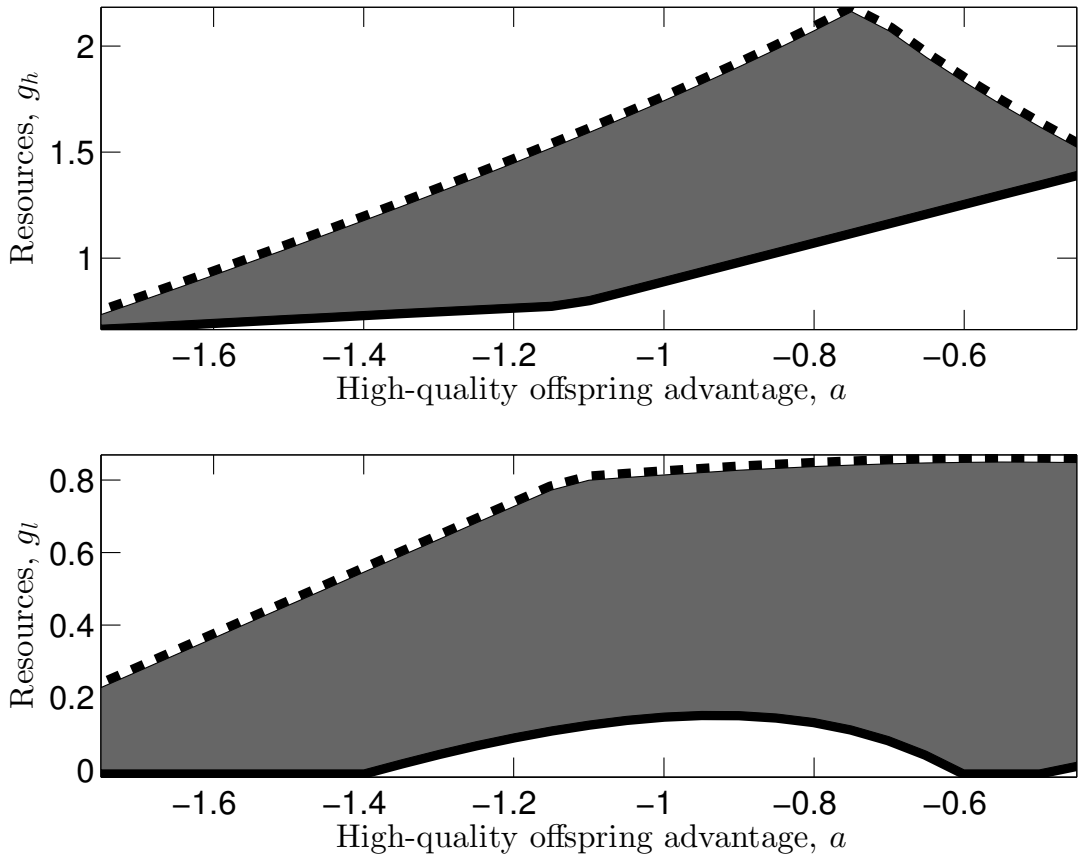

Figure 3.5.6: High-quality offspring advantage and its effect on the amount of resources required for the facultative outcome to be stable in good environments (top panel) and in poor environments (bottom panel). The region between the maximum amount of resources (blue lines) and the minimum amount of resources (red lines) constitute the amount of resources necessary for the stability of the facultative outcome. Results were generated using $d = 1$, $c = \min(0.05, \frac{1}{1+e^{-t}})$, $R = r = 0.5$, and $b = 0.1$.

High-quality offspring advantage

The relationship between the high-quality offspring advantage and the region of stability for the facultative outcome is quite complex (Figure 3.5.6), though summarily the facultative outcome is stable only if the high-quality offspring's advantage is moderate.

If the advantage is sufficiently small, the inclusive fitness benefit from the high-quality offspring's perspective of allowing its sibling to be fed does not outweigh the direct fitness advantage of being fed, even if the parent feeds randomly. Consequently, the facultative outcome

is never stable since the high-quality offspring will always signal (D3 not satisfied). The parent prefers to feed randomly because the efficiency benefit of not using cues outweighs the fact that the low-quality offspring would benefit slightly more from the resource. As the relative advantage of the high-quality offspring increases, the minimum g_h in the region of stability decreases. If the amount of resources in good environments, g_h, is sufficiently low, the parent may prefer to feed the high-quality offspring rather than the low-quality offspring (D1 not satisfied), since the fitness function of both offspring will be sufficiently far away from the domain of diminishing returns, and so the high-quality offspring will experience greater fitness gains for smaller levels of investment.

As the advantage becomes greater, lower amounts of resources are required to push the fitness function of the high-quality offspring into the domain of diminishing returns, thereby decreasing the minimum g_h. When a increases, maximum g_h in the region of stability increases initially, reaches a peak, then decreases. If g_h is sufficiently large, the high-quality offspring begins to prefer that the parent feeds randomly rather than allow the low-quality offspring to signal, and thus signals (D3 not satisfied). This is because, with large g_h, the direct benefit of receiving resources, even if randomly, outweighs the inclusive fitness benefit of its low-quality sibling getting the resource, even though the resource will increase its sibling's direct fitness more than it would its own. As the advantage of high-quality offspring increases, the offspring's fitness reaches the point of diminishing returns for lower levels of investment, and as such higher levels of g_h are required for the direct fitness benefit of being fed randomly to outweigh the indirect fitness benefit of letting the low-quality offspring be fed more. However, if the offspring advantage is sufficiently large, the low-quality offspring will no longer signal. The parent no longer prefers to feed randomly and will instead use direct cues to determine which offspring will be fed (D2 not satisfied). This is because, with such a high-fitness advantage, it is in the best interest of the parent to feed the low-quality offspring, and the efficiency advantage of the feeding randomly is outweighed by the greater fitness gains of feeding only

the low-quality offspring. The cost of signalling outweighs the efficiency benefit of avoiding the need to investigate cues, and so the low-quality offspring will choose not to signal. As the advantage of the higher-quality offspring increases, there is greater incentive for the parent to feed the low-quality offspring even for relatively low g_l levels, so the low-quality offspring is less likely to signal, and the minimum g_l decreases as a decreases. If the relative advantage of the high-quality offspring is sufficiently large, it never is in the best interest for the parent to feed the high-quality offspring, and so it is in the best interest of both offspring to not signal and for the parent to access using cues, thus the facultative outcome is never satisfied.

As a increases, the maximum g_l in the region of stability decreases. If g_l is sufficiently large, the low-quality offspring will signal, as it will prefer the parent to feed randomly rather than feed the high-quality offspring (D4 not satisfied). Since g_l is so large, the direct fitness benefit of being fed randomly outweighs the inclusive fitness benefit of allowing its sibling to be fed, even if the sibling would benefit more from being fed. As the fitness advantage of the high-quality offspring increases (a increases), the high-quality offspring's fitness function will be closer to the domain of diminishing returns for smaller g_l; as such, the higher-quality offspring benefits less per unit of resource, and so the low-quality offspring will signal for smaller g_l levels. As a increases (high-quality offspring advantage increases), the minimum value of resources, g_l, for which the parent prefers to feed randomly as opposed to using cues when neither offspring signals initially increases, reaches a peak, then decreases as a continues to decrease (Figure 3.5.7). The high-quality offspring refuses to signal when its parent prefers to feed using cues because it would rather the parent feed according to cues than to bear the costs of signalling (D5 not satisfied).

When the fitness advantage of the high-quality offspring is small, there is little difference between the marginal benefits of feeding the high-quality offspring versus the low-quality offspring for most values of g_l, and so the parent gains more from using the efficiency that comes

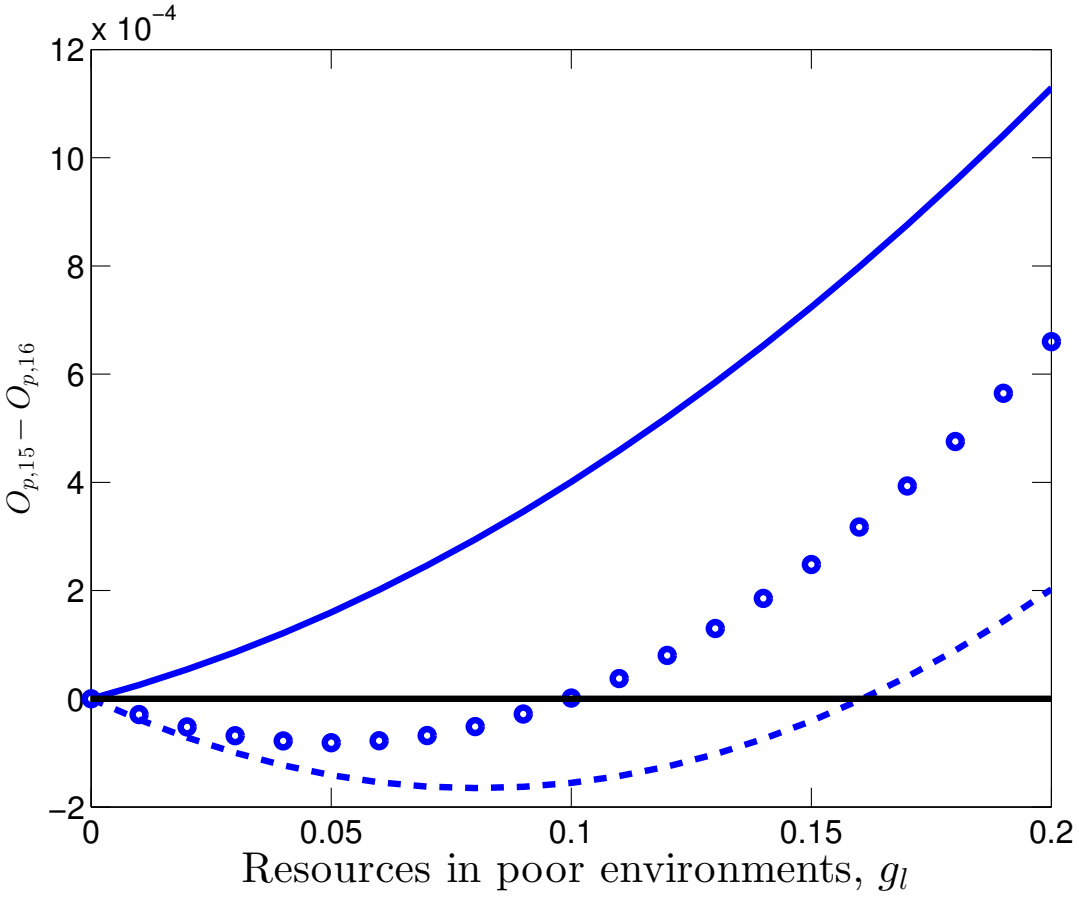

Figure 3.5.7: The difference between the parent's payoff when feeding randomly compared to using signals, plotted as a function of resources available in poor environments. The dotted, dashed, and solid lines represent $O_{p,15} - O_{p,16}$ as a function of g_l at $a = 1.2$, $a = 0.9$, and $a = 0.5$, respectively. Note that parents prefer to feed using cues for a greater range of g_l when a is moderate; if a is very large or very small, parents always prefer to feed randomly. Results were generated using $d = 1$, $c = \min(0.05, \frac{1}{1+e^{-t}})$, $R = r = 0.5$, and $b = 0.1$.

from feeding randomly as opposed to investigating cues. The result is that the minimum g_l in the region of stability is initially small. As the fitness advantage becomes larger, it is better for the parent to use cues rather than feed randomly for small values of g_l since feeding the high-quality offspring is significantly better than feeding the low-quality offspring, as the marginal rates of return are much higher for it than for the low-quality offspring when g_l is sufficiently low. The high-quality offspring would rather not bear the cost of signalling and thus allows the parent to feed via investigating cues. However, as a increases further, eventually the fitness function of the high-quality offspring is in the domain of diminishing returns even for very small amounts of resource investment, and so the fitness benefit of feeding one offspring over the other begins to shrink once again, and the parent is better off feeding randomly. The high-quality offspring will once again prefer to signal, and this results in the minimum g_l in the region of stability to decrease for very large values of a.

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Chapter 4

Sex differences in begging behaviour

Abstract

There are significant differences between the begging behaviours of males and female in many bird species. It has been hypothesized that these differences may be the result of sex differences in the need of nestlings. However, this theory remains untested theoretically and is unlikely to be a universal explanation since there are species that exhibit sex differences in begging behaviours but do not appear to have significant sex differences in need. We devise a simple evolutionary model to confirm that, all else equal, the sex in greater need the sex with lower baseline survival or greater per-unit benefit of additional provisioning will generally evolve to beg more intensely. We also propose and test the idea that sex differences in provisioning rates could promote the down-regulation of begging behaviour in females if there are genes in the female sex-chromosome that can modify begging behaviour. We find that this inclusive fitness effect can even be more important than sex differences in need, as females may evolve to be less intensely even when they are technically in greater need.

4.1 Introduction

The observation that male offspring in several species beg more than their female nestmates [1, 2, 3] has not been adequately explained. Price et al. (1996) proposed that male nestling

yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, tend to be larger, and therefore have greater long-term needs [1]. While perhaps appropriate for the particular species, this explanation cannot explain the sex-specific begging that has been observed in species that have little sex differences in size, such as the zebra finch [3], *Taeniopygia guttata*, and the barn swallow [4], *Hirundo rustica*. Saino et al. (2003) argue that the sex-specific differences in begging behaviour common in nestling barn swallows may be necessary for parents to identify the sex of their offspring as no obvious sexual dimorphism in morphology exists [2]. However, it has not been demonstrated that parents are unable to distinguish males from females in the absence of begging. Further, such a system may be susceptible to cheating.

We propose that sex-specific differences in begging behaviour may be driven by sex differences in the inclusive fitness effect of louder begging. Males of many species, including barn swallows, provide less care and are less reactive to increased levels of begging [5, 6, 7, 8]. Since any mutation which prompts an offspring to beg more loudly may inherited by the mutant's offspring, mutant mothers will be forced to provide a greater increase in care as a consequence of having mutant offspring compared to mutant fathers. Since the inclusive fitness cost of providing for loudly begging offspring is greater for mothers than for fathers, selection can cause females to beg less intensely than males if begging behaviour can be influenced by sex-linked genes. Here, we evaluate the hypothesis that long-term need should result in higher levels of begging using a full life-cycle model. We then model the inclusive fitness effect of begging behaviour to demonstrate that sex differences in provisioning behaviour are sufficient to explain sex-specific begging levels.

4.2 Methods

4.2.1 The long-term need hypothesis

We construct a caricature model of real biological systems to emphasize the core arguments of the long-term need hypothesis. Consider a finite wildtype population that consists of four distinct classes: female offspring, male offspring, female breeders, and male breeders, with population sizes of U_1, U_2, V_1, and V_2, respectively (Table 4.1 lists all variables and parameters used). In each generation, for mathematical simplicity, a male-female breeding pair creates exactly one offspring: with probability p, this offspring is female, and with probability $1 - p$, the offspring is male. The wildtype offspring of sex i begs with intensity x_i, where $i = f$ denotes females, and $i = m$ denotes males. We assume, as is frequently observed in many species, that greater levels of begging translate to greater parental care for that offspring [9, 10]. Suppose an offspring that begs with intensity x_i survives to fledge with probability $0 < s_i(x_i) < 1$, where s_i is an increasing function.Two unlinked autosomal genes will influence begging behaviour in the following manner: the gene controlling female (resp. male) begging levels influences only female (resp. male) begging rates but can be inherited and transmitted by the opposite sex.

Table 4.1: Variables and parameters used in the main text

Symbol	Explanation
U_i	Number of female ($i = 1$) and male ($i = 2$) offspring
V_i	Number of female ($i = 1$) and male ($i = 2$) breeders
x_i	Female ($i = f$) and male ($i = m$) begging intensity
$s_i(x_i)$	Survival rate for female ($i = f$) and male ($i = m$) offspring
$s_p(x_i)$	Survival rate for mothers with daughters ($i = f$) and sons ($i = m$)
r_2	Relatedness between offspring and father
a	Coefficient inversely proportional to carrying capacity
p	Primary sex ratio

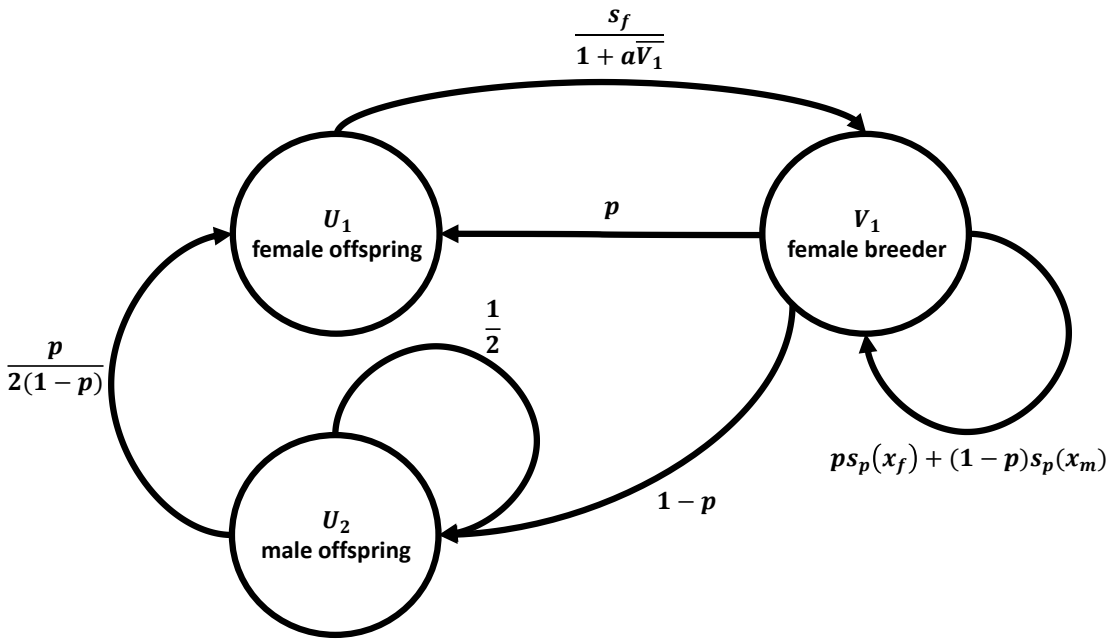

Figure 4.2.1: Lifecycle of the wildtype population at equilibrium. Note that since it is assumed male die after breeder once, one does not need to explicitly track the population dynamics surrounding male breeders, V_2.

$b_{i,1}$	Baseline survival rate of female ($i = f$) and male ($i = m$) offspring
$b_{i,2}$	Per-unit benefit of parental care for females ($i = f$) and males ($i = m$)
c	Baseline survival of mothers
c_1	Per-unit cost of parental provisioning

It is costly for parents to increase their level of care. To emphasize the role of sex-specific provisioning behaviour on the evolution of sex-specific begging, we assume that only females respond to offspring begging. Continuing with the assumption that increased begging levels results in increased care, if an offspring begs with intensity x_i, the mother survives with probability $0 \leq s_p(x_i) < 1$, where s_p is some decreasing function.

Offspring remain in the offspring class for exactly one generation, then they compete to become breeders. To ensure the population cannot grow without bound, suppose that there is a finite number of breeding territories, and each territory is 'owned' by up to one female breeder.

The probability that a female offspring that begs with intensity x_f in the current generation inherits one of these territories in the next generation is equal to $\frac{s_f(x_f)}{1+aV_1}$, where a is some constant inversely proportional to the carrying capacity. Any female breeder that survives in one generation will retain their territory in the next generation. Because begging does not influence the survival of fathers, we can assume for mathematical convenience the extreme case in which male breeders die immediately after their first breeding season. Any male offspring that survive will enter the male breeder class in the next generation, and these males will compete against each other for breeding opportunities.

The number of female breeders at equilibrium, $\bar{V}_1$, can be found by equating the expected number of females that lose territories in a given generation and the number of females that obtain a territory, $(1 - ps_p(x_f) - (1 - p)s_p(x_m))\bar{V}_1 = \frac{p\bar{V}_1 s_f(x_f)}{1+a\bar{V}_1}$. Solving for the number of female breeders, we find $\bar{V}_1 = \frac{1}{a}(\frac{ps_f(x_f)}{1-ps_p(x_f)-(1-p)s_p(x_m)} - 1)$. It is simple to conclude that $\bar{U}_1 = p\bar{V}_1$, $\bar{U}_2 = (1 - p)\bar{V}_1$, $\bar{V}_2 = (1 - p)s_m(x_m)\bar{V}_1$.

