

THE EVOLUTION OF NON-KIN COOPERATION IN JOINT-NESTING

TAIWAN YUHINAS, *YUHINA BRUNNEICEPS*

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

Sheng-Feng Shen

January 2009

© 2009 Sheng-Feng Shen

THE EVOLUTION OF NON-KIN COOPERATION IN JOINT-NESTING

TAIWAN YUHINAS, *YUHINA BRUNNEICEPS*

Sheng-Feng Shen, Ph. D.

Cornell University 2009

Cooperation among individuals occurs throughout nature. However, how diverse forms of social organizations are shaped by natural selection in different ecological and social conditions remains a puzzle. In this thesis, I use evolutionary game theory and inclusive fitness theory to model social conflict and its resolutions. I use Taiwan yuhinas, a passerine bird species in which multiple, non-related females lay eggs jointly in the same nest and then all group members cooperate in rearing the young, as a model system to study the formation and stability of non-kin groups. Based on the theory of reproductive skew, I derive the necessary prerequisite condition for the evolution of any stable social group: The reproductive productivity of the group must exceed that of the sum of all of its members if they attempted to reproduce solitarily. I argue that different types of group benefits have different influences on the properties and composition of cooperative breeding groups. I develop the “boarded tug-of-war model”, which synthesizes previous transactional and tug-of-war models of reproductive skew, to obtain the general ecological and social conditions for a stable social group to evolve. This synthesis model predicts that different conflict resolution mechanisms will be selected in different ecological and social conditions. I also model the general effect of parental investment on reproductive skew by relaxing the restrictive assumptions of existing models. My expanded model clarifies how adjustable parental effort can influence the resulting reproductive skew and social conflict. Finally, I use Taiwan yuhinas as an empirical case study of the evolution of

non-kin groups. I find that kin are more likely than non-kin to join groups, but only when group sizes are larger than the most productive sizes. I interpret this as suggesting that yuhinas still prefer to cooperate with kin. The reason yuhinas typically form non-kin groups is that maturing young have excellent opportunities for successful dispersal and reproduction elsewhere. This results in a high offspring dispersal rate, which limits the chance of adults recruiting their young (kin) into cooperative breeding groups. Studying the evolution of non-kin cooperation can help us understand the general principle of stable cooperation.

BIOGRAPHICAL SKETCH

Sheng-Feng Shen was born in Taipei, Taiwan on October 25, 1978. He grew up in the small towns in HsinChu, where he spent a lot of his time in nature. In the summer after the junior year of high school, after participating the Natural Conservation Camp hosted by Natural Conversation Student Club at National Taiwan University (NTU), he was convinced that he wants to study ecology and conservation at college. Sheng-Feng majored Botany at NTU and after volunteering in several ecological field researches, he found that he was most interested in behavioral ecology study in birds. His undergraduate study is on the basic breeding biology of Taiwan yuhinas. After graduating from department of Botany at NTU in 2000, Sheng-Feng began his MS in the Department of Zoology at NTU. He focused his study on the cost and benefit of the joint-nesting behavior in Taiwan yuhinas. In trying to understand the evolution of non-delayed dispersal yuhinas, he began interested in theoretical modeling. He obtain his MS in 2002 and after that, he worked as research assistant in a GIS lab, where he was in charge of a large scale avifauna studies, for a year. Sheng-Feng began his Ph.D. in the Department of Neurobiology and Behavior at Cornell in 2003, and having now finished his dissertation, he receives the Postdoctoral Research Abroad Fellowship from National Science Council, Taiwan. He will start his postdoc at Cornell University and his study will focus on the cooperation and conflict in social wasps. Sheng-Feng also plans to do another postdoc focusing on theoretical modeling at Cambridge University, UK.