Suppose a mutant that influences male begging behaviour enters the population. Mutant males exhibit a deviant begging intensity, y_m. Females can carry the mutation, but their behaviour does not change as a result. Assuming the mutant is rare and that the population is both well-mixed and outbreeding, we need only track the population of mutant heterozygotes. To model the dynamics of the mutant population, we census the population after birth but before fledging. Since male breeders die after reproducing, it is sufficient to subdivide the population into mutant female offspring, mutant male offspring, and mutant mothers with mutant female offspring. The dynamics of the mutant allele at equilibrium satisfy

$[U_1, U_2, V_1]^T = A1[U_1, U_2, V_1]^T$, where

$$A1 = \begin{pmatrix} \frac{1-ps_p(x_f)-(1-p)s_p(x_m)}{2} & \frac{(1-p)(1-ps_p(x_f)-(1-p)s_p(x_m))}{2p} & \frac{1-ps_p(x_f)-(1-p)s_p(x_m)}{p} \\ \frac{ps_m(y_m)}{2s_m(x_m)(1-p)} & \frac{s_m(y_m)}{2s_m(x_m)} & 0 \\ \frac{p(ps_p(x_f)+(1-p)(\frac{s_p(x_m)+s_p(y_m)}{2})}{2} & \frac{(1-p)(ps_p(x_f)+(1-p)(\frac{s_p(x_m)+s_p(y_m)}{2})}{2} & ps_p(x_f) + (1-p)(\frac{s_p(x_m)+s_p(y_m)}{2}) \end{pmatrix}.$$

Here, $A1$ is the Jacobian and the entries are the rates at which each class (U_1, V_1, and U_2) moves to other classes. We will illustrate the calculations used to generate the entries of $A1$ with an example. The number of male mutant offspring in the next generation produced by a male mutant offspring in the current generation is equal to the probability that he survives to become an adult ($s_m(y_m)$) multiplied by the expected number of females he mates with ($\frac{V1}{V1(1-p)s_m(x_m)}$, equivalent to the total number of female breeders divided by the total number of male breeders), multiplied by the probability that the offspring is male (p), weighted by the probability that the new male offspring will be a mutant ($\frac{1}{2}$). The growth rate, or equivalently the fitness, of the mutant population is equivalent to the largest eigenvalue, λ, of $A1$. The growth rate of mutations influencing female begging are similarly solved. The two growth rates are used to model the coevolution of male and female begging behaviour (see Appendix 4.4).

Results

Suppose $s_f = b_{f,1} + b_{f,2}x_f$ and $s_m = b_{m,1} + b_{m,2}x_m$. Here, $b_{f,1} > 0$ and $b_{m,1} > 0$ represent the baseline survival of females and males, respectively, while $b_{f,2} > 0$ and $b_{m,2} > 0$ are measures of the per-unit benefit of increasing parental care for females and males, respectively. We assume mothers survive with probability $s_p = c - c_1 x_i$, where x_i is the begging intensity of the offspring, $0 < c < 1$ is the baseline survival of the mother, and $c_1 > 0$ is the per-unit cost of investment. Males and females evolve to beg with equal intensity whenever there is no difference in their survival as a function of provisioning (i.e. $s_f(x) = s_m(x)$ for all x). All else equal, the sex with the greater per-unit provisioning benefit, $b_{i,2}$, will generally evolve to beg more intensely in a wider variety of situations. All else equal, the sex with the lower baseline survival will always

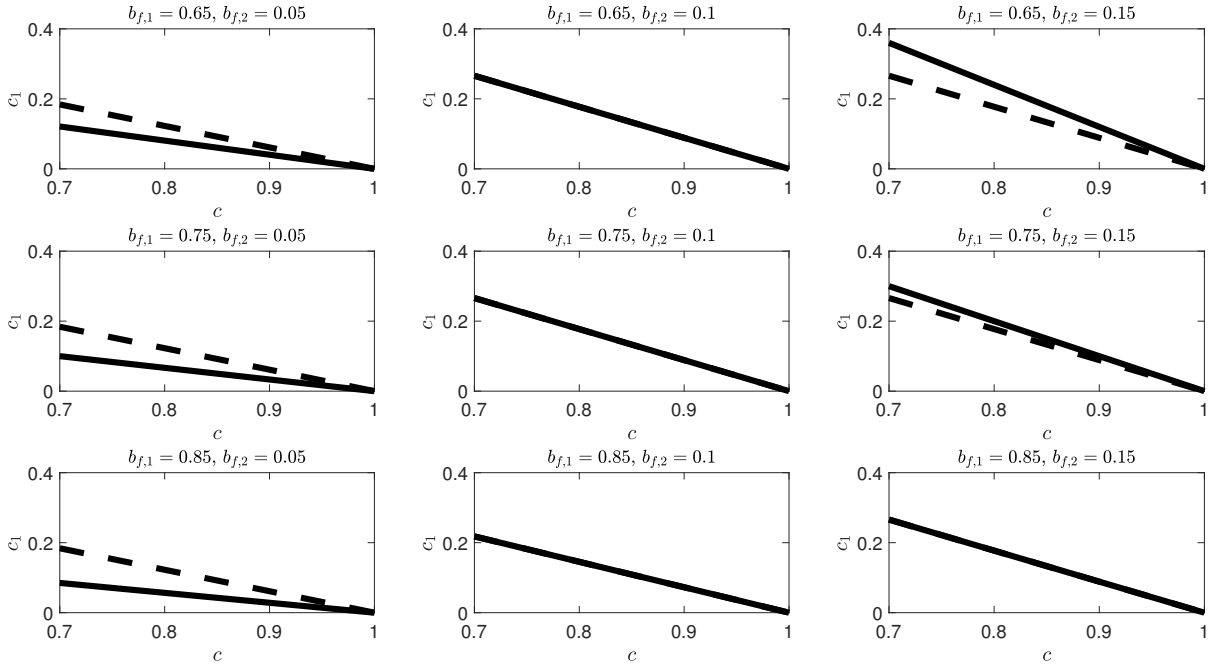

Figure 4.2.2: Sex-differences in begging behaviour at equilibrium. The areas under the solid (resp. dashed) lines show the range of per-unit previsioning costs, c_1, in which females (resp. male) evolve to beg maximally, $x_i = 1$, at equilibrium. All results were generated using $p = 0.5$, dashed lines were generated using $b_{m,1} = 0.75$ and $b_{m,2} = 0.1$, and solid lines were generated using the values given in the title of each panel.

beg with equal or greater intensity compared to the sex with higher baseline survival (Figure 4.2.2).

4.2.2 Potential influence of the sex-chromosome on sex-specific begging behaviour

Suppose begging levels are instead partially influenced by genes on the sex chromosome. Since most species noted to have sex differences in begging behaviour are birds, we assume ZW sex determination. Autosome genes completely determine male begging levels and influence female begging levels. Suppose there is a gene on the W sex chromosome that influences female begging levels. We can create a Jacobian to track the evolution of begging when influenced by an autosome, and another to model evolution when begging is controlled by an allosome (see Appendix 4.4.2 & 4.4.3).

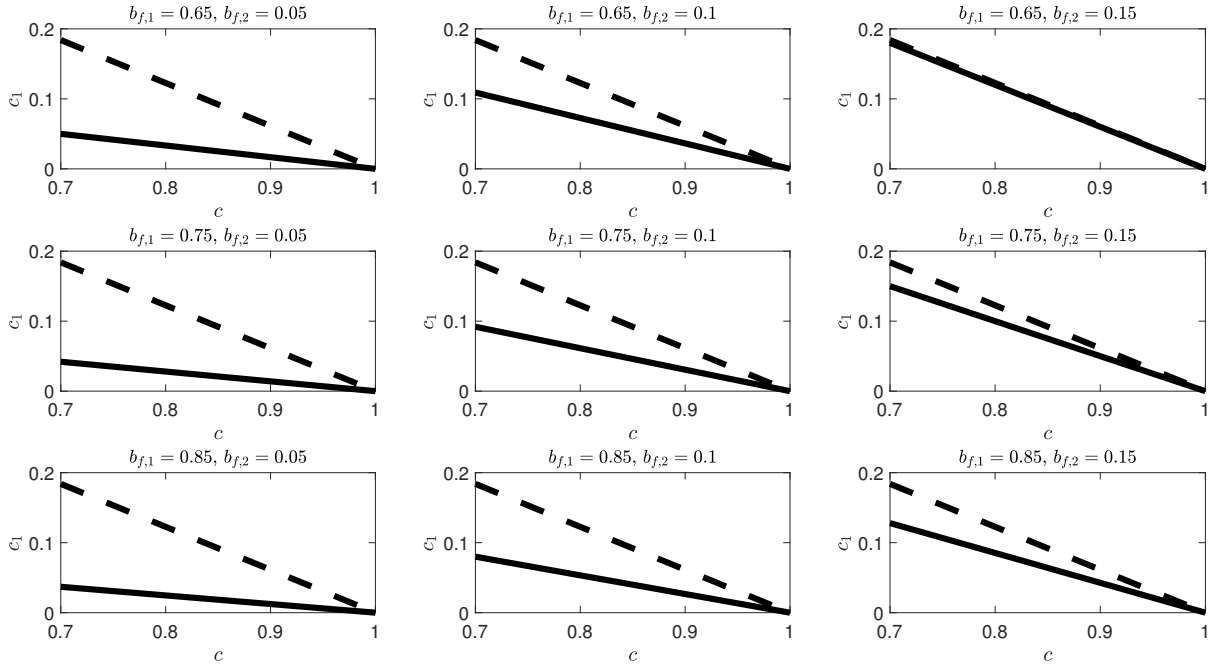

Figure 4.2.3: Sex-differences in begging behaviour at equilibrium when female begging is influenced by the sex chromosome. The areas under the solid (resp. dashed) lines show the range of per-unit previsioning costs, c_1, in which females (resp. male) evolve to beg maximally, $x_i = 1$, at equilibrium when female begging is controlled by genes on the sex chromosome. As with Figure 4.2.2, all results were generated using $p = 0.5$ and $x_m = x_f = 0$, dashed lines were generated using $b_{m,1} = 0.75$ and $b_{m,2} = 0.1$, and solid lines were generated using the values given in the title of each panel.

Results

Following the general method described in the long-term need model, we can compare the conditions under which begging can emerge if controlled by an allosome as opposed to an autosome. We assume that $p = \frac{1}{2}$. The result indicates that the autosomal mutation more readily allows for increased begging intensity compared to the sex-chromosome mutation (comparing Figures 4.2.2 & 4.2.3 reveals females evolve to beg more intensely under a small range of parameter conditions when the mutation is on the W sex chromosome; see Appendix 4.4.5 for a precise analytic version of this comparison). Mutations on the sex chromosome can even override sex differences in long-term need: if female begging behaviour is influenced by genes on the sex chromosome, greater per-unit benefits of provisioning and lower baseline survival rates for females compared to males does not necessarily mean that females will evolve to beg more loudly (Figure 4.2.3).

4.3 Discussion

All else equal, the sex with greater long-term need, as measured by baseline survival rates, $b_{i,1}$, and per-unit benefits of parental investment, $b_{i,2}$, will evolve to beg more intensely. The efficiency of parental investment, $b_{i,2}$, typically influences sex-differences in begging intensity most significantly (Figure 4.2.2). Male offspring in many species, such as the yellow-headed blackbirds [1], are larger than their female counterparts, meaning that they would be less likely to survive without additional parental care ($b_{f,1} > b_{m,1}$) but also that larger amounts of investment are required to sustain offspring of the larger sex ($b_{f,2} > b_{m,2}$). Our models thus provide mixed support for Price's hypothesis that males evolve more loudly because they are larger in size and therefore require greater amounts of care [1]. The larger males, in fact, may be less inclined to beg more intensely because their per-unit benefit of begging is lower. Consequently, the benefits of increased begging are less likely to outweigh the indirect fitness cost incurred through the parent's increased provisioning levels.

The term c_1 not only represents the per-unit cost of parental investment but is equal to the maximum parental investment in our model since maximal begging effort, x_i, was set to unity (a limit is necessary to ensure positive population sizes and fitness levels). Results indicate offspring either increase their begging maximally, $x_i = 1$, or not at all $x_i = 0$. Differences in the maximum begging intensity, $max(x_m) \neq max(x_f)$ can lead to differences in begging intensity. Sex differences in maximum begging intensity — which in our model is equal to the realized begging intensity if both offspring decide to beg — can either represent the physical limit of offspring begging intensity or sex-specific variance in fitness (without requiring sex differences in parental investment costs).

When begging intensities were allowed to coevolve with the primary sex ratio, p, mothers will skew the sex ratio toward the sex that is less costly to raise, all else being equal (see Appendix 4.4.4). Noteworthy is the fact that offspring are less likely to beg if the survival of

mothers, c, is high, since maternal fitness exponentially increases with increased annual survival. This can remain true even when there are significant sex differences in the cost of raising offspring. As such, one would expect smaller absolute sex differences in begging intensities in longer-lived species.

Note that the middle column of Figure 4.2.2 suggests that males and females may evolve to beg with the same intensity even if their need differs. This occurs because the evolution of male and female begging intensities influence one another (expounded more explicitly in Appendix using Frank & Taylor analysis). Consider, for example, the situation in which male offspring gain more from increased levels of provisioning (i.e. they are needier). In this case, compared to daughters, sons are more willing to inflict survival costs onto mothers. Since the expected fitness of a mother increases exponentially with survival, the indirect fitness costs of begging more loudly declerate with increased begging. Therefore, once one sex begins to beg – males, in this case – the opposite sex will be more willing to beg since the indirect fitness costs (i.e. the expected decrease in the residual fitness of the mother) has diminished.

Why begging rates are necessary for parents to provide males with relatively greater levels of care is less clear. Begging has been found in many species to increase predation [11, 12, 13] and to have metabolic costs [14, 15, 16], and thus a system in which parents could differentiate offspring by sex without begging would be largely beneficial. Our models suggest that sex differences in long-term need are a sufficient but not necessary explanation for observed sex differences in begging behaviour. As offspring, the sexes will benefit equally by increasing begging intensity assuming no differences in long-term need or cost. However, if mothers often provide greater levels of provisioning and are more responsive to offspring begging compared to males, mothers suffer larger costs for bearing the 'increased begging intensity' mutation. Therefore, if begging intensity is genetically influenced, as is suggested by several studies [17, 18, 19], the inclusive fitness effects of begging behaviour can lead females to beg less in-

tensely than males even in the absence of sex-differences in long-term need. With evidence for the genetic inheritably of begging behaviour being mostly species-specific and indirect, studies that focus on identifying precisely which genes influence begging behaviour, with special attention paid to sex chromosomes, may be a direction for future study.

The models here were constructed with the assumption of well-mixed, outbreeding populations, though sex-specific dispersal patterns can potentially influence sex differences in begging behaviour. All else equal, the non-dispersing sex may be expected to beg less intensely since that sex encounters more local resource and mate competition, and therefore one would expect the per-unit efficiency of parental investment, $b_{i,2}$, into the non-dispersing sex to be lower. Although some of the sex differences in dispersal rates can be represented by the parameter $b_{i,2}$, the full complexity of sex-specific dispersal, including local resource and mate competition and inbreeding, and its implications on sex-specific begging behaviour cannot be captured by our model.

It is important to note that our model assumes the parent's response to increased begging will always translate to increases in provisioning. While this is indeed true of many species [9, 10], exceptions have been noted, with parents of certain species and populations allocating resources entirely independently of offspring begging behaviour. Ultimately, due to the fact that ours is a one-offspring model, we assume that begging signals need rather than quality or hunger [20]. Models with multiple-offspring broods together with more dynamic allocation strategies that assume sex-differences in long-term need (i.e. quality) would be more realistic representations of signalling systems used by species in environments that are particularly resource-limited.

4.4 Appendix

4.4.1 Numerical analysis

Given any initial wildtype male begging intensity, $x_{m,0}$, we can approximate the selection gradient acting on this phenotype by finding the derivative of the leading eigenvalue. We can then iterate this process, with $x_{m,t+1} = x_{m,t} + k\frac{\partial\lambda}{\partial y_m}|_{x_{m,t}}$, where k is related to the mutation rate. This continues until we find $|x_{m,t+1} - x_{m,t}| < \epsilon$, for some sufficiently small ϵ such that we can be confident that we have identified the evolutionarily stable begging levels for males. We simulatenously track the dynamics of a mutation that exclusively influences female begging behaviour (see below) to find the male and female begging rates at equilibrium.

4.4.2 Female allosome mutation

Female carriers of this mutation beg with intensity y_m. Males can carry the mutation, but their behaviour does not change as a result. The Jacobian relating to the invasion of this mutation is given by

$$A2 = \begin{pmatrix} \frac{s_f(y_f)(1-ps_p(x_f)-(1-p)s_p(x_m))}{2s_f(x_f)} & \frac{(1-p)(s_f(y_f))(1-ps_p(x_f)-(1-p)s_p(x_m))}{2s_p(x_f)p} & \frac{s_f(y_f)(1-ps_p(x_f)-(1-p)s_p(x_m))}{s_f(x_f)p} \\ \frac{p}{2(1-p)} & \frac{1}{2} & 0 \\ \frac{p(p(\frac{s_p(y_f)+s_p(x_f)}{2})+(1-p)s_p(x_m))}{2} & \frac{(1-p)(p(\frac{s_p(y_f)+s_p(x_f)}{2})s_p(y_f)+(1-p)s_p(x_m))}{2} & p(\frac{s_p(y_f)+s_p(x_f)}{2}) + (1-p)s_p(x_m) \end{pmatrix}.$$

We then find the evolutionarily stable female begging levels. The same results can be derived using a Taylor-Frank analysis [21] of the model (see below).

4.4.3 Female autosomal mutation

To model the influence of the gene on the sex chromosome, we need only track two population classes:

- female offspring with a mutation on the sex chromosome, w_1

- mothers with a mutation on the sex chromosome, w_2

Suppose that a mutant begging with intensity y_f invades a wildtype population that begs with intensity x. The dynamics of the gene on the female sex chromosome can be modelled using the Jacobian

$$\mathbf{A4} = \begin{pmatrix} p\frac{s_f(y_f)}{1+a\bar{V}_1} & \frac{s_f(y_f)}{1+a\bar{V}_1} \\ p(p(\frac{s_p(y_f)+s_p(x_f)}{2}) + (1-p)s_p(x_m)) & p(\frac{s_p(y_f)+s_p(x_f)}{2}) + (1-p)s_p(x_m) \end{pmatrix}$$

4.4.4 Variable sex-ratio

We model the sex-ratio as evolving completely under the female's control, due to the assumed ZW sex determination. Suppose a mutation influencing female behaviour invades, causing mothers to produce female offspring with probability q. We are concerned with three population classes

- mutant female offspring, u_1
- male offspring, u_2
- mutant mothers, u_3

The Jacobian relating to the invasion of this mutation is given by

$$\mathbf{A3} = \begin{pmatrix} \frac{q(1-ps_p(x_f)-(1-p)s_p(x_m))}{2p} & \frac{(1-q)(1-ps_p(x_f)-(1-p)s_p(x_m)}{2p} & \frac{1-ps_p(x_f)-(1-p)s_p(x_m)}{p} \\ \frac{p}{2(1-p)} & \frac{1}{2} & 0 \\ \frac{q(qs_p(x_f)+(1-q)s_p(x_m))}{2} & \frac{(1-q)(qs_p(x_f)+(1-q)s_p(x_m))}{2} & qs_p(x_f) + (1-q)s_p(x_m) \end{pmatrix}.$$

To allow the coevolution of sex-ratio and offspring begging, we simultaneously update x_f, x_m, and p until an equilibrium is reached.

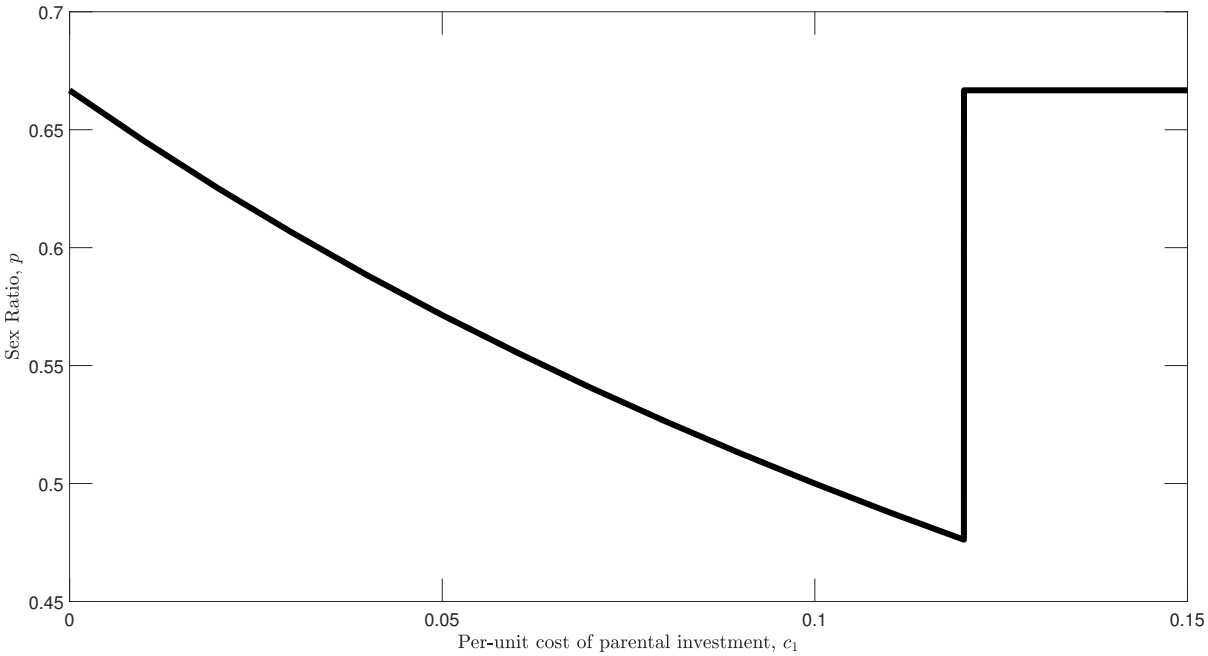

Figure 4.4.4: Equilibrium sex ratio as a function of parental investment costs. The solid line represents the sex ratio when adjusting the per-unit cost of investing in daughters, while holding the per-unit investment cost into offspring of the opposite sex is set to a constant, $c_1 = 0.1$. If investment costs for one sex is sufficiently high, that sex will not beg at all. Consequently, the equilibrium sex ratio will favour that sex. Results were generated using $b_{f,1} = b_{f,1} = 0.5$, $b_{f,2} = b_{m,2} = 0.15$, and $c = 0.9$.

Results

The sex ratio, p, is now assumed to coevolve with begging levels, x_i. There is a threshold for female (resp. male) baseline offspring survival, $b_{f,1}$ (resp $b_{m,1}$), above which female (resp. male) offspring do not signal. The sex ratio is then biased toward the sex that does not beg. If the benefit of begging, as measured by $b_{i,2}$, is too low for a specific sex, that sex will not beg at all, causing the sex ratio to favour that sex. If the baseline survival of the parent, c, is sufficiently high, neither offspring will beg. Increasing the per-unit cost of begging, c_1, of one sex causes the sex ratio to favour the opposite sex, until the per-unit cost of investing in one sex is sufficiently high such that offspring of that sex cease to beg, and consequently that sex is favoured (Figure 4.2.3).

4.4.5 Taylor & Frank Analysis

The following analysis is used to derive more precise conditions under which the mutations listed above may invade a population, and the results that follow agree with the analysis above. Let $\mathbf{A} = [w_{ij}]$, where w_{ij} represents the number of class-i offspring of a class-j individual. Suppose $\mathbf{v} = v_i$ is the dominant left eigenvector of $\mathbf{A}$, and represents the individual reproductive values of each class. Additionally, $\mathbf{u} = u_i$ is the dominant right eigenvector of $\mathbf{A}$, and represents the class frequencies at equilibrium. Then we note that the average fitness can be written as $W = \mathbf{vAu}$. To look at the effects of mutant behaviour, we can take the derivative of W with respect to the variable x that controls individual behaviour. We seek to find evolutionarily stable levels x^* of this behaviour. As such, we are interested in $\frac{dW}{dx} = \mathbf{v}\frac{d\mathbf{A}}{dx}\mathbf{u}$; the mutant invades whenever $\frac{dW}{dx} > 0$. The following analysis is done setting the baseline survival of sons equal to that of daughters, $b_{f,1} = b_{m,1} = b$, while $s_f = b + b_{f,2}x_f$, $s_m = b + b_{m,2}x_m$, and $s_p = c - c_1 x_i$.

Female mutant invasion

The classes of interest, $i = 1, 2, 3$, are mutant male offspring, mutant female offspring, and mutant mothers, respectively. Then we have

$$W = \begin{pmatrix} 1 & 1 & \frac{p(ps_p(x_f)+(1-p)s_p(x_m)}{1-ps_p(x_f)-(1-p)s_p(x_m)} \end{pmatrix} \mathbf{A1} \begin{pmatrix} \frac{\bar{V}_1}{2} \\ \frac{\bar{V}_1}{2} \\ \bar{V}_1 \end{pmatrix},$$

, we conclude the mutant will invade whenever $c_1 < \frac{2b_{f,2}(1-c)}{bp-2b_{f,2}x_m-b_{f,2}px_f+2b_{f,2}px_m}$. When $x_m = x_f = 0$, this reduces to the requirement that $c_1 < \frac{2b_{f,2}(1-c)}{bp}$. Note that these inequalities can only be used if the sex ratio has been allowed to reach equilibrium, otherwise the reproductive value between males and females would differ and the vector, $\mathbf{v}$, used above would not be valid.

Male-mutant invasion

Using the same population classes as before, we find with male mutation that

$$\frac{dW}{dx} = \begin{pmatrix} 1 & 1 & \frac{p(ps_p(x_f)+(1-p)s_p(x_m)}{1-ps_p(x_f)-(1-p)s_p(x_m)} \end{pmatrix} \mathbf{A1} \begin{pmatrix} \frac{\bar{V}_1}{2} \\ \frac{\bar{V}_1}{2} \\ \bar{V}_1 \end{pmatrix}.$$

The invasion condition simplifies to $c_1 < \frac{2b_{m,2}(1-c)}{b(1-p)}$ when $x_m = x_f = 0$. Note that when $p = \frac{1}{2}$ and $x_m = x_f = 0$, the requirement for the male-influencing mutation is equivalent to the requirement for the female-influencing mutation.

Sex-ratio mutation

The condition for mutant invasion simplifies to $x_m < x_f$. That is, the sex-ratio will be biased toward the sex that begs less intensely since it is less costly to raise.

Sex-chromosome mutation

The condition for mutant invasion is $c_1 < \frac{b_{f,2}(1-c)}{bp-b_{f,2}x_m+b_{f,2}px_m}$, which simplifies to $c_1 < \frac{b_{f,2}(1-c)}{bp}$ whenever $x_m = x_f = 0$. Note that by comparison to the autosomal case, it is clear that this mutation on the sex-chromosome invades under fewer conditions.

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Chapter 5

Cooperative breeding and clutch size

Koykka, C. & Wild, G. (2016) The association between the emergence of cooperative breeding and clutch size. *J. Evol. Biol.* 29(1): 58-76.

Abstract

Previous theoretical work has suggested that smaller brood sizes helped facilitate the emergence of cooperative breeding in birds. However, recent empirical evidence has found no statistically significant difference between the clutch sizes of cooperative breeders and that of non-cooperative breeders. One explanation for this finding is that, while small clutch sizes may predispose species to cooperative breeding, the emergence of cooperative breeding itself may influence the evolution of clutch size. Here, we develop a set of models using population dynamics to describe how the emergence of cooperative breeding influences clutch size. We find, in contrast to previous theoretical work, that the emergence of cooperative breeding does not necessarily decrease and, under certain conditions, may actually increase clutch size. In particular, clutch size may increase after the emergence of cooperative breeding if helpers – philopatric individuals that assist their breeding relatives – are able to substantially improve breeder fecundity at low costs to their own survival, and if the association between breeder and helper is brief. In many cases, clutch size increases following the emergence of cooperative breeding not because it is optimal for the breeder, but as the result of breeder-helper conflict over resource allocation.

5.1 Introduction

Cooperative breeding is a social system in which individuals forego reproductive opportunities to help raise offspring that are not their own [1]. In the majority of cooperatively breeding birds, helpers delay dispersal and assist breeding relatives on their natal patch [2]. Two widely accepted theories delineate the proximate causes of delayed dispersal and cooperative breeding. The habitat saturation hypothesis suggests that individuals will not disperse if it is is unlikely to result in independent reproduction [3, 1]. The benefits of philopatry hypothesis is a complimentary explanation which focuses on the benefits of staying, such as the possibility of territory inheritance, rather than the costs of dispersing [1, 4].

It has been proposed that certain life-history characteristics can increase the costs of dispersal and the benefits of philopatry, and thus facilitate the emergence of delayed dispersal and cooperative breeding [5]. That the presence of cooperative breeders is not randomly distributed in avian species suggests it is possible that there are characteristics predisposing certain lineages to exhibit cooperative breeding [5]. Both theoretical [6, 7, 8] and empirical [9, 10, 5, 11, 12] evidence has indicated that low juvenile and adult mortality, which can lead to highly dense populations with infrequent opportunities for independent breeding, is a life-history trait that may have played a particularly important role in the evolution of cooperative breeding in birds.

Previous work has suggested that because greater reproductive output often translates to reduced survival [13], cooperatively breeding birds may also tend to have smaller clutch sizes than non-cooperative breeders [3]. Recent comparative analyses have consistently provided support for the association between high longevity and cooperative breeding in birds [5, 11, 12], but have provided mixed support for the association between clutch size and cooperative breeders. The most recent analysis [12] found that cooperative breeders did not have statistically significant smaller clutch sizes than non-cooperative breeders. In contrast to previous studies, Beauchamp controlled for correlates such as body size, and used a larger sample size taken

from avian species world-wide [12].

An obvious explanation for the discrepancy between theoretical work and recent empirical results is that while small brood sizes may predispose species to breed cooperatively, cooperative breeding itself may drive an increase in clutch size. This idea has been proposed previously by Hardling & Kokko, who developed a simple model to study how the emergence of cooperative breeding affects clutch sizes. The model indicates that cooperative breeding uniformly increases clutch size. However, this model suffers from several key limitations.

First, the model assumes that the offspring depreciation hypothesis - that the reproductive value of offspring born later in the season is strictly less than that of those born earlier - holds true for every cooperatively breeding avian species. Yet certain species produce more offspring than their natal territory can sustain should they remain philopatric, and so several offspring from a single brood can become floaters [14]. As the reproductive value of these floaters need not necessarily differ significantly, the assumption that older offspring have strictly higher reproductive value than any offspring subsequently produced does not uniformly hold. Additionally, the model asserts that offspring birth determines the rank of auxiliaries in the queue for breeding positions, but this relies on the assumption that auxiliaries stay permanently. There are, however, species in which helpers stay only temporarily before dispersing to become floaters, helpers, or breeders on other territories [15].

Second, the model does not use population dynamics, and therefore may not properly account for the inclusive fitness effects resulting from changes in clutch sizes. Further, the model considers only the breeder's optimal resource distribution between fecundity and survival. It therefore neglects the potential conflict between breeder and auxiliary, which may cause selection on resource distribution and consequently brood size to deviate from the breeder's optimum.

Lastly, the model assumes a particular type of trade-off between fecundity and survival in the presence of helpers - that help increases longevity with the same factor independent of clutch size - but as Johnstone [16] demonstrates, this relationship is complex and can vary significantly depending on ecological and life-history factors.

Here we develop a set of population dynamics models to investigate how the emergence of cooperative breeding itself may influence clutch sizes at evolutionary equilibrium. These models improve upon previous theoretical work by examining how clutch size changes under a variety of ecological and life-history assumptions, including those regarding the nature of help provided by auxiliaries and the relationship between breeder fecundity and survival. The model also describes how conflict between breeder and auxiliary can affect clutch sizes at evolutionary equilibrium. The results of the model are then compared to recent comparative analyses investigating the association between cooperative breeding and clutch size.

5.2 The Model

5.2.1 Model Design

Following Wild & Koykka [17], we design an inclusive-fitness model by first considering a population of diploid, simultaneous hermaphrodites. Each individual in the population is a breeder, a helper, or a floater. Each breeder inhabits a territory on which they produce a number of offspring per season through female function by mating with another breeder, selected uniformly at random from the population. These offspring either become helpers, floaters, or breeders in the next season, depending on the circumstances and the assumptions about the ecology of the species. Each helper lives on a territory occupied by a breeder: they assist breeders by increasing their fecundity, decreasing their mortality rate, or both. Should a breeder not survive the offspring-production stage of the life-cycle, the helper, assuming it survives, inher-

its the breeding territory. In the absence of any suitable successor, breeding territories become vacated. Floaters await the opportunity to inhabit vacant breeding territories. In these models, breeders first produce offspring, and then it is determined whether they survive the breeding season.

For simplicity, suppose that there can be at most one helper per breeder at any given time. This assumption is used for mathematical convenience, but is biologically reasonable: perhaps there is enough resources to support only a limited number of breeders and helpers per territory [14], or the benefits of helping for both helpers and breeders diminish greatly per additional helper [18], or there is a limit on the number of offspring breeders can coerce to help[19].

While there are many ways in which helpers can assist breeders, ultimately helpers - assuming they are truly helpful - allow breeders to exert less energy, thereby increasing breeders' fecundity, survival, or both [16]. Breeders exhibit either additive or compensatory reactions to the presence of helpers: they can either choose to redirect their efforts away from reproductive efforts and toward increasing survival (load-lightening) or they can exert the same amount of effort toward reproduction, regardless of the presence of helpers so that total reproductive output is greater when helpers are available. The degree to which breeders 'lighten their load' in the presence of helpers varies between and occasionally within cooperatively breeding species [20].

To account for load-lightening and the different forms of helpful behaviour, suppose breeders and helpers each have a certain amount of resources which they allocate toward breeder survival and breeder fecundity. In the presence of a helper, a breeder allocates portion p of its resources to offspring production while the helper allocates q to offspring production, such that the expected number of offspring produced is $\lambda(p, q)$ and the probability that the breeder will survive a given season is $s_B(p, q) = s_B$. We assume that the actual number of offspring pro-

duced follows a Poisson distribution with mean $\lambda(p, q)$. The way in which helpers and breeders allocate their resources may also affect helper survival, so that the helper survives a given season with probability $s_H(p, q)$. Assume that in the absence of a helper, a breeder allocates a proportion p_0 of resources to offspring production and $1 - p_0$ toward survival. Then the solitary breeder expects to produce $\alpha(p_0)$ offspring and survives the breeding season with probability $s_B(p_0, 0) = s_{B_0}$.

Let V, W, and U represent the number of breeders without helpers, breeders with helpers, and floaters in the population, respectively. We impose ecological constraints by assuming that the probability with which a floater obtains a breeding territory in a given season is a function of the number of currently occupied territories. In particular, a floater survives a given season with probability t and surviving floaters obtain a breeding territory with probability $\frac{1}{1+a(V+W)}$ (and thus remains a floater with probability $1 - \frac{1}{1+a(V+W)}$), where a is a constant inversely correlated with the carrying capacity of the population.

Each of the models created adhere to the description above, and differ only in the assumptions made about the hierarchy of nest-mates. First, we must make an assumption about the presence of direct local kin competition for breeding positions. If it is assumed that there is no direct local kin competition, then only helpers may inherit breeding territories should a breeder die; should both the breeder die and there are no helpers on the territory, any offspring produced on that territory that season become floaters. As there is only one helper per territory, relatives are not in direct competition. Conversely, if there is direct local kin competition, then in the event that breeder dies, both helpers and offspring residing on the territory (those recently produced through maternal function) have the opportunity to inherit the territory, although preference is given to helpers, such that in order for an offspring to inherit the territory immediately after its birth, both helper and floater must be absent. After the role of breeder and helper are filled (say, without loss of generality, by 'oldest' two offspring), any remaining off-

spring become floaters. A second assumption that must be addressed is whether auxiliaries stay only temporarily to help breeders on their natal patch, after which time they become floaters, or if they stay indefinitely (i.e. until either it or the breeder dies).

Since the general results derived from our models are independent of these two assumptions (see Results), to demonstrate the analysis of our models we will assume the presence of local kin competition and that helpers stay for only one breeding season before dispersing. See Appendix for the complementary analysis of the remaining models.

5.2.2 Population Dynamics

If U, V, and W represent the population of floaters, breeders without helpers, and breeders with helpers, respectively, then the next generation of these populations is given by (U', V', W', respectively)

$$
\begin{aligned}
U' =& (1 - \frac{1}{1 + a(V + W)})tU && \text{I}\\
&+ s_{B_0} V \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((k-1)(1-d^k) + kd^k) && \text{II}\\
&+ (1 - s_{B_0}) V \sum_{k=2}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((k-1)d^{k-1} + (k-2)(1-d^{k-1})) && \text{III}\\
&+ s_B W \sum_{l=1}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}((l-1)(1-d^l) + ld^l) && \text{IV}\\
&+ (1 - s_B)(1 - s_H) W \sum_{l=2}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}((l-1)d^{l-1} + (l-2)(1-d^{l-1})) && \text{VI}\\
&+ (1 - s_B) s_H W \sum_{l=1}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}((l-1)(1-d^l) + ld^l) && \text{VII}\\
&+ s_B s_H W && \text{VIII}
\end{aligned}
$$

(I) The proportion of floaters that fail to obtain breeding sites.

(II) The expected number of dispersing offspring from territories on which there is no helper and the breeder survives.

(III) The expected number of dispersing offspring from territories on which there is no helper and the breeder dies.

(IV) The expected number of dispersing offspring from territories on which there is a helper and the breeder survives.

(V) The expected number of dispersing offspring from territories on which there is a helper and both the breeder and the helper die.

(VI) The expected number of dispersing offspring from territories on which there is a helper and the breeder dies.

(VII) The expected number of territories on which there is a helper who survives.

We can similarly define the recursive equations for breeders with helpers and floaters

$$\begin{aligned}
V' =& \frac{1}{1+a(V+W)}tU \\
&+ s_{B_0}V\sum_{k=0}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}d^k \\
&+ (1-s_{B_0})V\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}d^{k-1} \\
&+ s_B W\sum_{l=0}^{\infty}\frac{\exp(-\alpha)\alpha^l}{l!}d^l \\
&+ (1-s_B)s_H W\sum_{l=0}^{\infty}\frac{\exp(-\alpha)\alpha^l}{l!}d^l \\
&+ (1-s_B)(1-s_H)W\sum_{l=1}^{\infty}\frac{\exp(-\alpha)\alpha^l}{l!}d^{l-1}
\end{aligned}$$

$$
\begin{aligned}
W' =& W_{S_B} \sum_{l=1}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}(1-d^l) \\
&+ (1-s_B)s_H W \sum_{l=1}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}(1-d^l) \\
&+ (1-s_{B_0})(1-s_H)W \sum_{l=2}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}(1-d^{l-1}) \\
&+ s_{B_0} V \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1-d^k) \\
&+ (1-s_{B_0})V \sum_{k=2}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1-d^{k-1})
\end{aligned}
$$

The above set of recursive equations can be written in the compact form

$$
\begin{aligned}
\bar{U} &= \frac{a(V+W)}{1+a*(V+W)} S_{11}U + F_{12}V + F_{13}W \\
\bar{V} &= \frac{1}{1+a(V+W)} S_{21}U + S_{22}V + S_{23}W \\
\bar{W} &= S_{32}V + S_{33}W
\end{aligned}
$$

The basic reproduction number is given by

$$
R_0 = \frac{F_{12}(1-S_{33})S_{21}}{1-(S_{22}+S_{33})+(S_{22}S_{33}-S_{23}S_{32})} + \frac{F_{13}F_{32}S_{21}}{1-(S_{22}+S_{33})+(S_{22}S_{33}-S_{23}S_{32})},
$$

and the population avoids extinction if $R_0 > 1$.

Setting $U = \bar{U}$, $W = \bar{W}$, and $V = \bar{V}$, we can solve for the positive equilibrium (say U_E, V_E, W_E). We find

$$V_E = \frac{(1 - S_{33})(R_0 - 1)}{a(1 - S_{11})(S_{32} - S_{33} + 1)}$$
$$W_E = \frac{S_{32}(R_0 - 1)}{a(1 - S_{11})(S_{32} - S_{33} + 1)}$$

5.2.3 Mutant Fitness

Suppose a rare mutation causes heterozygous individuals to allocate $\bar{p}$, rather than p, to offspring production once they become a breeder. For simplicity, assume there is no inbreeding. While the mutant is rare, we have five classes of individuals, and can describe the population as follows

- u_1, density of mutant floaters
- u_2, density of solitary mutant breeders
- u_3, density of mutant breeders with wildtype helpers
- u_4, density of mutant breeders with mutant helpers
- u_5, density of wildtype helpers with mutant helpers

The fitness of the mutant is given by the largest eigenvalue of the 5×5 Jacobian matrix J_1,

$$J_1 = \begin{bmatrix} j_{11} & j_{12} & j_{13} & j_{14} & j_{15} \\ j_{21} & j_{22} & j_{23} & j_{24} & j_{25} \\ 0 & j_{32} & j_{33} & j_{34} & j_{35} \\ 0 & j_{42} & j_{43} & j_{44} & 0 \\ 0 & j_{52} & j_{53} & j_{54} & 0 \end{bmatrix},$$

where each entry, j_{ij} represents the proportion of individuals from class j that will move to class i in the next season. Similar Jacobian matrices, J_2 and J_3, can be constructed for the invasion of mutants that allocate $\bar{q}$, rather than q, when they become a helper, and the invasion of individuals that allocate $\bar{p_0}$, rather than p_0, when they are breeding without helpers, respectively.