To my parents, who give me freedom to pursuit my dream and
to my thesis advisor, Stephen T. Emlen, who is a true mentor
to my scientific career

ACKNOWLEDGMENTS

First I thank my advisor Steve Emlen for his great help on every aspect of my Ph.D. study. I feel really honored to have the chance to learn from a master like him. His guidance is always very useful and full of wisdom. My advisor, Sandy Vehrencamp, is very supportive and patient in helping the yuhina research and my writing. I really appreciate her support and guidance. Kern Reeve is literally my third advisor, who has profound influences on my thinking on behavioral ecology. He is one of the smartest scientists I have ever met and it is a real privilege to work with him closely in these years. I also thank my graduate committee, David Winker and David McCobb, for their encouragement and guidance.

It is not possible to complete this research without my collaborator Hsiao-Wei Yuan's full support with her lab's man power and resources. I thank Mark Liu introduced me to yuhina's research and teach me many useful field skills. I appreciate the dedications to this research by current and previous members of the yuhina group, including my tireless field assistant, Karimi Sylvester, K-Y Lin, Q-D Zhong, S-Y Fu, F-Y Huang, J-W Lin, C-J Chang, Y-H Chang, I-F Liao, M-Y Huang, Z-N Yuan, D-L Lin, S-J Chen, W-Y Liao, K-Z Cheng, S-J Chen and, more than 50 volunteers mainly from natural conservation student club, Department of life science, Forestry of National Taiwan University. I acknowledge the great helps from staffs of Mei-Feng Experimental Farm of National Taiwan University, especially Barsar and Wiwi.

For inspiring scientific discussion, friendship and help, I thank Pei-Fen Lee, Mike Cant, Walt Koenig, Paul Sherman, Tom Seeley, Janis Dickinson, Jessie Barker, Lynn Fletcher, Charalotte Jander, Judith Scarl, Chris Wilson, Troy Murphy, Jonathan Lee, Carlos Botero, Andrea Townsend, Stephanie Correa and Natalia Demong/Emlen. I especially thank my previous officemate, Dustin Rubenstein, for many helpful advices to my scientific career and good discussions and collaboration on research.

The staff in the Department of Neurobiology & Behavior made my time here more enjoyable and productive. I especially thank Terri Natoli for helping me survive better in the system.

Thanks to my family, which has been very supportive along the way, and of course, I thank my wife, I-Ho Chang, who is willing to quit her bank job to come to Ithaca with me, helped my field work and is always very supportive and patient.

My research was supported by fellowships from Cornell University College of Agriculture and Life Sciences, Cornell Laboratory of Ornithology, Cornell East Asia Program Hu-Shih Memorial Award, Cornell University Graduate School, Cornell University Department of Neurobiology and Behavior.

TABLE OF CONTENTS

BIOGRAPHICAL SKETCH.....	iii
DEDICATION.....	iv
ACKNOWLEDGMENTS.....	v
TABLE OF CONTENTS.....	vii
LIST OF FIGURES.....	viii
LIST OF TABLES.....	xi
CHAPTER ONE:	
Group benefits and the evolution of cooperative breeding.....	1
CHAPTER TWO:	
Reproductive skew theory unified: The general bordered tug-of-war model.....	26
CHAPTER THREE:	
Parental care, costly young and reproductive skew: a general model of parental investment in cooperatively breeding societies.....	60
CHAPTER FOUR:	
Why do cooperatively breeding Taiwan yuhinas cooperate with non-relatives?.....	82

LIST OF FIGURES

Figure 1.1	(a) Effects group size and resource quality on group productivity and (b) Effects group size and resource quality on per capita group productivity.....8	8
Figure 1.1	(c) Effects group size and resource quality on group productivity, and (d) Effects group size and resource quality on per capita group productivity.....10	10
Figure 1.2	Group control version of insider-outsider conflict model.....	13
Figure 2.1	(a) Dynamics of decision-making in the synthetic model.....	36
Figure 2.1	(b) A numerical example shows that a mutant strategy of simultaneously decreasing selfish effort.....	37
Figure 2.2	Transitions of different sub-models in relation to group resource (G) and genetic relatedness (r)	40
Figure 2.3	Transitions of different sub-models in relation to the subordinate are relative competitive efficiency of the subordinate (b) and direct fitness of leaving the group (S)	41
Figure 2.4	The inclusive fitness of the dominant and the subordinate compared to their non-cooperative option in relation to (a) genetic relatedness (r) and (b)direct fitness of leaving the group (S)	42
Figure 2.5	(a) The reproductive skew in relation to group productivity (G) and relatedness (r) (b) The reproductive skew in relation to solitary payoff of losing (S) and relative competitive efficiency of the subordinate (b)	49
Figure 2.6	The level of destruction in relation to (a)group productivity (G) and relatedness (r); and (b) solitary payoff of losing (S) and relative	