Table 5.1: Variables and parameters used in the main text

Symbol	Explanation
p	Proportion of breeder resources allocated toward reproduction
q	Proportion of helper resources allocated toward reproduction
d	Probability with which offspring are unwilling to help
λ	Expected number of offspring produced per season by a breeder with a helper
α	Expected number of offspring produced per season by a lone breeder
s_{B_0}	Probability that a lone breeder will survive the season
s_B	Probability that a breeder who is aided by an auxiliary will survive the season
t	Probability that floaters survive from one season to the next
V_E	Population of lone breeders at equilibrium
W_E	Population of breeders with auxilliares at equilibrium
U_E	Population of floaters at equilibrium

The fitness of a mutant who allocates a deviant amount to offspring production, $\bar{p}$, whenever it is a breeder with a helper is given by the largest eigenvalue of J_1, λ_1. Here, λ_1 measures the growth rate of a rare mutant. Similarly, the fitness of mutant helpers (resp. mutant solitary breeders) that allocate $\bar{q}$ (resp. $\bar{p_0}$) to offspring production is given by the largest eigenvalue of J_2 (resp. J_3), λ_2 (resp. λ_3). To verify that the Jacobian is correct, computer simulation reveals $\lambda_1 = 1$ when $\bar{p} = p$; that is to say, a neutral mutation introduced in the resident population will be neither selected for nor against.

We can solve for the equilibrium strategy set by taking the derivative of λ_1, λ_2, and λ_3 with respect to $\bar{p}$, $\bar{q}$ and $\bar{p_0}$, respectively, setting each equal to zero evaluated at $p = \bar{p}, q = \bar{q}, p_0 = \bar{p_0}$. That is, the candidate evolutionarily stable strategy (ESS) set, (p, q, p_0), can be derived by

solving the system of equations:

$$\left(\frac{\delta\lambda_1}{\delta\bar{p}}\right)\Bigg|_{p=\bar{p},q=\bar{q},p_0=\bar{p_0}} = 0$$
$$\left(\frac{\delta\lambda_2}{\delta\bar{q}}\right)\Bigg|_{p=\bar{p},q=\bar{q},p_0=\bar{p_0}} = 0$$
$$\left(\frac{\delta\lambda_3}{\delta\bar{p_0}}\right)\Bigg|_{p=\bar{p},q=\bar{q},p_0=\bar{p_0}} = 0$$

This system can not be solved analytically, but convergent stable equilibria can be found numerically. The convergent stable allocation strategy, (p, q, p_0), can then be used to calculate the expected clutch size of breeders with and without helpers, $\lambda(p, q)$ and $\alpha(p_0)$, respectively.

5.2.4 Breeder-auxiliary conflict

The above analysis tacitly assumes that breeders and helpers control only their own resource allocation strategy. Breeders and helpers may differ in their optimal resource allocation strategies. As such, clutch sizes at equilibria derived using the above method (henceforth called the 'realized' clutch size) are the product of conflict between breeder and auxiliary over resource allocation. Hardling & Kokko, however, do not incorporate this conflict in their model, and instead assume that realized clutch size is equivalent to breeder's optimal clutch size. To highlight the consequences of neglecting this conflict, we compare the breeder's optimal clutch size, the helper's optimal clutch size, and the realized clutch size.

To determine breeders' optimal clutch size, suppose a rare mutation causes breeders to control both the proportion of resources that they and their helpers allocate toward offspring production; that is, the mutant allocates $\bar{p}$, rather than p, to offspring production, and its helpers allocate $\bar{q}$, rather than q. The method used to solve for candidate ESS sets is the same as that delineated in Section 2.3, except the entries in the Jacobians may change. For example, con-

sider the expected number of offspring produced by mutants breeders with wildtype helpers (class u_3). If we assume that breeders and helpers control only their resource allocation strategy, then the number of offspring produced is $\lambda(\bar{p}, q)$, whereas if we assume breeder control over helper allocation strategy, the expected number of offspring is $\lambda(\bar{p}, \bar{q})$.

Similarly, to calculate helpers' optimal clutch size, we suppose a rare mutation causes helpers to control both the proportion of resources that they and their breeder allocate toward offspring production; that is, the mutant allocates $\bar{q}$, rather than q, to offspring production, and its breeder allocate $\bar{p}$, rather than p.

5.3 Results

To understand how the emergence of cooperative breeding affects clutch size at evolutionary equilibrium, we examined how clutch sizes changed as a function of offspring willingness to help, $1 - d$. Before the emergence of cooperative breeding (i.e. $d = 0$), clutch size can be measured in only one way - the value of α, as all breeders are without helpers. After the emergence of cooperative breeding, clutch size at equilibrium can be measured in two ways. The first measure of clutch size, $\lambda p, q$, is the expected number of offspring produced by a breeder-auxiliary pair per season. This is the measure studied in Hardling & Kokko's model. Alternatively, clutch size can be measured by, $c = \frac{V_E}{V_E+W_E}\alpha + \frac{W_E}{V_E+W_E}\lambda$, which denotes the weighted average clutch size, or the expected number of offspring produced per season by a given breeder within the population sampled uniformly at random. This was what is measured in comparative analyses [12]. There is an important distinction between these two measurements: clutch size data collected by empirical studies are very frequently derived from non-obligate cooperative breeders. As such, when comparing the result of our model to empirical data, the weighted average clutch size is most important, and when comparing Hardling & Kokko's model to ours, λ is the quantity of interest.

For each of the models, whether or not the helper stays, and whether or not there is local kin competition, there is a wide set of biological reasonable parameter conditions that allow for both measurements of clutch size of cooperative breeders, c and λ, to be the same or larger than that of non-cooperative breeders (Figures 5.3.1, 5.3.2). That is, biologically meaningful functions of the model's parameters (s_B, s_{B_0}, λ, and α) can be selected such that the convergent stable clutch size (both c and λ) are uniformly larger once cooperative breeding has emerged ($d > 0$) than before it evolves ($d = 0$). However, the effects of the emergence of cooperative breeding on clutch are variable, and depend on parameter conditions. Ultimately we found that clutch size can increase, decrease or remain unaffected by the emergence of helping behaviour. That the emergence of cooperative breeding can affect the two different measurements of brood size in different ways (Figure 5.3.1) highlights the importance of distinguishing c and λ: the emergence of helping behaviour may not affect the clutch sizes of breeders without help and breeders with help in same way. For example, if helpers are far more effective at increasing breeder survival than fecundity, then the clutch size of breeders with helpers may smaller than that of breeders before the emergence of helping behaviour. But after the emergence of help, breeders without helpers may try to increase their clutch size in the attempt to gain greater levels of help in subsequent seasons. The result is that while Hardling & Kokko's model would have accurately concluded that λ decreases after the emergence of cooperative breeding, empirical studies, which instead measure c, may reach the opposite conclusion.

Whenever clutch size increases after the emergence of cooperative breeding, the cause is frequently though not always the conflict between the breeder and the auxiliary over resource allocation (Figure 5.3.1b). That is, if the realized allocation strategy was equivalent to the optimal allocation strategy from the breeder's perspective rather than a compromise between the optimal strategies of the breeder and of the follower, there would be fewer conditions that favour larger clutch sizes as the propensity to help increases. Still, in many situations the op-

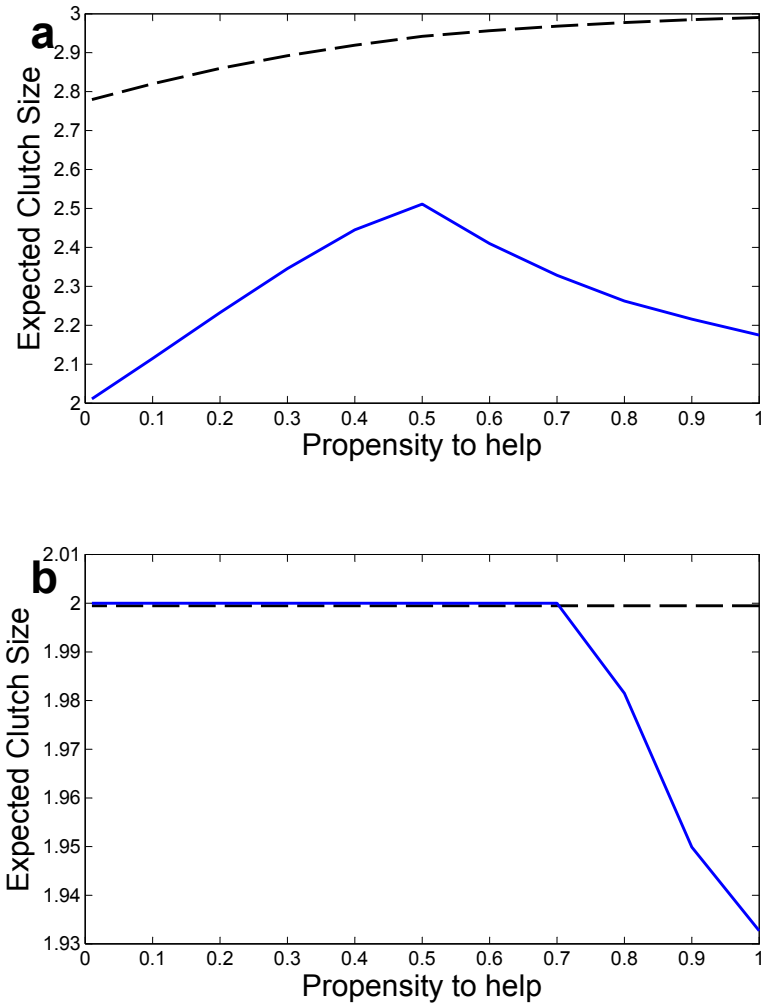

Figure 5.3.1: Cooperative breeders may have larger clutch sizes than non-cooperative breeders. The dotted black line in (a) represents the expected clutch size created by a breeder-auxiliary pair. The solid blue line (a) represents the expected clutch size of a given breeder in the population. In both cases, a population that does not breed cooperatively will have a smaller clutch size than a non-cooperatively breeding population, under the same life-history conditions. The dotted black line and the solid blue in (b) represent the expected clutch size created by a breeder-auxiliary pair and by a given breeder in the population, respectively, if the outcome of the conflict between breeder and helper was exactly equal to the strategy set favoured by the breeder. Note that in the absence of the breeder-auxiliary conflict, one concludes that clutch size does not increase (and indeed, may decrease) as helping behaviour becomes more prevalent. Results were generated assuming both that helpers stay only temporarily and that there is no local kin competition, and using $s_B = 0.7 + 0.1p + 0.25(2q - 1)$, $s_{B_0} = 0.7 + 0.1p_0$, $\lambda = 2(1 - p + 0.5(1 - q))$, $\alpha = 2(1 - p_0)$, $s_H = 1 - 0.1q - 0.3(1 - q)$.

timal strategy of the breeder favours a decrease in brood size as helping behaviour increases in frequency (Figure 5.3.3). For example, if indeed helping behaviour is truly beneficial to the breeder, and if helpers are able to improve fecundity far more significantly than survival, then breeders with greater levels or frequency of help should be expected to produce a greater number of offspring.

On occassion, the emergence of helping behaviour affects clutch size in non-uniform ways: in many cases, the clutch size of a cooperative breeding system may be higher than that of breeders before cooperative breeding emerged only for certain dispersal rates. For example, if helping behaviour is common (d is low) and clutch size can be significantly increased with greater investment, then the probability of receiving helping is largely contingent upon allocating a significant proportion of resources to offspring production. As helping becomes rarer, producing more offspring does little to improve the chances of receiving help, so breeders use a greater share of resources on survival rather than fecundity. This ultimately translates to a decrease in brood size as dispersal rates increase, and thus cooperative breeding promotes larger clutch sizes only when d is sufficiently small.

5.4 Discussion

5.4.1 Revisiting Previous Theory

The influence of the emergence of cooperative breeding on clutch size is not as simple as Hardling & Kokko's model may suggest. In our model, the relationship between clutch size and the emergence of cooperative breeding is highly variable, and depends heavily on how resource allocation influences survival and fecundity. We therefore conclude that the effect of cooperative breeding on clutch size is likely to vary between species. This result is supported by Beauchamp's comparative analysis, which indicates that while the difference between the clutch size of pairs of closely related cooperative and non-cooperative breeders is, on average,

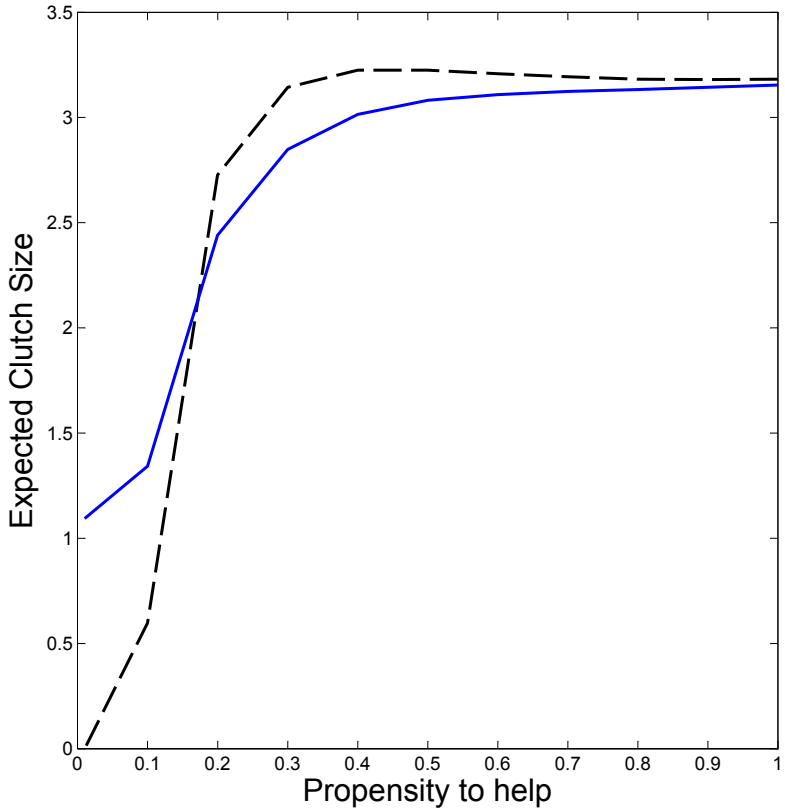

Figure 5.3.2: The clutch size of cooperative breeders may be larger than that of non-cooperative breeders under a wide variety of life-history assumptions. The dotted black line in (a) represents the expected clutch size created by a breeder-auxiliary pair. The solid blue line (a) represents the expected clutch size of a given breeder in the population. Results were generated assuming helpers remain on their natal patch and that there is local kin competition, and using $s_B = 0.7 + 0.1p + 0.25(2q - 1)$, $s_{B_0} = 0.7 + 0.1p_0$, $\lambda = 2(1 - p + 0.5(1 - q))$, $\alpha = 2(1 - p_0)$, $s_H = 1 - 0.1q - 0.3(1 - q)$.

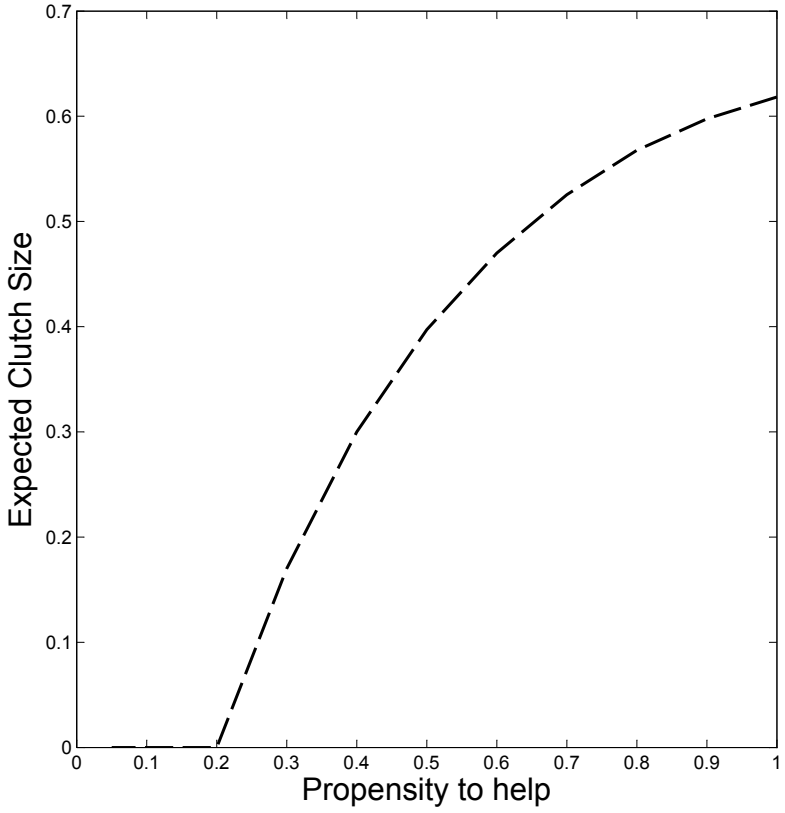

Figure 5.3.3: The breeder's optimal clutch size for cooperative breeders may be significantly larger than that of non-cooperative breeders. Under the conditions used to generate these results, the realized allocation strategy set was equivalent to that of the breeder's optimal strategy set. Note that brood size in this situation approaches zero as the propensity to help increases because breeders with helpers have extremely low mortality, and thus it optimal for the breeder to breed only through male function. Results were generated assuming helpers remain on their natal patch and that there is local kin competition, and using $s_B = 0.7 + 0.3\sqrt{\frac{1.3(p+q)}{3.5}}$, $s_{B_0} = 0.7 + 0.3\sqrt{\frac{1.3p_0}{3.5}}$, $\alpha = 3(1 - p_0)$, $s_H = 1 - 0.1q + 0.2(1 - q)$.

negligible, it varies considerately between pairs, with some cooperatively breeding species having substantially larger clutch sizes than their non-cooperatively breeding counterparts, while in other pairs the opposite trend is present.

The differences in the conclusions generated in our model compared to that of Hardling & Kokko's model are not simply the product of different assumptions about the ecology of cooperatively breeding species. Indeed, even when the main assumption used in Hardling & Kokko's model - that philopatric offspring are better off than dispersing offspring - is maintained in our model (see Appendix 5.6), one still finds that clutch size does not necessarily (Figure 5.3.1) decrease after the emergence of cooperative breeding.

It is also important to note that the emergence and frequency of helpful behaviour in our model does not influence the carrying capacity of the population, which is a function only of the constant a. Thus clutch size may increase after the emergence of cooperative breeding even though there are diminishing returns on the reproductive value of each offspring. Put simply, if helpers increase the reproductive output of breeder's far more efficiently than they improve breeder survival, a greater total amount of effort will be allocated toward fecundity by a breeder-auxiliary pair than a lone breeder in a non-cooperatively species, all else being equal. Even though each offspring is unlikely to ever become a breeder, and even though increasing clutch size augments this competition, the cost on survival for the production of more offspring is relatively small.

5.4.2 Conflict Over Helping Behaviour

The idea that conflict exists between breeder and auxiliary is not new. In addition to conflict over breeding opportunities [21, 22], past research has noted and examined conflict between breeder and auxiliary over helping effort [23, 16]. Although increased helping effort often ultimately allows breeders to produce more offspring, thus providing auxiliaries with indirect

fitness benefits, it is also associated with direct fitness costs in the form of decreased survival. This sets the stage for conflict between breeder and auxiliary: the optimal level of help from the perspective of the breeder often differs from that of the helper [16]. We propose that a similar conflict can exist over the form, rather than the amount, of helping behaviour. Although many forms of help increase both breeder survival and fecundity, certain forms of help from auxiliaries often play a relatively larger role in either increasing the reproductive output of breeders (e.g. nest building, provisioning of offspring) or increasing the survival of the breeder (e.g. territory defense), [24]. Often, the forms of help differ between individuals and across species. Different forms of help provide different costs and benefits for both breeder and auxiliary. Thus helpers may be selective in the forms of helping they which to provide. Breeders also can influence the total amount of effort dedicated toward survival and reproduction in the form of load-lightening.

If territory inheritance is a primary incentive for helping behaviour, then for cooperative breeding to evolve, helpers require a relatively high probability of inheriting the territory on which they provide help. Should breeders exhibit load-lightening in response to the effort of helpers, they increase their own survival, which decreases the probability that a given helper will ever receive the benefits of philopatry. Increasing the reproductive output of breeders is unlikely to affect the probability with which helpers inherit the territory (assuming queue is determined by age), and is likely to increase the number of helpers available once the helper becomes the dominant breeder. Thus in many situations helpers would fare better if breeders do not lighten their load. Breeders on the other hand likely want to increase their survival rather than increasing their annual reproductive effort because, as Hardling & Kokko suggest, increasing brood size often translates to greater kin competition, and therefore diminishing returns on increases in fitness with each additional offspring produce. Thus while load-lightening may be advantageous to breeders in many situations, too much emphasis on survival rather than reproduction will disincentivize the emergence of helping. While the influence of this conflict

on the evolution of cooperative breeding was not fully studied here, it can easily be analyzed by either allowing dispersal frequency, d, to evolve, in addition to p, q, and p_0, or by allowing the total helping effort, in addition to resource allocation strategies, to evolve. If resource allocation strategies and cooperative breeding co-evolve, it is expected that the resolution of the conflict between breeder and auxiliary will more highly favour helpers since they are able to reduce helping effort whenever they are unlikely to inherit breeding territories.

In our model, conflict between breeder and auxiliary is not necessarily won by either breeder or helper. Instead, the realized allocation strategies are the result of a compromise. This compromise will favour the party whose fitness is more greatly influenced by the outcome of the conflict. The favoured party will, in general, be the breeder, and this is true for two reasons. First, the helper has some significant probability of never becoming a breeder. Thus even if the helper wins the conflict, there is a greater probability that the direct fitness of the helper rather than that of the breeder is unaffected by the outcome of the conflict. This explains why the resolution of the conflict seems to favour the breeder more significantly if helpers only temporarily assist the breeder, a situation in which helpers are less likely to inherit breeding territories. Second, there is a significant probability that the allocation strategy employed by the helper will also be used by the helper's offspring. Thus, if the helper uses a strategy that is significantly detrimental to the breeder, it may suffer for this strategy once it becomes a breeder. That a mutant helper's offspring are not guaranteed to use the same allocation strategy drives the outcome of the conflict between breeder and helper to not uniformly favour the breeder's optimal strategy.

5.4.3 Limitations & Future Directions

Our model assumes that strategies regarding helpful behaviour are biologically rather than socially acquired. That is, individuals have a single strategy set which they use regardless of the

actions of those with whom they interact. While there has been suggestion that the type of helpful behaviour individuals display can actually be influenced or determined by inherit personality traits [25], it is likely that in nature, both the degree and form helping behaviour and load-lightening can be adapted based on interaction partners. Following McNamara et al. [26], one can modify our model to incorporate a form of negotiation between breeder and auxiliary in order to identify evolutionary stable negotation rules. However, since conflict between breeder and helper is not necessary for the emergence of cooperative breeding to increase clutch size, this modification will not alter the general conclusions of this study. However, it may help to identify how ecological, life-history, and social factors influence load-lightening and both the form and degree of helping behaviour, a topic which has received little attention.

Although in many species breeders commonly have multiple helpers, extending our model to allow the presence of multiple auxiliary will likely serve only to highlight the fact that the emergence of cooperative breeding increases clutch size so as to increase the expected level of help breeders receive in subsequent seasons. It might, however, provide interesting insight into how allocation strategies and helping effort change as a function of the number of auxiliaries present [16].

Since this is a model of hermaphrodites rather than dioecious species, breeders are always able to produce offspring through paternal function, and so clutch size - the number of offspring produced through maternal function - and total offspring produced are not equivalent in our model. Thus the fitness of an individual is less affected by allocation strategies than the parameters α and λ may indicate. Consequently, we are limited in our ability to directly translate empirical data into parameter values in our model. One could extend our model to describe the behaviour of dioecious species. Doing so may allow for direct and precise predictions regarding the relationship between the emergence of cooperative breeding and brood size of specific species. This would also allow for greater exploration of the conflict between

parents, in addition to the conflict between breeder and auxiliaries, over helping effort and form.

Modelling dioecious species populations may also allow one to examine how genomic imprinting affects both auxiliary helping effort and the form of helpful behaviour (namely whether help favours increase fecundity or survival). For example, in some cooperatively breeding species, maternal investment is significantly higher than paternal investment [27, 16]. If in these species males are frequently successful in finding new mates in the event that their current mates die, then their fitness is relatively independent of the mother's probability of surviving to the next breeding season. Naturally, fathers will be concerned about offspring survival. This may allow for genomic imprinting to influence helping behaviour [28]: if the father is only concerned with the mother's fecundity and not her survival, his genes may influence offspring to focus their effort in increasing breeder fecundity rather than survival once they become auxiliaries. As we have shown here, it is unclear what resource allocation strategy is optimal for the mother, though it may differ from the optimal allocations strategy of the father.

5.5 Conclusions

In agreement with recent empirical data but in contrast to previous theoretical work, our model demonstrates that the emergence of cooperative breeding does not necessarily lead to smaller clutch sizes. As such, even though small clutch sizes may predispose species to breeder cooperatively, clutch size may not be a trait that has a clear association with cooperative breeding. While the connection between longevity and cooperative breeding has received greater support from empirical studies, it too is a life-history trait whose association with cooperative breeding been recently been questioned [29]. We echo Hardling & Kokko on the importance of analyzing both how a life-history trait may pre-dispose a species to cooperative breeding and how cooperative breeding influences the evolution of the life-history, but stress that to do so, thorough inclusive-fitness models that incorporate population dynamics are required.

Acknowledgements

Funding was provided by NSERC.

5.6 Population Dynamics

5.6.1 Example calculations: Model #1 (No local kin competition; helper leaves)

$$
\begin{aligned}
U' =& (1 - \frac{1}{1 + a(V + W)})tU \\
&+ s_{B_0} V \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((k-1)(1-d^k) + kd^k) \\
&+ (1 - s_{B_0}) V \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!} k \\
&+ s_B W \sum_{l=1}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}((l-1)(1-d^l) + ld^l) \\
&+ (1 - s_B)(1 - s_H) W \sum_{l=1}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!} l \\
&+ (1 - s_B) s_H W \sum_{l=1}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}((l-1)(1-d^l) + ld^l) \\
&+ s_B s_H W
\end{aligned}
$$

$$
\begin{aligned}
V' =& \frac{1}{1 + a(V + W)} tU \\
&+ s_{B_0} V \sum_{k=0}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!} d^k \\
&+ s_B W \sum_{l=0}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!} d^l \\
&+ (1 - s_B) s_H W \sum_{l=0}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!} d^l
\end{aligned}
$$

$$\begin{aligned} W' =& W_{S_B} \sum_{l=1}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}(1-d^l) \\ &+ (1-s_B)s_H W \sum_{l=1}^{\infty} \frac{\exp(-\alpha)\alpha^l}{l!}(1-d^l) \\ &+ s_{B_0} V \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1-d^k) \end{aligned}$$

Suppose a rare mutation causes heterozygous individuals to allocate $\bar{p}$, rather than p, when they become a breeder (any terms with bars over them are a function of $\bar{p}$, and therefore represent mutant behaviour or the product of mutant behaviour). For simplicity, assume there is no inbreeding. While the mutant is rare, we have five classes of individuals

Matrix Entry	Expression
Column 1	
j_{11}	$(1-\frac{1}{1+a(V_E+W_E)})t$
j_{21}	$\frac{t}{1+a(V_E+W_E)}$
Column 2	
j_{12}	$\frac{1}{2}(1+\frac{V_E}{V_E+W_E})(s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_{B_0})\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}k)+\frac{1}{2}\frac{W_E}{V_E+W_E}((1-s_B)s_H\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_B)(1-s_H)\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}k+s_B\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k))$
j_{22}	$s_{B_0}\sum_{k=0}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}d^k$
j_{32}	$\frac{1}{2}s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}(1-d^k)$
j_{42}	$\frac{1}{2}s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}(1-d^k)$
j_{52}	$\frac{1}{2}((1-(1-s_B)(1-s_H))\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}(1-d^k)\frac{W_E}{W_E+V_E}+S_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}(1-d^k)\frac{V_E}{W_E+V_E})$
Column 3	

j_{13} $\frac{1}{2}(1-\bar{s_B})\bar{s_H}\sum_{k=1}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}((1-d^k)(k-1)+kd^k)+\frac{1}{2}(1-\bar{s_B})(1-\bar{s_H})\sum_{k=1}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}k+\frac{1}{2}\bar{s_B}\sum_{k=2}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}((1-d^k)(k-1)+kd^k))+\frac{1}{2}(\frac{V_E}{V_E+W_E}(s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_{B_0})\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}k))+\frac{W_E}{V_E+W_E}((1-s_B)s_H\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_B)(1-s_H)\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}k+s_B\sum_{k=2}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k))$

j_{23} $\bar{s_B}\sum_{k=0}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}d^k$

j_{33} $\frac{1}{2}\bar{s_B}\sum_{k=1}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}(1-d^k)$

j_{43} $\frac{1}{2}\bar{s_B}\sum_{k=1}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}(1-d^k)$

j_{53} $\frac{1}{2}(1-\bar{s_B})\bar{s_H}\sum_{k=1}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}(1-d^k)+\frac{1}{2}((1-(1-s_B)(1-s_H))\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}(1-d^k)\frac{W_E}{W_E+V_E}+s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}(1-d^k)\frac{V_E}{W_E+V_E})$

Column 4

j_{14} $\bar{s_H}\bar{s_B}+\frac{1}{2}(1-\bar{s_B})\bar{s_H}\sum_{k=1}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}((1-d^k)(k-1)+kd^k)+\frac{1}{2}(1-\bar{s_B})(1-\bar{s_H})\sum_{k=1}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}k+\frac{1}{2}\bar{s_B}\sum_{k=2}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}((1-d^k)(k-1)+kd^k)+\frac{1}{2}(\frac{V_E}{V_E+W_E}(s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_{B_0})\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}k))+\frac{W_E}{V_E+W_E}((1-s_B)s_H\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_B)(1-s_H)\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}k+s_B\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k))$

j_{24} $\bar{s_B}\sum_{k=0}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}d^k+(1-\bar{s_B})\bar{s_H}\sum_{k=0}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}d^k$

j_{34} $\frac{1}{2}(1-(1-\bar{s_B})(1-\bar{s_H}))\sum_{k=1}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}(1-d^k)$

j_{44} $\frac{1}{2}(1-(1-\bar{s_B})(1-\bar{s_H}))\sum_{k=1}^{\infty}\frac{\exp(-\bar{\lambda})\bar{\lambda}^k}{k!}(1-d^k)$

j_{54} $\frac{1}{2}((1-(1-s_B)(1-s_H))\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}(1-d^k)\frac{W_E}{W_E+V_E}+S_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}(1-d^k)\frac{V_E}{W_E+V_E})$

Column 5

j_{15} $s_B s_H$

j_{25} $(1-s_B)s_H\sum_{k=0}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}d^k$

j_{35}	$(1-s_B)s_H\sum_{k=0}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}(1-d^k)$

Suppose a rare mutation causes heterozygous individuals to allocate $\bar{q}$, rather than q, when they become a helper(any terms with dots over them are a function of $\bar{q}$, and therefore represent mutant behaviour or the product of mutant behaviour).

Matrix Entry	Expression
Column 1	
j_{11}	$(1-\frac{1}{1+a(V_E+W_E)})t$
j_{21}	$\frac{t}{1+a(V_E+W_E)}$
Column 2	
j_{12}	$\frac{1}{2}(1+\frac{V_E}{V_E+W_E})(s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_{B_0})\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}k)+\frac{1}{2}\frac{W_E}{V_E+W_E}((1-s_B)s_H\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_B)(1-s_H)\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}k+s_B\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k))$
j_{22}	$s_{B_0}\sum_{k=0}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}d^k$
j_{32}	$\frac{1}{2}s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}(1-d^k)$
j_{42}	$\frac{1}{2}s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}(1-d^k)$
j_{52}	$\frac{1}{2}((1-(1-s_B)(1-s_H))\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}(1-d^k)\frac{W_E}{W_E+V_E}+S_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}(1-d^k)\frac{V_E}{W_E+V_E})$
Column 3	
j_{13}	$\frac{1}{2}(1-s_B)s_H\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k)+\frac{1}{2}(1-s_B)(1-s_H)\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}k+\frac{1}{2}s_B\sum_{k=2}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k))+\frac{1}{2}(\frac{V_E}{V_E+W_E}(s_{B_0}\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_{B_0})\sum_{k=1}^{\infty}\frac{\exp(-\alpha)\alpha^k}{k!}k))+\frac{W_E}{V_E+W_E}((1-s_B)s_H\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k)+(1-s_B)(1-s_H)\sum_{k=1}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}k+s_B\sum_{k=2}^{\infty}\frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k))$

j_{23} $s_B \sum_{k=0}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!} d^k$

j_{33} $\frac{1}{2} s_B \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!} (1 - d^k)$

j_{43} $\frac{1}{2} s_B \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!} (1 - d^k)$

j_{53} $\frac{1}{2}(1 - s_B)s_H \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k) + \frac{1}{2}((1 - (1 - s_B)(1 - s_H)) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)\frac{W_E}{W_E+V_E} + s_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}(1 - d^k)\frac{V_E}{W_E+V_E})$

Column 4

j_{14} $\dot{s_H}\dot{s_B} + \frac{1}{2}(1-\dot{s_B})\dot{s_H} \sum_{k=1}^{\infty} \frac{\exp(-\dot{\lambda})\dot{\lambda}^k}{k!}((1-d^k)(k-1)+kd^k) + \frac{1}{2}(1-\dot{s_B})(1-\dot{s_H}) \sum_{k=1}^{\infty} \frac{\exp(-\dot{\lambda})\dot{\lambda}^k}{k!}k + \frac{1}{2}\dot{s_B} \sum_{k=2}^{\infty} \frac{\exp(-\dot{\lambda})\dot{\lambda}^k}{k!}((1-d^k)(k-1)+kd^k) + \frac{1}{2}(\frac{V_E}{V_E+W_E}(s_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}((1-d^k)(k-1)+kd^k) + (1-s_{B_0}) \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}k)) + \frac{W_E}{V_E+W_E}((1 - s_B)s_H \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1 - d^k)(k - 1) + kd^k) + (1 - s_B)(1 - s_H) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}k + s_B \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1 - d^k)(k - 1) + kd^k))$

j_{24} $\dot{s_B} \sum_{k=0}^{\infty} \frac{\exp(-\dot{\lambda})\dot{\lambda}^k}{k!} d^k + (1 - \dot{s_B})\dot{s_H} \sum_{k=0}^{\infty} \frac{\exp(-\dot{\lambda})\dot{\lambda}^k}{k!} d^k$

j_{34} $\frac{1}{2}(1 - (1 - \dot{s_B})(1 - \dot{s_H})) \sum_{k=1}^{\infty} \frac{\exp(-\dot{\lambda})\dot{\lambda}^k}{k!}(1 - d^k)$

j_{44} $\frac{1}{2}(1 - (1 - \dot{s_B})(1 - \dot{s_H})) \sum_{k=1}^{\infty} \frac{\exp(-\dot{\lambda})\dot{\lambda}^k}{k!}(1 - d^k)$

j_{54} $\frac{1}{2}((1 - (1 - s_B)(1 - s_H)) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)\frac{W_E}{W_E+V_E} + S_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}(1 - d^k)\frac{V_E}{W_E+V_E})$

Column 5

j_{15} $\dot{s_B}\dot{s_H}$

j_{25} $(1 - \dot{s_B})\dot{s_H} \sum_{k=0}^{\infty} \frac{\exp(-\dot{\lambda})\dot{\lambda}^k}{k!} d^k$

j_{35} $(1 - \dot{s_B})\dot{s_H} \sum_{k=0}^{\infty} \frac{\exp(-\dot{\lambda})\dot{\lambda}^k}{k!}(1 - d^k)$

Suppose a rare mutation causes heterozygous individuals to allocate $\bar{p_0}$, rather than p_0, when they become a helper(any terms with tildes over them are a function of $p\bar{0}1$, and therefore represent mutant behaviour or the product of mutant behaviour).

Matrix Entry	Expression
Column 1	
j_{11}	$(1 - \frac{1}{1+a(V_E+W_E)})t$
j_{21}	$\frac{t}{1+a(V_E+W_E)}$
Column 2	
j_{12}	$\frac{1}{2}(s\tilde{}_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\tilde{\alpha})\tilde{\alpha}^k}{k!}((1 - d^k)(k - 1) + kd^k) + (1 - s\tilde{}_{B_0}) \sum_{k=1}^{\infty} \frac{\exp(-\tilde{\alpha})\tilde{\alpha}^k}{k!}k) + \frac{1}{2}\frac{V_E}{V_E+W_E} \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}((1 - d^k)(k - 1) + kd^k) + (1 - s_{B_0}) \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}k) + \frac{1}{2}\frac{W_E}{V_E+W_E}((1 - s_B)s_H \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1 - d^k)(k - 1) + kd^k) + (1 - s_B)(1 - s_H) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}k + s_B \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1 - d^k)(k - 1) + kd^k))$
j_{22}	$s\tilde{}_{B_0} \sum_{k=0}^{\infty} \frac{\exp(-\tilde{\alpha})\tilde{\alpha}^k}{k!}d^k$
j_{32}	$\frac{1}{2}s\tilde{}_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\tilde{\alpha})\tilde{\alpha}^k}{k!}(1 - d^k)$
j_{42}	$\frac{1}{2}s\tilde{}_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\tilde{\alpha})\tilde{\alpha}^k}{k!}(1 - d^k)$
j_{52}	$\frac{1}{2}((1 - (1 - s_B)(1 - s_H)) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)\frac{W_E}{W_E+V_E} + S_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}(1 - d^k)\frac{V_E}{W_E+V_E})$
Column 3	
j_{13}	$\frac{1}{2}(1 - s_B)s_H \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1 - d^k)(k - 1) + kd^k) + \frac{1}{2}(1 - s_B)(1-s_H) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}k + \frac{1}{2}s_B \sum_{k=2}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k)) + \frac{1}{2}(\frac{V_E}{V_E+W_E}(s_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}((1-d^k)(k-1)+kd^k) + (1-s_{B_0}) \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}k)) + \frac{W_E}{V_E+W_E}((1 - s_B)s_H \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1 - d^k)(k - 1) + kd^k) + (1 - s_B)(1 - s_H) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}k + s_B \sum_{k=2}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1 - d^k)(k - 1) + kd^k))$
j_{23}	$s_B \sum_{k=0}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}d^k$
j_{33}	$\frac{1}{2}s_B \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)$
j_{43}	$\frac{1}{2}s_B \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)$

j_{53} $\frac{1}{2}(1 - s_B)s_H \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k) + \frac{1}{2}((1 - (1 - s_B)(1 - s_H)) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)\frac{W_E}{W_E+V_E} + s_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}(1 - d^k)\frac{V_E}{W_E+V_E})$

Column 4

j_{14} $s_H s_B + \frac{1}{2}(1-s_B)s_H \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k) + \frac{1}{2}(1-s_B)(1-s_H) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}k + \frac{1}{2}s_B \sum_{k=2}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1-d^k)(k-1)+kd^k) + \frac{1}{2}(\frac{V_E}{V_E+W_E}(s_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}((1-d^k)(k-1)+kd^k) + (1-s_{B_0}) \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}k)) + \frac{W_E}{V_E+W_E}((1 - s_B)s_H \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1 - d^k)(k - 1) + kd^k) + (1 - s_B)(1 - s_H) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}k + s_B \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}((1 - d^k)(k - 1) + kd^k))$

j_{24} $s_B \sum_{k=0}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}d^k + (1 - s_B)s_H \sum_{k=0}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}d^k$

j_{34} $\frac{1}{2}(1 - (1 - s_B)(1 - s_H)) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)$

j_{44} $\frac{1}{2}(1 - (1 - s_B)(1 - s_H)) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)$

j_{54} $\frac{1}{2}((1 - (1 - s_B)(1 - s_H)) \sum_{k=1}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)\frac{W_E}{W_E+V_E} + S_{B_0} \sum_{k=1}^{\infty} \frac{\exp(-\alpha)\alpha^k}{k!}(1 - d^k)\frac{V_E}{W_E+V_E})$

Column 5

j_{15} $s_B s_H$

j_{25} $(1 - s_B)s_H \sum_{k=0}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}d^k$

j_{35} $(1 - s_B)s_H \sum_{k=0}^{\infty} \frac{\exp(-\lambda)\lambda^k}{k!}(1 - d^k)$

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Chapter 6

Concessions and the Evolution of Coalitionary behaviour

Koykka, C. & Wild, G. (2016) Concessions, lifetime fitness consequences, and the evolution of coalitionary behaviour. *Behav. Ecol*. 28(1): 20-30.