	competitive efficiency of the subordinate (b); and the level of aggression in relation to (c) group productivity (G)and relatedness (r); and (d) solitary payoff of losing (S) and relative competitive efficiency of the subordinate (b)	50
Figure 2.7	The relative level of destruction in relation to (a) group productivity (G) and relatedness (r); and (b) solitary payoff of losing (S) and relative competitive efficiency (b); and the relative level of aggression in relation to (c) group productivity (G) and relatedness (r); and (d) solitary payoff of losing (S) and relative competitive efficiency of the subordinate (b)	52
Figure 3.1	Results of the incomplete-control costly young model. (a) clutch size in relation to relative cost of young; The effect of relatedness on (b) Beta’s reproductive share, (c) clutch size and (d) total group output. Relaxing the complete-control assumption changes the properties of the costly young models.....	68
Figure 3.2	The effect of relatedness on (a) clutch size, (b) level of parental care, (c) Beta’s reproductive share, and (d) total group output in the parental investment models of reproductive skew, which relaxes the fixed group productivity of costly young models.....	72
Figure 4.1	Percentage of related dyads in small and large compared to the distribution of all dyads.....	89
Figure 4.2	The relationship between proportion of fledglings staying in the study area in the following season and the nest success rate of the season.....	89

Figure 4.3	The relationship between percentage of fledglings staying in the study area in the following season and fledged date of the fledglings.....	90
Figure 4.4	The group size distribution of Taiwan yuhinas groups.....	90
Figure 4.5	The hypothetical figure showing the relationship between insider yuhinas' average inclusive fitness and group size in breeding season and non-breeding season.....	91

LIST OF TABLES

Table 2.1	Summary of skew predictions of different sub-models.....	43
Table 2.2	Summary of level-of-conflict predictions of different sub-models.....	48
Table 3.1	Predictions of the effect of relatedness on different phenomena in different models. The effect of relatedness assumes that other parameters and group size are held constant.....	71
Table 4.1	Cases of individuals who lived with related group members.....	94
Table 4.2	Resolutions of reproductive vacancies in Taiwan yuhinas.....	95

CHAPTER 1

GROUP BENEFITS AND THE EVOLUTION OF COOPERATIVE BREEDING

INTRODUCTION

The selective forces favoring cooperative breeding, where more than two adults provide care in the rearing of young, are generally considered different from those favoring other types of group living (Dickinson & Hatchwell 2004; Emlen & Vehrencamp 1983). This is because, unlike many social groups, the per capita reproductive success in cooperatively breeding societies shows no consistent pattern with group size, and in most cases per capita reproductive success of single pairs is highest (Koenig 1981). Therefore, the formation of cooperatively breeding groups, especially in birds, is usually explained by the ecological constraints hypothesis: mature offspring delay dispersal and stay at home because they are “forced” to do so by severe ecological constraints, e.g. lack of high quality territories and/or mates, that limit the option of mature offspring to disperse and breed solitarily (Brown 1974; Emlen 1982a; Gaston 1978; Koenig & Pitelka 1981; Selander 1964). The benefit of philopatry hypothesis provided an alternative explanation for the evolution of cooperative breeding. It proposed that mature offspring delay dispersal because they can gain a net fitness benefit by doing so (Stacey & Ligon 1987; Stacey & Ligon 1991). There has been much debate on the distinctions between these two hypotheses, but now it is generally accepted that these two hypotheses are, in fact, two sides of the same coin and both are based on the cost-benefit analysis of leaving versus staying. The ecological constraints hypothesis was subsequently generalized to include both intrinsic benefits and extrinsic constraints and successfully accommodates the benefit of philopatry hypothesis (Emlen 1994; Hatchwell & Komdeur 2000; Koenig et al. 1992).