Abstract

The relationship between the costs of coalitionary behaviour and the evolution of such behaviour has not been closely examined by theoretical studies. Here, we create a set of life-history models for species whose coalitionary behaviour is genetically determined to investigate how different types of costs afflicted upon members of failed coalitions, in terms of survival, fecundity, and social rank, may influence the nature of coalitionary behaviour that emerges at evolutionary equilibrium. We also extend previous theory by examining the coevolution between coalitionary behaviour and concessions granted by dominant individuals to prevent dominants from being targeted by coalitions. We show that species that form coalitions to contest social rank evolve to regularly form bridging coalitions under a vast majority of social and ecological settings, whereas species that contest fecundity form all-up coalitions under most conditions. Further, dominant individuals concede resources to subordinates to prevent coalitionary attacks only in very few circumstances, and these concessions occur only to ensure another individual is a more attractive

coalition target. We compare and contrast results to empirical data to provide an evolutionary context for commonly observed coalitionary behaviours in the animal kingdom.

6.1 Introduction

In behavioural ecology, coalitions generally refer to two or more individuals that temporarily cooperate in joint action against a third party [1]. This widespread and complex phenomenon has been thoroughly studied by a large number of game theoretical models [for review see 2]. However, a recent comprehensive comparison [3] between these models and a vast amount of data collected by field biologists reveals an important lack of communication between theorists and empiricists. An aspect of coalitionary behaviour which has largely been left unexamined in the theoretical literature is the cost of forming coalitions [3], particularly if the coalitions are unsuccessful. Yet empiricists rely on theoretical models to identify the types of costs related to coalition formation and coalition failure since these costs are frequently intangible, difficult to observe directly [4], and may manifest in a variety of forms [5], such as decreased survival [6, 7] and opportunity costs (e.g. decreased fecundity or rank in the social hierarchy) [8, 7]. As has been demonstrated previously [9, 10], the evolution of certain social behaviours, such as altruism, is largely contingent upon how the particular life-history trait (fecundity vs. survival) is affected by the behaviour. Therefore, it is reasonable to assume that different forms of consequences resulting from coalitionary behaviour may influence the types of coalitionary behaviour (all-up, bridging, all-down) that evolves.

A second aspect of coalitionary behaviour that remains neglected especially by theoretical work is its connection to concessions — resources given to subordinates by dominants in order to prevent coalitionary action from targetting the dominant. It is challenging to study concessions empirically since it is difficult to distinguish between concessions and a dominant's inability to completely control subordinates, although theoretically it has been shown

that dominants can evolve to concede to their subordinates and that these concessions have the potential to influence group stability and dynamics. For example, concession models of cooperative breeders have demonstrated that the benefits of group augmentation and philopatry under certain conditions may encourage the dominant to concede fecundity to subordinates in the hopes of retaining them [11]. Whereas theoretically it has been shown [12, 13] that under certain conditions it may be favorable for dominant individuals to provide concessions to avoid conflict (i.e. peace incentives [12]), it is unclear whether and under what conditions dominants evolve to provide concessions in order to prevent coalitions from targeting them. Indeed, some animals, such as lions [14, 15], that exhibit coalitionary behaviour also engage in lethal competition over resources and, consequently, dominants of such species may provide peace incentives to prevent these costly engagements, which would explain the relatively low reproductive skew found in these species. In species whose coalitionary behaviour is governed by simple, genetically determined rules, concessions cannot be used to entice coalition formation because coalitionary behaviour does not respond dynamically to concessions; instead, concessions and coalitionary behaviour effectively manifest simultaneously. As such, we hypothesize that concessions will not evolve in species that are incapable of sophisticated cognitive ability.

Here, we create a suite of relatively simple models to better understand the influence of certain social and life-history characteristics on the evolution of coalitionary behaviour. We use these models to show how different types of costs (i.e. survival, fecundity, and rank-changes) affect the types of coalitions (i.e. all-up, all-down, bridging) that emerge. We also investigate the conditions that facilitate the coevolution between coalition formation and the concessions granted to subordinates by dominant individuals to prevent coalitions among subordinates. Our model provides important general conclusions regarding how simple social and life-history characteristics can influence the types of coalitions that form in species that may use simple rules when forming coalitions – species whose coalitionary behaviour has been largely left unexamined in empirical and theoretical studies [7, 3] despite being relatively common [16, 7].

6.2 Model

We follow previous work [17, 2] of many coalition models by focusing on triadic interactions in species with strict hierarchies. Consider a large number of territories, each inhabited by a trio consisting of an alpha, beta, and gamma individual (i.e. individuals in the top, middle, and bottom rank of the social hierarchy, respectively). Suppose initially that apart from their positions in social hierarchies this population is homogeneous, and that rank is simply determined by the order in which individuals arrive on each territory. Each trio produces a large number of offspring each season, and the alpha individual of each group initially has sole control over the distribution of the group's reproductive opportunities. At the beginning of each season, the alpha allocates portion p of all reproductive opportunities to the beta, and portion q to the gamma, and is left with the remaining portion $1 - p - q$ for its own use. We assume that these concessions are genetically controlled, and may evolve over time. Following the distribution of fecundity, individuals on the territory may choose to form a coalition. Each coalition is comprised of two individuals, and each trio can contain at most one coalition. The individual that is not a member of the coalition is the coalition's target. Three types of coalitions are possible in this model: alpha-beta ('all-down'), alpha-gamma ('bridging'), and beta-gamma ('all-up').

6.2.1 Coalition Solicitation

We create two sets of models that describe two different types of social dynamics. The first set assumes a specific pattern of coalition solicitation: following Stamatopoulos et al. [18], we assume that individuals higher in the hierarchy are socially dominant position and are thus able to prevent the formation of certain coalitions that may target them by first themselves forming a coalition (Figure 6.2.1). With probability $x_{1,2}$, the alpha first offers the beta the opportunity to form a coalition. We assume that both parties must be willing participants for a coalition to form. The beta individual accepts the alpha's offer with probability $x_{2,1}$. Should either be unwilling to form the coalition, the alpha next extends the coalition offer to the gamma with

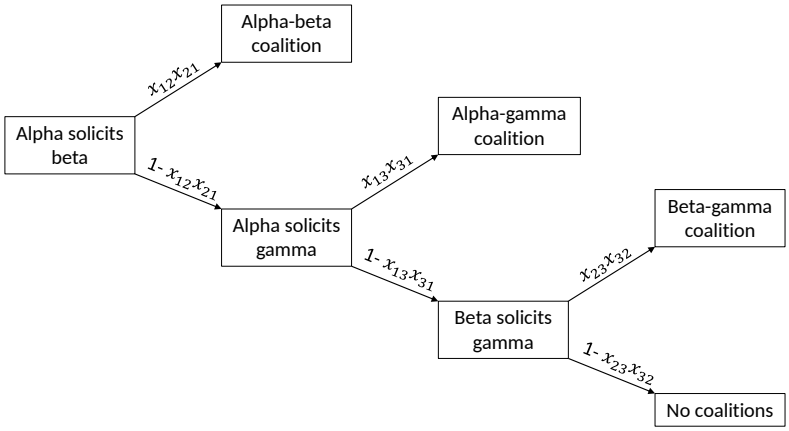

Figure 6.2.1: Scheme outlining sequential coalition solicitation. The probability of each scenario, which are functions of the trio's phenotypic values, is listed above each error. For example, for alpha-gamma coalitions to occur, the alpha must either not offer the beta a chance to form a coalition or the beta must decline (probability $1 - x_{12}x_{21}$), then the alpha must offer the gamma an opportunity to form a coalition and the gamma must accept (probability $x_{13}x_{31}$), and thus the probability of alpha-gamma coalitions is $(1 - x_{12}x_{21})x_{13}x_{31}$. It follows that higher ranked individuals are afforded more opportunities to prevent the formation of coalitions that target them.

probability $x_{1,3}$, and the gamma accepts with probability $x_{3,1}$. If either declines, the beta now gets the opportunity to offer the gamma the opportunity to form a coalition, and does so with probability $x_{2,3}$, while the gamma accepts with probability $x_{3,2}$. Each of these probabilities is genetically determined and may evolve over time. The loci controlling each phenotype is assumed to be on separate chromosomes, such that these phenotypes evolve independently of one another.

The second set of models assumes a scramble solicitation such that no individual has a social advantage during coalition formation. Let $x_{i,c}$ represent the probability that the individual in rank i is willing to form a coalition. Let $x_{i,h}$ represent the probability that the individual in rank i is willing to form a coalition with the higher ranked individual; with probability $1 - x_{i,h}$, the individual is willing to form a coalition with the lower ranked individual. With scram-

ble coalition formation, the probability that an alpha-beta coalition will form, for example, is $x_{1,c}x_{2,c}x_{1,h}x_{2,h}$. Since individuals in the population are homogeneous apart from rank, we assume the probability that coalitions between individuals i and j succeed is constant, given by $c_{i,j}$. The assumption that coalition success is rank-dependent rather than individual-dependent is made of mathematical convenience. Effectively, we assume that while individuals do not vary in intrinsic resource holding potential (RHP), differences in rank may provide individuals with different amounts of resources, information, and motivation [19] which ultimately affects the probability that specific coalitions are successful.

6.2.2 Coalition Consequences

Empirical observations suggest that coalitions can form to contest and maintain either tangible resources such as fecundity (non-rank-changing coalitions) [20, 21] or higher ranks in the hierarchy (rank-changing coalitions) [22, 23, 24]. Further, evidence suggests the cost of being a target of a successful coalition or a member of a failed coalitions may be in the form of reduced fecundity, lower survival and/or lowered rank in the hierarchy [3]. For each set of models (sequential and scramble solicitation), we create a separate model for each situation: (i) non-rank-changing coalitions with fecundity costs, (ii) non-rank-changing coalitions with survival costs, (iii) rank-changing coalitions with fecundity costs, (iv) rank-changing coalitions with survival costs, and (v) rank-changing coalitions with rank-lowering costs (that is, members of failed coalitions are assumed to usurped by the target, should the target not already be the residing alpha).

When coalitions form to contest fecundity, a successful coalition will obtain portion h of the target's resources. For example, should an alpha-beta coalition be successful, it is assumed that the gamma individual loses portion h, leaving it with portion $(1 - h)q$ of all breeding opportunities. This loss in fecundity is divided – not necessarily evenly – between the members of the coalition, with the higher-ranked (dominant) individual receiving portion h_1 of the spoils,

such that the alpha would receive h_1hq, in addition to the $1-p-q$ that it retained, and the beta would receive an additional $(1-h_1)hq$. Should the coalition fail, the dominant individual loses portion $(1-h_1)h(1-p-q)$ and the beta loses $h_1h(1-p-q)$, and this is given to the target of the failed coalition. A similar construction was used for survival cost, where the losing party lost portion h of its survival, although it the victorious party was not assumed to gained increased survival.

6.2.3 Selection gradient

Following coalition formation and the division of fecundity, offspring production occurs. All offspring become floaters that queue for opportunities to join these breeding trios. It is assumed that the reproductive value of all offspring is equal, and the population is at demographic equilibrium (i.e. the population is of constant size), such that the reproductive value of offspring is also equal across seasons. Following reproduction, individuals on breeding territories then have some probability of dying each season. An individual in rank i survives the season with probability s_i. Since each trio collectively produces a very large number of offspring, we assume that there is a sufficient number of individuals in queue to join these hierarchies, such that at the beginning of each season there are always three individuals on each territory (Figure 6.2.2). Hierarchies are determined by the order in which individuals arrive on each territory: individuals who have been on the territory the longest obtain more favorable positions in the hierarchy. Should individuals arrive at the same time, we assume the contest over hierarchy positions is randomly resolved. As relatives tend to form long-term alliances [1], coalitions are rarely observed among relatives [25, 3], and so we will ignore kinship. All variables in the main text are described in Table 6.1.

Table 6.1: Variables and parameters used in the main text

Symbol	Explanation

p	Portion of resources allocated to the beta individual
q	Portion of resources allocated to the gamma individual
$x_{i,j}$	Willingness of individual in rank i to form a coalition with rank j
$c_{i,j}$	Probability that coalition of i and j defeat its target
s_i	Per-season probability of survival for individuals in rank i
h	Proportion of resources lost by losing party
h_1	Proportion of resources lost by dominant individuals in unsuccessful coalitions
$W_{i,j}$	Future reproductive success of an individual in rank j in a trio in state i
$M_{i,j}$	The probability that an individual in state i will be in state j in the following season
$I_{i,j}$	Probability that an individual begins in rank j in a trio in state i

We demonstrate how to calculate the selection gradient for the scenario with sequential solicitation, non-rank-changing coalitions and fecundity costs. Analogous calculations can be applied to the remaining models (see supplementary data).

For each of the models, there are 12 states in which individuals may reside:

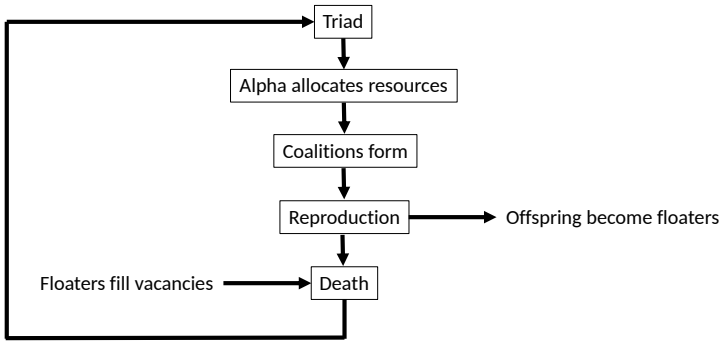

Figure 6.2.2: Lifecycle of individuals in the model. At the beginning of each generation, there is a triad on each territory. First, the alpha proposes a distribution of resources (assumed to directly translate to fecundity). Coalitions may then form, which can alter this distribution of resources or the ranks of individuals. Next, reproduction based on this adjusted distribution of fecundity occurs, with all offspring dispersing to become floaters. At the end of the breeding season, individuals on each territory may die, in which case it is assumed that floaters fill these vacancies, and thus a triad resides on each territory, and the cycle begins. Note we assume that there are a very largely number of territories and that the production of offspring is sufficiently large such that individuals on each territory are unrelated. Note that the population size is unchanging.

Table 6.2: List of positions each individual can hold in the triad

i=1	alpha in an alpha-beta coalition trio
i=2	beta in an alpha-beta coalition trio
i=3	gamma in an alpha-beta coalition trio
i=4	alpha in an alpha-gamma coalition trio
i=5	beta in an alpha-gamma coalition trio
i=6	gamma in an alpha-gamma coalition trio
i=7	alpha in a beta-gamma coalition trio
i=8	beta in a beta-gamma coalition trio
i=9	gamma in a beta-gamma coalition trio
i=10	alpha in a no-coalition trio
i=11	beta in a no-coalition trio
i=12	gamma in a no-coalition trio

To calculate the selection gradient acting on each phenotype, we first derive the future reproductive success associated with each state. We define W_i as the future reproductive success for an individual in state i (e.g. W_6 represents the residual fitness of a gamma in a trio that has formed an alpha-gamma coalition). Let F_i represent the fecundity of an individual in state i; that is, F_i is equal to the number of offspring produced by an individual in state i per season (e.g. $F_{10} = (1 - p - q)$). Lastly, let $M_{i,j}$ represent the probability that an individual in state i transitions into state j in the next generation (e.g. in order for an alpha in trio that contains an alpha-beta coalition in one generation to remain the alpha in a trio that contains an alpha-beta coalition in the next generation, it must survive [probability s_1] and an alpha-beta coalition must then form [probability $x_{1,2}x_{2,1}$]; that is, $M_{1,1} = s_1x_{1,2}x_{2,1}$). The values of each $M_{i,j}$ and F_i for this model are provided in the appendix (see supplementary data for these values in the remaining models). Following Kokko & Johnstone [11], we calculate the fitness of each state by adding the fecundity of an individual in the current breeding season to the future components of fitness, which are weighted by transition probabilities for each state; equivalently, $W_i = F_i + \sum_{j=1}^{12} M_{i,j}W_j$. The solution to these equations is derived analytically using computer software (not shown because of their length). We next use the reproductive success of each state to calculate the fitness of a wild type individual in a wild type population. Let I_i represent the probability that an individual begins its tenure in a trio in state i (e.g.

$I_{10} = (1/3)(1 - s_1)(1 - s_2)(1 - s_3)(1 - x_{1,2}x_{2,1})(1 - x_{1,3}x_{3,1})(1 - x_{2,3}x_{3,2}))$. Then the fitness of a wild type individual is given by $W = \sum_{i=1}^{12} I_i W_i$. In this way, we are able to track the lifetime fitness consequences of coalitionary behaviour, and understand how these consequences vary with respect to life-history and social characteristics.

Suppose now a mutant enters this wild type population and it exhibits deviant behaviour with respect to one of the eight phenotypes under selection; wild type individuals use strategy $s = (p, q, x_{1,2}, x_{1,3}, x_{2,1}, x_{2,3}, x_{3,1}, x_{3,2})$, whereas mutants use a deviant strategy $\bar{s}$. We will demonstrate the calculation of the selection gradient acting on a mutant phenotype by considering a mutation in phenotype, $x_{1,2}$. We now seek to calculate the mutant's future reproductive success in each state, $\bar{W}_i$. Instead of transition probabilities, $M_{i,j}$, being purely a function of the wildtype phenotypes, s, certain entries will be a function of the mutant gene, $\bar{s}$. The entries in which this particular mutation manifests itself are $\bar{M}_{1,k}, \bar{M}_{4,k}, \bar{M}_{7,k}, \bar{M}_{10,k}$ for all k – the remaining transition probabilities remain the same, since the mutant needs to be in the alpha position for its mutation $\bar{x_{1,2}}$ to potentially influence its reproductive output. We then solve the system of equations to calculate $\bar{W}_i$. We apply similar changes to the initial state vector, I to get the mutant's initial state vector, $\bar{I}$. Putting this together, we derive the expected lifetime fitness of an individual with a $\bar{x}_{1,2}$ mutation. We do this for each phenotype under selection in order to develop the following system of equations

$$\frac{\partial W}{\partial \bar{x}_{1,2}}|_{\bar{s}=s}, \frac{\partial W}{\partial \bar{x}_{1,3}}|_{\bar{s}=s}, \frac{\partial W}{\partial \bar{x}_{2,1}}|_{\bar{s}=s}, \frac{\partial W}{\partial \bar{x}_{2,3}}|_{\bar{s}=s}, \frac{\partial W}{\partial \bar{x}_{3,1}}|_{\bar{s}=s}, \frac{\partial W}{\partial \bar{x}_{3,2}}|_{\bar{s}=s}, \frac{\partial W}{\partial \bar{p}}|_{\bar{s}=s}, \frac{\partial W}{\partial \bar{q}}|_{\bar{s}=s} \tag{6.1}$$

This system cannot be solved analytically, but the ESS can be derived numerically by following the effect of the selection gradient given in (6.1) in an iterative fashion [26]. Effectively, under the assumption of weak selection, offspring may have small mutations, and beneficial mutations changes in phenotypic values which would increase an individual's fitness emerge and become fixed in the population [27], such that changes in phenotypic values over time

are travelling along the selection gradients given by (6.1). Specifically, we change the value of each phenotype by some amount proportional to its selection gradient and repeat until, for each of the phenotypes, the selection gradient approaches zero or reaches a boundary imposed by the biologically relevant parameter space $0 \leq p, q, x_{i,j} \leq 1$ (see supplementary material).

6.3 Results

6.3.1 Non-rank-changing coalitions

We first examine coalitionary behaviour arranged to contest fecundity with the costs of failed coalitions shared evenly among members (i.e. $h_1 = 0.5$). Regardless of whether coalition solicitation is performed sequentially or in a scramble, and regardless of whether the costs of failed coalitions are losses in fecundity or survival, alphas generally evolve never to concede any fecundity to the beta and gamma, and beta-gamma coalitions form in response; in fact, this is always the ESS whenever $c_{1,2} > c_{1,3} > c_{2,3}$, a condition expected to hold true whenever those higher in the hierarchy have greater success rates in fights – a common although by no means universal trait of animal hierarchies [7]. The exception is if the probability of alpha-gamma coalition success is substantially lower than the probability of beta-gamma coalition success, $c_{1,3} < c_{2,3}$, in which case oscillations in the degree of concessions as well as the frequency of beta-gamma and alpha-beta coalitions occur (Figure 6.3.3); alphas concede some fecundity to the gamma individual, and consequently both beta-gamma and alpha-beta coalitions evolve. Note that such cyclic equilibria may be the product of the homogeneous population assumption. Survival rates, as well as the degree of fecundity lost by failed coalitions and the targets of successful coalitions have no effect on the outcome of evolution. The fact that the relation between $c_{1,3}$ and $c_{2,3}$ but not the absolute value of $c_{1,3}$ perturbs the system from a pure beta-gamma ESS despite not affecting the payoff structure of an beta-gamma equilibrium suggests that the transient dynamics are important to consider. However, it should also be noted that all listed results are not contingent upon initial conditions.

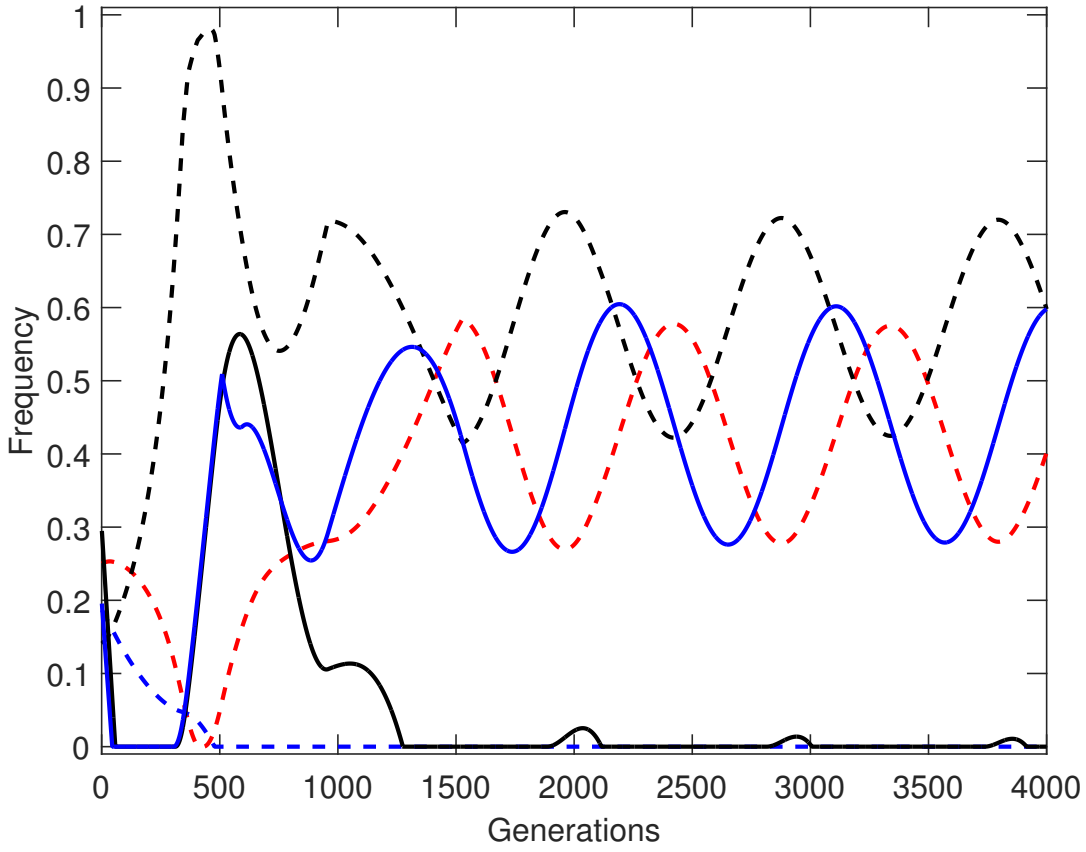

Figure 6.3.3: Change in coalition types and concessions over time when the probability of success for alpha-gamma coalitions is lower than that of beta-gamma coalitions. The solid black and blue lines represent concessions granted to the beta and gamma, respectively. The dashed red, blue, and black lines represent the frequency of alpha-beta, alpha-gamma, and beta-gamma coalitions, respectively. The cycle can be described as follows. Alphas have initially evolved to concede to the gamma and in turn alpha-beta coalitions are initially frequent. However, gamma individuals are then receptive to coalition offers from the beta in order to retain their share of fecundity; beta individuals are willing to align with gammas because alphas are still retain a larger share of fecundity. Eventually, as beta-gamma coalitions become more frequent, the alpha is gaining less from concessions and so concedes less to the gamma, and soon more alpha-beta coalitions occur coalitions occur. The cycle then repeats. Results were generated using $s_1 = 0.9$, $s_2 = 0.85$, $s_3 = 0.8$, $h = 0.9$, $c_{1,2} = 0.95$, $c_{1,3} = 0.55$, $c_{2,3} = 0.75$, $h_1 = 0.5$, and a mutation rate of 0.01.

A relatively common feature in some species [28] is that subordinates bear a greater cost for failed coalitions than do dominants, and dominants receive a greater benefit for successful coalitions than do subordinates (i.e. $h_1 < 0.5$). As before, all-up coalitions are the ESS whenever $c_{1,2} > c_{1,3} > c_{2,3}$ even when $h_1 \neq 0.5$. Little changes because alphas do not share fecundity and are thus usually the target of coalitions; as such, regardless of the value of $0 < h_1 < 1$, subordinate can only improve their fecundity by forming a coalition against the alpha. If $c_{1,3} < c_{2,3}$ and higher-ranked individuals in coalitions receive substantially more than lower-ranked individuals ($0.5 >> h_1 > 0$), then the alpha evolves to concede some fecundity to the gamma, and although beta-gamma coalitions are still the only coalition type to form, the frequency of this coalition oscillates (Figure 6.3.4). In contrast, if lower-ranked individuals in coalitions receive substantially more than higher-ranked individuals ($1 > h_1 >> 0.5$), oscillating levels of beta-gamma coalitions occur but the alpha concedes some fecundity to the beta instead. By conceding to the subordinate that receives the greatest penalty as a result of a failed coalition, the alpha is assured to re-obtain a significant portion of these concessions back if the beta-gamma coalition fails, and by making these concessions the alpha also loses a smaller portion of its fecundity should the coalition succeed.

6.3.2 Rank-changing coalitions

When coalitions are formed with the intent to alter ranks and solicitation occurs sequentially, we once again find that generally alpha individuals evolve to concede nothing to their subordinates; however, alpha-gamma coalitions evolve under a wide range of conditions. There are two exceptions. First, if the survival of beta individuals is significantly less than the survival of gamma individuals, alpha-beta coalitions evolve (while dominant individuals in many species experience greater survival, there are certain species in which dominant individuals suffer greater mortality [29, 30]). Second, if the probability of alpha-gamma coalition success is lower than beta-gamma success, then oscillating levels of beta-gamma and alpha-gamma coalitions evolve.

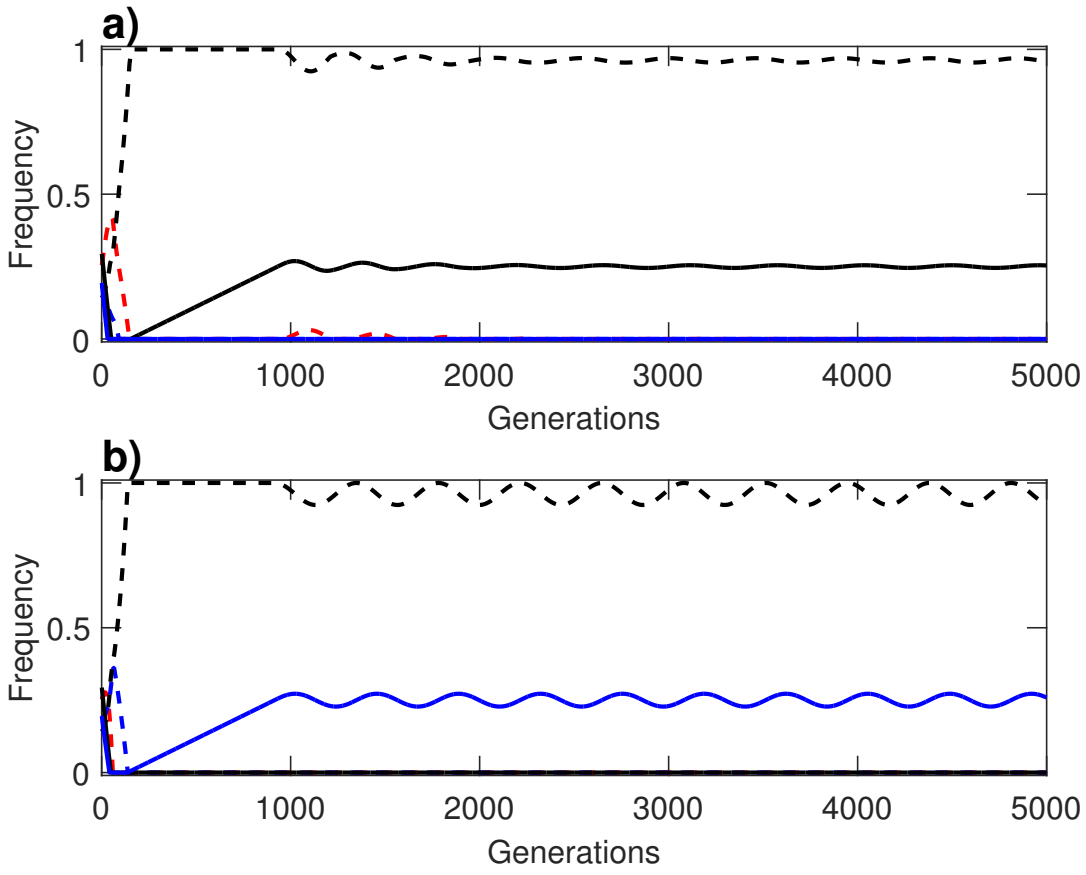

Figure 6.3.4: Frequencies of coalition types and concessions when dominants bear a greater cost and gain less from coalitions (panel a, $h_1 = 0.9$) compared to when subordinates bear a greater cost and gain less from coalitions (panel b, $h_1 = 0.1$). The solid black and blue lines represent concessions granted to the beta and gamma, respectively. The dashed red, blue, and black lines represent the frequency of alpha-beta, alpha-gamma, and beta-gamma coalitions, respectively. Results were generated using $s_1 = 0.9$, $s_2 = 0.85$, $s_3 = 0.8$, $h = 0.9$, $c_{1,2} = 0.95$, $c_{1,3} = 0.55$, $c_{2,3} = 0.75$, and a mutation rate of 0.01.

Alternatively, when coalitions form with scramble solicitation, beta-gamma coalitions evolve unless the survival of beta individuals is low relative to gamma individuals, in which case oscillating levels of alpha-beta coalitions occur.

6.4 Discussion

6.4.1 Rank-changing vs. non-rank-changing coalitions

Our model provides the general, testable prediction that, among species in which dominants are able to monopolize resources, species that use coalitions to contest rank should be more likely to form alpha-gamma, or 'bridging' coalitions, compared to species that form coalitions primarily to contest fecundity, in which beta-gamma, or 'all-up' coalitions, should be favored. The fact that under the majority of parameter conditions alpha-gamma coalitions form when social ranks are being contested and sequential solicitation occurs is expected. The gamma can automatically ascend to the beta position by forming an alliance with either the beta or the alpha. Since the only way for the beta to immediately take over the alpha position is to form a coalition with the gamma, the beta is willing to form a coalition with the gamma. As such, the alpha seeks to pre-empt the opportunity for the beta-gamma coalition to form by themselves forming a coalition with the gamma. With scramble solicitation, the alpha is unable to prevent the beta-gamma coalition, and so beta-gamma coalitions generally evolve. Alternatively, beta-gamma coalitions generally form when fecundity is contested simply because the alpha tends to monopolize resources, and thus there is little for subordinates to lose and much to gain by forming a beta-gamma coalition.

6.4.2 Costs of coalitions

It is difficult to theoretically investigate the costs of coalitionary behaviour because technically it requires models that track the fitness consequences of an individual's decisions through its entire life cycle, rather than identifying evolutionarily stable strategies in single situations, as most previous analytic models have done [31, 32, 33, 34, 35, 36, 37, 2]. By finding what is rational behaviour at each stage of an individual's life cycle in isolation, previous models examine only the immediate, direct fitness consequences of coalitionary behaviour rather than the influence of coalitionary behaviour on an individual's lifetime fitness. The potential need for thorough life-history models of coalitionary behaviour is made further evident by the fact that previous theory has established that in social hierarchies with heritable rank, future benefits and costs may affect current behaviour [11, 38].

Available data suggests that the time and energy invested in coalition formation is negligible, and that injuries and especially death as a consequence of failed coalitions are rare, yet it is unclear whether this is because such events have gone unrecorded or whether they are in fact unusual [7]. There are, however, data to suggest that there may be opportunity costs, including failure to achieve higher ranks, reduced mating access, and various other consequences that can only be addressed with models that capture entire life cycles, associated with coalition formation, particularly if the coalition fails [4]. Yet our model, which does track the fitness consequences of behaviour thorough an individual's entire life cycle, suggests that whether or not coalitions are rank-changing is far more influential in affecting the evolution of coalitionary behaviour than the types of costs (fecundity versus survival) experienced by failed coalitions or the targets of successful ones. Future empirical research may benefit from identifying differences in the frequency of types of coalitions that emerge in species that regularly engage in rank-changing coalitions compared to species in which rank-changes as a result of coalition formation is rare.

6.4.3 Concessions

Our model predicts that the threat of all-up coalitions may lead high-ranked individuals to concede a greater amount of resources toward lower ranked individuals, without changing ranks, only in a specific set of circumstances. Concessions only occur when alpha-gamma coalitions are unlikely to succeed compared to beta-gamma coalitions, implying (under the assumption that the competitiveness of a coalition is the sum of the competitiveness of its members) that the beta must be more competitive than the alpha for concessions to be granted. In this case, the alpha evolves to concede fecundity to one of the subordinates; which subordinate the dominant concedes to depends on the division of risk and reward between dominants and subordinates in coalitions. In doing so, the subordinate that receives the concession then becomes an excellent target for the coalition, which encourages the remaining subordinate to form a coalition with the alpha. Ultimately, selection never favors alphas that concede to both subordinates; instead, the alpha concedes to only one subordinate. Further, our model suggests that these concessions do not occur so that the subordinate afforded a portion of fecundity will have more to lose and should therefore be less willing to be a part of beta-gamma coalitions, since generally they hold more risk for the beta than alpha-beta coalitions; instead, concession are made so that the subordinate receiving the concession is a more compelling target for coalitions.

Our work differs from most previous reproductive skew theory because it focuses on the influence of direct aggression, rather than the threat of departure of eviction; our work is unique because this aggression is in the form of coalition formation, rather than binary conflict [13]. Since our model is triadic, we are able to clearly demonstrate that dominants may be willing to concede fecundity, but we consistently find that this concession is to a single subordinate only. It is thus likely true that should other concession models be extended to three or more individuals, one would find that the dominant concessions to subordinates likely follow an uneven distribution, and the amount that each subordinate receives will depend on rank and various other social and ecological factors. For example, dominants likely need to concede

less to subordinates in higher rank since they are more likely to inherit breeding territories and therefore need less incentive to remain in the group. We have ignored factors related to ecological constraints, which often motivate concessions in models of cooperative breeders, in order to exclusively investigate and precisely describe the relationship between concessions and coalitions.

6.4.4 A Comparison to Empirical Data

A comparison between our results and empirical data yields mixed agreement. In what follows we explore some of the similarities between our results and empirical observations, and provide an evolutionary context for these findings. We also highlight discrepancies between our results and the data, identify possible deficiencies in the available data and limitations of our model, and propose future studies of coalitionary behaviour and concessions that may help resolve the disagreement between theory and data.

It is difficult to compare our results to previous models and empirical data since the relation between concessions and coalitions has not previously been investigated. Comparisons are particularly problematic for non-rank-changing coalitions because it is unclear whether the social hierarchy as it is recorded by field biologists coincides with the rank as it is imposed in our model or rather the distribution of fecundity – these hierarchies are not necessarily equivalent. Indeed, there are no rank changes in our models if fecundity is contested (aside for succession due to deaths), yet based on the outcome of coalitionary behaviour individuals in lower ranks may actually have greater fecundity and thus may appear to be of higher social rank if their coalitions are successful. This stated, we make comparisons where possible.

The frequency of certain types of coalitions is known to vary significantly across [25] and within species [3], and our model does suggests that the type of coalitions that evolve may vary with survival, the manner of coalition solicitation, and whether it is social rank or fecun-

dity that is being contested. However, observations indicate that among unrelated individuals all-down coalitions are the most common form of coalitionary behaviour [39]. In contrast, our model suggests that coalitions contesting fecundity should be all-down only when $c_{1,3} < c_{2,3}$, and coalitions contesting rank should be all-down only if the survival of beta individuals is generally much lower than that of gamma individuals ($s_2 << s_3$). In our model, few conditions favor alpha-beta coalitions because, assuming dominants have control over resource allocation, alpha individuals will naturally evolve to take a greater share of resources, which makes them an excellent target for coalitions. We find this to be true regardless of whether the cost of failed coalitions is survival or fecundity. If the costs and benefits are unequal for individuals within coalitions (i.e. the dominants both gain more and risk less relative to subordinates), no coalitions other than beta-gamma coalitions evolve under any parameter conditions; however, oscillating levels of beta-gamma coalitions evolve, as well as oscillating amounts that alpha individuals concede to the gamma individuals.

Whereas previous studies [1, 40] have assumed that the distribution of fecundity (or whichever limiting resource is being contested) is environmentally determined, here we assume the degree of despotism – at least before the formation of coalitions – is controlled by the dominant individual. The degree to which the dominant individuals in species exhibiting coalitionary behaviour are actually able to monopolize resources is of course variable and difficult to determine, as it is often unclear whether subordinates who reproduce are able to do so due to concessions or a lack of control from dominant breeders [41]. At least in certain species, there are high degrees of monopolization which seem to be dominant-controlled [42, 43, 44, 45]. Our results, in contrast to empirical data, suggest that all-up coalitions should be common under a wide range of parameter conditions, and this may indicate that the type of coalitions that evolve may be related to the ability for the dominant individuals of a species to make concessions, which naturally is contingent upon the ability of dominant individuals to monopolize resources if dominant individuals are unable to control the distribution of resources, they are

unable to make concessions, and thus the results of our models are not applicable. Our models suggest then that the variance in the prevalence of all-down coalitions between species may be due to species-level differences in the ability of dominant individuals to monopolize resources and their willingness to concede resources to subordinates as peace offerings, and this may be a promising direction for future empirical work.

Bissonnette et al. [3] state that their unpublished data reveals all-up coalitions are particularly uncommon across species in mixed-sex groups, in which coalitions to contest fecundity are common. They posit that this is likely the result of unequal distribution of mating opportunities among successful coalitions, which is in agreement with the fact that when h_1 in our model deviates significantly from 0.5 (an equal distribution), beta-gamma coalitions are no longer ubiquitous.

All-up, rank-changing coalitions have also been found to be relatively rare, and it has been proposed that this is the result of high-costs involved with contesting rank [3]. The existence of other types of rank-changing coalitions is often more difficult to prove because they may not result in readily observable changes (e.g. alpha-beta coalitions formed to prevent rank-changes are unlikely to produce rank-changes). There has, however, been recordings of the alpha male forming coalitions with lower-ranking members to remove higher-ranking social threats to the alpha [46, 3], and this is the very type of coalition (i.e. bridging) our model predicts is most likely to form.

All-down, rank-changing coalitions are fairly common in both primate and non-primate species [3], which is in contrast to our findings that the formation of coalitions among high ranking individuals to pre-emptively deter all-up coalitions should be relatively rare. Again, this discrepancy may be the result of the assumption that the alpha is able to control resources, and we expect that the frequency of all-down coalitions should vary with the alpha's ability

to monopolize resources. Another possible explanation for the dissimilarities between our model and the data is the fact that our model population has been divided into triads. Although alpha-gamma coalitions evolve in our rank-changing model while all-down coalitions are most common in nature, both of these coalitions can, from the perspective of the alpha, be viewed as rank-stabilizing: they are formed so that the alpha can preserve its rank. The reason all-down coalitions may be more prevalent in reality than our model suggests is that in many populations exhibiting coalitionary behaviour group sizes are larger than three [3], and in such groups there are a greater number of viable all-up coalitions that can target the alpha and, indeed, the beta. As such, there may be greater incentive for all-down coalitions. Unfortunately, creating models of coalitionary behaviour that calculate lifetime fitness consequences become exponentially more complex with larger group sizes, and thus agent-based simulation would likely be required. Models as well as empirical data that are able to describe changes in coalitionary behaviour as a function of group size are profitable lines of inquiry for future work.

Other theories for the relative rarity of all-up coalitions include the high cost of targeting dominant individuals, and the fact that all-up coalitions can be countered by all-down coalitions, which often consist of more dominant individuals [3]. Yet our models show that all-up and bridging coalitions can readily emerge even when the probability with which alpha-beta coalitions succeed is much higher than that of other coalitions. This is due to the dominant's general tendency to retain most of the group's fecundity, ensuring that subordinates have much to gain from targeting alpha individuals, but also little to lose in the event that the coalition fails.