The ecological constraints hypothesis has been supported by many excellent studies (Baglione et al. 2006; Dickinson & McGowan 2005; Komdeur 1992; Pruett-Jones & Lewis 1990; Rubenstein & Lovette 2007). However, many authors have argued that an apparent weakness of this hypothesis is that numerous species also face strong ecological constraints but they are *not* cooperative breeders (Brockmann 1997; Covas & Griesser 2007; Hatchwell & Komdeur 2000; Koenig et al. 1992; Kokko 2007; Smith 1990). Theoretical models have also shown the possibility that ecological constraints might not lead to delayed offspring dispersal and cooperative breeding (Pen & Weissing 2000). Moreover, there are many cooperatively breeding societies, including most insect societies and marine fishes, that are not formed through delayed offspring dispersal (Cockburn 1998; Costa 2006). For example, marine fish larvae are usually swept far from their natal territory by currents, and helpers in these cooperative fish societies are mostly comprised of non-kin individuals (e.g. Buston et al. 2007). Therefore, the ecological constraints hypothesis, with its foundation in delayed dispersal, is difficult to apply to these non-kin cooperatively breeding societies in the current framework. Consequently, delayed dispersal and ecological constraints, although important for many societies, might be neither necessary nor sufficient conditions for the evolution of cooperative breeding. It has also been pointed out that hypotheses based on delayed offspring dispersal could “potentially divert us from recognizing parallels between families and societies formed through coalitions of unrelated individuals”(Cockburn 1998). The overly general definition of ecological constraints also makes it difficult to obtain useful predictive power and can lead to facile post hoc identification of constraints (Hatchwell & Komdeur 2000; Kokko & Ekman 2002).

In this paper, we argue that distinguishing different types of group benefits is the key to develop a unified framework for understanding various cooperative breeding

societies (see also Koenig 1981; Koenig et al. 1992; Rankin et al. 2007; Vehrencamp 1983). We will first show that a group benefit is the necessary condition for the evolution of cooperative breeding by developing a simple Hamiltonian model. We will then distinguish two major types of group benefits, namely resource benefit and social benefit. Instead of focusing on delayed offspring dispersal, the social and resource benefits framework can be applied to various cooperatively breeding societies. The insider-outsider conflict model will then be introduced to overcome the problem of focusing on delayed offspring dispersal. Consequently, the “typical” cooperatively breeding groups, formed through delayed offspring dispersal, in most birds and mammals can be understood in the same general framework with “untypical” groups, not formed by delayed offspring dispersal, in most insects and fishes.

NECESSARY CONDITION FOR THE EVOLUTION OF A SOCIAL GROUP

Based on Hamilton’s rule, for an individual to prefer joining a social group over being solitary, the inclusive fitness of joining must be higher than being solitary. Using the above logic, we derive the necessary condition for forming a social group, which is simply

$$G(n,r) > L_1 + L_2 + \dots + L_n = \sum_{i=1}^n L_i \quad (1),$$

where $G(n,r)$ is the group productivity with n group members with average relatedness of r and L_i is direct fitness for the i^{th} individual of being solitary (box 1). In other words, for a social group to form and be stable, the group productivity has to be higher than the sum of the solitary payoff of each group member, regardless of the relatedness between group members. However, relatedness does affect group productivity by affecting level of social conflict and/or individuals’ investment in creating group resources. Using inequality (1), it is clear that the original ecological

constraint hypothesis represents a low solitary payoff (small L_n), but it is not sufficient for the evolution of cooperative breeding. This also explains the lack of predictive power of the ecological constraint hypothesis, as many authors have pointed out (Brockmann 1997; Covas & Griesser 2007; Hatchwell & Komdeur 2000; Koenig et al. 1992; Kokko 2007; Smith 1990). Similarly, the benefit of philopatry hypothesis is a special case of the group benefit hypothesis, that emphasizes the benefit offspring can obtain by staying in the natal territory.