The general conclusions derived from our model are unlikely to apply to species with facultative and highly sophisticated coalitionary behaviour that are able to flexibly and dynamically respond to the behaviour of others, such as many primates. However, our model does describe coalition formation in the growing number of species with lower cognitive capacities that have been observed to regularly form coalitions, including many species of birds and social carni-

vores [7]. Indeed, there is mounting evidence to suggest that cognition is not as important as socioecology in determining whether a species will evolve to use coalitions [7]. Based on our results, we expect that species incapable of sophisticated cognition are far more likely to form all-up and bridging rather than all-down coalitions. Our model calculates the influence of coalitionary behaviour on an individual's lifetime fitness rather than the fitness that may be gained from separate stages of an individual's life cycle. Few studies [25] have sought to understand the relationship between coalitions and lifetime fitness; that is, previous models do not account for the fact that individuals may adjust behaviour based on their future reproductive success [47, 48].

From its inception [17], theory regarding coalition formation has focused extensively on the effects of initial ranks and RHP distributions of a group on coalition formation [2] with few exceptions [49], yet empirical studies have regularly demonstrated across species that coalition partners are often selected based on features related to but distinct from RHP such as kinship [50, 51, 52, 53], sex [54], and age [55, 24].The call for models to delineate the relationship between coalitionary behaviour and life-history characteristics would require a class-structure analogue of the model provided here. Each distinct class would then require a separate set of phenotypes controlling for behaviour in each distinct group structure. Unfortunately, such a model is unlikely to be numerically, much less analytically, tractable; agent-based models are likely to be more profitable for this endeavor. While agent-based modelling has been previously used to investigate coalitionary behaviour, those models have focused on how individual differences in RHP rather than pertinent life-history traits may affect coalitionary behaviour [56].

6.5 Appendix

6.5.1 Complete Fitness Calculation

To calculate the selection gradient acting on each phenotype, we first derive the future reproductive success associated with each state. We define W_i as the future reproductive success for an individual in state i (e.g. W_6 represents the residual fitness of a gamma in a trio that has formed an alpha-gamma coalition). Let F_i represent the fecundity of an individual in state i; that is, F_i is equal to the number of offspring produced by an individual in state i (e.g. $F_{10} = (1 - p - q)$). Lastly, let $M_{i,j}$ represent the probability that an individual in state i transitions into state j in the next generation (e.g. $M_{1,1} = s_1 x_{1,2} x_{2,1}$). We calculate the fitness of each state by adding the fecundity of an individual in the current breeding season to the future components of fitness, which are weighted by transition probabilities for each state; equivalently, we solve the solution vector $[W_1, W_2, ..., W_{12}]$ to the following system of equations

$$\begin{pmatrix} W_1 \\ \vdots \\ W_{12} \end{pmatrix} = \begin{pmatrix} M_{1,1} & M_{1,2} & \cdots & M_{1,12} \\ M_{2,1} & M_{2,2} & \cdots & M_{2,12} \\ \vdots & \vdots & \vdots & \vdots \\ M_{12,1} & M_{12,2} & \cdots & M_{12,12} \end{pmatrix} \begin{pmatrix} W_1 \\ \vdots \\ W_{12} \end{pmatrix} + \begin{pmatrix} F_1 \\ \vdots \\ F_{12} \end{pmatrix}.$$

6.5.2 Entries in System of Equations

In a homogeneous, wild type population of constant size

$$
\begin{aligned}
M_{1,1} &= s_1 x_{21} x_{12} \\
M_{1,2} &= 0 \\
M_{1,3} &= 0 \\
M_{1,4} &= s_1 s_1 (1 - x_{21} x_{12}) x_{31} x_{13} \\
M_{1,5} &= 0 \\
M_{1,6} &= 0 \\
M_{1,7} &= s_1 s_1 (1 - x_{21} x_{12})(1 - x_{31} x_{13}) x_{23} x_{32} \\
M_{1,8} &= 0 \\
M_{1,9} &= 0 \\
M_{1,10} &= s_1 (1 - x_{21} x_{12})(1 - x_{31} x_{13})(1 - x_{23} x_{32}) \\
M_{1,11} &= 0 \\
M_{1,12} &= 0 \\
M_{4,1:12} &= M_{7,1:12} = M_{10,1:12} = M_{1,1:12}.
\end{aligned}
$$

$$M_{2,1} = (1 - s_1)s_2x_{21}x_{12}$$

$$M_{2,2} = s_1s_2x_{21}x_{12}$$

$$M_{2,3} = 0$$

$$M_{2,4} = (1 - s_1)s_2(1 - x_{21}x_{12})x_{31}x_{13}$$

$$M_{2,5} = s_1s_2(1 - x_{21}x_{12})x_{31}x_{13}$$

$$M_{2,6} = 0$$

$$M_{2,7} = (1 - s_1)s_2(1 - x_{21}x_{12})(1 - x_{31}x_{13})x_{23}x_{32}$$

$$M_{2,8} = s_1s_2(1 - x_{21}x_{12})(1 - x_{31}x_{13})x_{23}x_{32}$$

$$M_{2,9} = 0$$

$$M_{2,10} = (1 - s_1)s_2(1 - x_{21}x_{12})(1 - x_{31}x_{13})(1 - x_{23}x_{32})$$

$$M_{2,11} = s_1s_2(1 - x_{21}x_{12})(1 - x_{31}x_{13})(1 - x_{23}x_{32})$$

$$M_{2,12} = 0$$

$$M_{5,1:12} = M_{8,1:12} = M_{11,1:12} = M_{2,1:12}.$$

$$M_{3,1} = (1-s_1)(1-s_2)s_3x_{21}x_{12}$$

$$M_{3,2} = s_3(s_1(1-s_2)+s_2(1-s_1))x_{21}x_{12}$$

$$M_{3,3} = s_1s_2s_3x_{21}x_{12}$$

$$M_{3,4} = (1-s_1)(1-s_2)s_3(1-x_{21}x_{12})x_{31}x_{13}$$

$$M_{3,5} = s_3(s_1(1-s_2)+s_2(1-s_1))(1-x_{21}x_{12})x_{31}x_{13}$$

$$M_{3,6} = s_1s_2s_3(1-x_{21}x_{12})x_{31}x_{13}$$

$$M_{3,7} = (1-s_1)(1-s_2)s_3(1-x_{21}x_{12})(1-x_{31}x_{13})x_{23}x_{32}$$

$$M_{3,8} = s_3(s_1(1-s_2)+s_2(1-s_1))(1-x_{21}x_{12})(1-x_{31}x_{13})x_{23}x_{32}$$

$$M_{3,9} = s_1s_2s_3(1-x_{21}x_{12})(1-x_{31}x_{13})x_{23}x_{32}$$

$$M_{3,10} = (1-s_1)(1-s_2)s_3(1-x_{21}x_{12})(1-x_{31}x_{13})(1-x_{23}x_{32})$$

$$M_{3,11} = s_3(s_1(1-s_2)+s_2(1-s_1))(1-x_{21}x_{12})(1-x_{31}x_{13})(1-x_{23}x_{32})$$

$$M_{3,12} = s_1s_2s_3(1-x_{21}x_{12})(1-x_{31}x_{13})(1-x_{23}x_{32})$$

$$M_{6,1:12} = M_{9,1:12} = M_{12,1:12} = M_{3,1:12}.$$

Entries in the reproductive output vector are given by

$$F_1 = (1-p-q) + h_1 c_{1,2} hq - (1-c_{1,2})(1-h_1)h(1-p-q)$$

$$F_2 = p + (1-h_1)c_{1,2}hq - (1-c_{1,2})h_1 hp$$

$$F_3 = q - c_{1,2}hq + (1-c_{1,2})h(h_1 q + (1-h_1)(1-p-q))$$

$$F_4 = (1-p-q) + h_1 c_{1,3} hp - (1-c_{1,3})(1-h_1)h(1-p-q)$$

$$F_5 = p - c_{1,3}hp + (1-c_{1,3})h((1-p-q)(1-h_1) + qh_1)$$

$$F_6 = q + (1-h_1)c_{1,3}hp - h_1(1-c_{1,3})hq$$

$$F_7 = (1-p-q) - c_{2,3}h(1-p-q) + (1-c_{2,3})h((1-h_1)p + h_1 q)$$

$$F_8 = p + h_1 c_{2,3} h(1-p-q) - (1-c_{2,3})h(1-h_1)p$$

$$F_9 = q + (1-h_1)c_{2,3}h(1-p-q) - (1-c_{2,3})hh_1 q$$

$$F_{10} = (1-p-q)$$

$$F_{11} = p$$

$$F_{12} = q.$$

Entries in the initial state vector are given by

$$I_1 = (1/3)(1 - s_1)(1 - s_2)(1 - s_3)x_{1,2}x_{2,1}$$

$$I_2 = ((1/3)(1 - s_1)(1 - s_2)(1 - s_3) + (1/2)((1 - s_1)(1 - s_2)s_3$$
$$+ (1 - s_1)(1 - s_3)s2 + (1 - s_2)(1 - s_3)s_1))x_{1,2}x_{2,1}$$

$$I_3 = ((1/3)(1 - s_1)(1 - s_2)(1 - s_3) + (1/2)((1 - s_1)(1 - s_2)s_3$$
$$+ (1 - s_1)(1 - s_3)s2 + (1 - s_2)(1 - s_3)s_1)$$
$$+ s_1s_2(1 - s_3) + s_1(1 - s_2)s_3 + (1 - s_1)s_2s_3))x_{1,2}x_{2,1}$$

$$I_4 = (1/3)(1 - s_1)(1 - s_2)(1 - s_3)(1 - x_{1,2}x_{2,1})x_{1,3}x_{3,1}$$

$$I_5 = ((1/3)(1 - s_1)(1 - s_2)(1 - s_3) + (1/2)((1 - s_1)(1 - s_2)s_3$$
$$+ (1 - s_1)(1 - s_3)s2 + (1 - s_2)(1 - s_3)s_1))(1 - x_{1,2}x_{2,1})x_{1,3}x_{3,1}$$

$$I_6 = ((1/3)(1 - s_1)(1 - s_2)(1 - s_3) + (1/2)((1 - s_1)(1 - s_2)s_3$$
$$+ (1 - s_1)(1 - s_3)s2 + (1 - s_2)(1 - s_3)s_1)$$
$$+ s_1s_2(1 - s_3) + s_1(1 - s_2)s_3 + (1 - s_1)s_2s_3))(1 - x_{1,2}x_{2,1})x_{1,3}x_{3,1}$$

$$I_7 = (1/3)(1 - s_1)(1 - s_2)(1 - s_3)(1 - x_{1,2}x_{2,1})(1 - x_{1,3}x_{3,1})x_{2,3}x_{3,2}$$

$$I_8 = ((1/3)(1 - s_1)(1 - s_2)(1 - s_3) + (1/2)((1 - s_1)(1 - s_2)s_3$$
$$+ (1 - s_1)(1 - s_3)s2 + (1 - s_2)(1 - s_3)s_1))(1 - x_{1,2}x_{2,1})(1 - x_{1,3}x_{3,1})x_{2,3}x_{3,2}$$

$$I_9 = ((1/3)(1 - s_1)(1 - s_2)(1 - s_3) + (1/2)((1 - s_1)(1 - s_2)s_3$$
$$+ (1 - s_1)(1 - s_3)s2 + (1 - s_2)(1 - s_3)s_1)$$
$$+ s_1s_2(1 - s_3) + s_1(1 - s_2)s_3 + (1 - s_1)s_2s_3))(1 - x_{1,2}x_{2,1})(1 - x_{1,3}x_{3,1})x_{2,3}x_{3,2}$$

$$I_{10} = (1/3)(1 - s_1)(1 - s_2)(1 - s_3)(1 - x_{1,2}x_{2,1})(1 - x_{1,3}x_{3,1})(1 - x_{2,3}x_{3,2})$$

$$I_{11} = ((1/3)(1 - s_1)(1 - s_2)(1 - s_3) + (1/2)((1 - s_1)(1 - s_2)s_3$$

$$+ (1 - s_1)(1 - s_3)s2 + (1 - s_2)(1 - s_3)s_1))(1 - x_{1,2}x_{2,1})(1 - x_{1,3}x_{3,1})(1 - x_{2,3}x_{3,2})$$

$$I_{12} = ((1/3)(1 - s_1)(1 - s_2)(1 - s_3) + (1/2)((1 - s_1)(1 - s_2)s_3$$

$$+ (1 - s_1)(1 - s_3)s2 + (1 - s_2)(1 - s_3)s_1)$$

$$+ s_1s_2(1 - s_3) + s_1(1 - s_2)s_3 + (1 - s_1)s_2s_3))(1 - x_{1,2}x_{2,1})(1 - x_{1,3}x_{3,1})(1 - x_{2,3}x_{3,2})$$

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Chapter 7

Conclusions

Throughout this thesis, we created evolutionary models to better understand a variety of scenarios involving social groups wherein resources and control over resources were asymmetrically divided. Motivated largely by empirical studies which indicate cooperation commonly occurs among individuals in different social ranks [1, 2, 3, 4], even when they are in conflict, we developed theory to better explain unintuitive mixes of conflict and cooperation throughout the animal kingdom.

Our work began by exploring what may motivate the evolution of social groups involving individuals with asymmetries in resources and social roles. In Chapter 2, we investigated the emergence of leader-follower relationships in the context of group dispersal, a common biological phenomenon [5], by examining the inclusive fitness incentives for leading and following. Our work showed that leader-follower relationships are more likely to evolve among groups with high relatedness, especially when there were significant group augmentation benefits associated with participating in leader-follower relationships. Despite the common perception that leaders monopolize resources [6], these relationships were found to be more likely to evolve when reproductive skew in favour of followers. Our results were used to conclude that at evolutionary equilibrium the incentives for leading can be either selfish or altruistic, de-

pending on ecological and social conditions, like relatedness between leaders and followers. Ultimately, our model revealed that kin selection is sufficient and that individual differences in condition and ability are not necessary for the evolution of leader-follower relationships.

We next explored conflict and cooperation in non-egalitarian groups of kin. The most basic unit of non-egalitarian kin groups is the parent-offspring pair, and these relationships can be subject to intense conflict over parental care [7]. Our work in Chapter 3 evaluated that offspring begging has on resolving this conflict. Our work here shows that whether offspring begging conveys need or demonstrates quality depends on environmental conditions. Motivated by a recent meta-analysis of begging behaviours in bird species [4], we constructed a model to show that in stable environments, needy offspring beg and are preferentially fed, while in unpredictable environments, high-quality offspring beg and are fed when conditions are poor. This shift occurs fundamentally because in poor and unpredictable environments, parents often have more offspring than they can possibly rear, and so it is frequently best for parents to invest their meager resources in the highest quality offspring, as these are frequently the offspring to gain most from small amounts of investment. In contrast, parents provide greater care for needier offspring when environmental conditions are stable, since parents are more reliably able to successfully raise their entire brood. High signalling costs coupled with lower relatedness between offspring, or low signalling costs together with moderate levels of relatedness between siblings, allow for the shift between signals of need and signals of quality to occur in more volatile environments. Species whose offspring are highly dependent on parents for survival are not expected to use both signals of need and of quality.

Chapter 4 was dedicated to understanding how asymmetric outcomes to conflict between parents over provisioning can lead to sex differences in behaviour in the begging behaviour of offspring. We validate the previously untested hypothesis that sex differences in long-term need can cause selection to favour sex differences in begging behaviour [8]. However, these

results do not seem to match empirical data [9]. By tracking the full lifetime inclusive fitness consequences of begging behaviour, we develop a more parsimonious theory — females, who often provide greater care for their offspring, ultimately suffer larger costs compared to males by increasing their begging intensity. As such, even when females are in greater need, they may evolve to beg at lower intensities than males.

In Chapter 5, we explored conflict between helpers and breeders in cooperatively breeding species. Smaller brood sizes were previously thought to be a precursor to cooperative breeding [10], though recent empirical evidence does not support this theory [11]. Our thorough inclusive fitness model reveals that while small clutch sizes may predispose species to cooperative breeding, cooperative breeding itself can affect the evolution of clutch size. We show that, in contrast to previous theoretical work, cooperative breeding does not need to lead to smaller clutch size and under very general conditions may actually increase clutch size at evolutionary equilibrium. Conflict between breeder and auxiliary may motivate the helper to promote larger clutch sizes, which may harm the breeder's survival to increase the probability of territory inheritance. Moreover, clutch sizes can lead to increases in the expected level of help breeders will receive in the future.

We then shift focus to cooperation and conflict in non-egalitarian social groups comprised of unrelated individuals. In Chapter 6 we attempt to resolve the lack of agreement between empirical observation and theoretical research on coalitionary behaviour in the animal kingdom [3]. Using a life-history model, we explore how coalitionary behaviour may differentially evolve depending on the types of costs afflicted upon members of failed coalitions, in terms of survival, fecundity, and social rank. We find that bridging coalitions under a clear majority of social and ecological settings are formed to contest social rank, whereas species that contest fecundity should be expected to form all-up coalitions under most conditions. We then model the coevolution of coalitionary behaviour and dominant concessions toward subordinates to

demonstrate that dominant individuals rarely evolve to make concessions to their subordinates, even when threatened by coalitions.

Social interactions, particularly among relatives, can make the inclusive fitness consequences of certain traits difficult to predict. A theme common to the models presented in this thesis is the importance of properly calculating the inclusive fitness consequences of a trait. This is accomplished by building models which tracks the consequences of a trait through an individual's full life-cycle. That there is a requirement for models which track the consequences of a behaviour throughout an individual's lifetime explains why some of the behaviours being modelled appear, at first glance, counterintuitive and even maladaptive. Evolutionary models often seek to determine whether a trait can be expected to evolve by measuring the inclusive fitness associated with the trait. Unfortunately, with inclusive fitness frequently being defined, even in textbooks [7], as the genetic contribution to the gene pool of the population in next generation, the true currency of evolutionary biology – the contributions to the gene pool of populatons in the distant future – is sometimes neglected, and thus the trajectory of evolution is frequently miscalculated.

Conflict and cooperation sometimes appear to be arbitrary distinctions, particularly from a gene's perspective of evolution. For instance, the helping behaviour of auxiliaries studied in Chapter 5 revealed that while auxiliaries may appear to help breeders raise their offspring, territory inheritance can motivate them to do so in ways that are not optimal for the parent, even reducing the parent's survival. However, as outlined in Chapter 2, if both parties gain in terms of inclusive fitness by participating in voluntary cooperative behaviour, the cooperative behaviour can evolve. Cooperation can emerge even when certain individuals enjoy a complete monopoly over resources. These dominant individuals are motivated to share their resources for a wide variety of resources, from kin selection — as is evident with parental care in Chapters 3 and 4, — to appeasement — studied through the concessions made by domi-

nant individuals in Chapter 6 — to group augmentation — referenced in the leader-follower relationships in Chapter 2. Conflict, however, can still arise even with cooperative behaviours as each party attempts to maximize their gains from their interaction, usually at the cost of their social partners. Modelling and understanding how these conflicts within cooperation are resolved is core of much of the work presented here.

Many of these models also demonstrate the importance of communication between empiricists and theoreticians. The work in Chapter 6, for example, was motivated by a lack theoretical literature that analyzed how certain social and ecological conditions, such as the costs of failed coalitions, influenced the evolution of coalitionary behaviour, even when an abundance of empirical data indicated their importance to coalition formation [3]. Chapter 3 was, in part, motivated by a lack of realism in the fitness functions of offspring used in previous models [12]. Unfortunately, there is a trade-off between biological realism and analytic tractability. Even so, as demonstrated by the offspring fitness functions in Chapter 3 and the full life-cycle models in Chapter 5, simplifying biological assumptions sometimes need to be more rigorously tested. When simple analytic results cannot be generated in this pursuit, even general results from numerical analysis can provide important insights into the evolutionary biology of the systems being studied.

Naturally, this thesis did not examine all observed cooperative behaviour among individuals in conflict in non-egalitarian groups. Possible avenues for future research specific to each behaviour examined are outlined in the discussion of each chapter. Left almost unexplored in this thesis is conflict and cooperative behaviour unique to humans. Due to the unique cognitive capacity of humans, the evolution of human conflict and cooperation is influenced by behaviours and traits that are exclusive to or uncommonly extensive in our species. For example, humans frequently engage in cooperative behaviour even in large groups of unrelated individuals when interactions are not repeated [13]. No theory has yet been able to definitively explain this

phenomenon, although many have been proposed and tested theoretically [14, 15]. These theories and mechanisms used to explain the phenomenon – including extensive rewarding [16] and punishment [17] on the individual and institutional level [18, 19], and reputation and reciprocity [20] – rely on the fact that humans are uniquely able to rapidly recognize, remember, and adapt social behaviour by observing the behaviour and payoffs of others [13, 21].

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