The general conclusion of combining the ecological constraint and benefit of philopatry hypotheses is equivalent to comparing the inclusive fitness between staying versus leaving, which is overly generous and basically the restatement of Hamilton's rule. Interestingly, by applying Hamilton's rule, inequality (1) shows that group benefit is the necessary condition for the evolution of all social groups, regardless of relatedness. Therefore, to develop a general framework for understanding various cooperatively breeding societies, we start with proposing that there are two key different types of group benefits, i.e. resource and social benefits, and then discuss how to separate different types of group benefits (see also Koenig 1981; Koenig et al. 1992; Rankin et al. 2007; Vehrencamp 1983).

Box 1

We employed Hamilton's rule for deciding whether joining a group or breeding solitarily will be favored by the natural selection (Hamilton 1964, Grafen 1984). For simplicity, we first consider a two-player group. Let G be the group productivity, p_1 be individual 1's share, and p_2 be individual 2's share of group productivity. Thus, the direct fitnesses of joining a group is Gp_1 for individual 1 and Gp_2 for individual 2. Also, let the payoff of being solitary be L_1 and L_2 for individual 1 and 2, respectively. Joining a group will be favored over be solitary for individual 1 if

$$(Gp_1 - L_1) + r(Gp_2 - L_2) \geq 0, \text{ (B1)}$$

where r is the coefficient of relatedness.

By setting (B1)=0 and solve for p_1 , we can obtain the minimum share that individual 1 needs to favor joining a group over being solitary, which is

$$p_1^* = \frac{L_1 + r[L_2 - Gp_2]}{G}. \text{ (B2a)}$$

Similarly, the minimum share for individual 2 to favor joining a group is

$$p_2^* = \frac{L_2 + r[L_1 - Gp_1]}{G}. \text{ (B2b)}$$

The sum of individual minimum shares, p_1^* and p_2^* , has to be smaller than one, so that both individuals would prefer joining a group. This can be expressed as follows:

$$1 - (p_1^* + p_2^*) > 0. \text{ (B3)}$$

Substituting (B2a) and (B2b) into (B3), we get

$$1 - \frac{L_1 + L_2 + r[L_1 + L_2 - G(p_1 + p_2)]}{G} > 0. \text{ (B4)}$$

Since individual 1 and 2 share all the group resources, we substitute $p_1 + p_2 = 1$ into

(B4) and obtain

$$\frac{[G - (L_1 + L_2)][1 + r]}{G} > 0. \text{ (B5)}$$

Therefore, for (B5)>0, the following inequality must be true

$$G > L_1 + L_2 \text{ (B6)}$$

Now, let $G(n,r)$ represent the group productivity function, which is determined by group size, n , and r represent relatedness between group members. Using the same logic, we find that the minimum share, p_i^* , for i^{th} individual in a n - player group is

$$p_i^* = \frac{L_i + r[G(n,r) \sum_{j=1}^n p_j - \sum_{j=1}^n L_j] \Big|_{i \neq j}}{G(n,r)}. \text{ (B7)}$$

Similarly, the sum of all group members' minimum shares has to be smaller than one,

$$1 - \sum_{i=1}^n p_i^* \geq 0. \text{ (B8)}$$

By substituting (B7) into (B8), we get

$$\frac{[G(n,r) - (L_1 + L_2 + \dots + L_n)][1 + (n-1)r]}{G(n,r)} \geq 0. \quad (\text{B9})$$

Thus, based on (B9), we prove that

$$G(n,r) > L_1 + L_2 + \dots + L_n = \sum_{i=1}^n L_i \quad (\text{B10})$$

TYPES OF GROUP BENEFITS

Resource benefit

Resource is defined here as something from the environment that an animal needs, such as food, territories, and nesting sites (Johnson et al. 2002). Although shortage of mates is often considered as a type of ecological constraint, we do not include potential mates as a type of resource. Mates are not environmental features and the key issue with mate shortage is what causes the imbalance of sex ratio, which is beyond the scope of this review. The definition of the resource benefit is that group productivity is determined by the quality of resources and cannot be increased by cooperation between group members. If resource benefit is the key benefit of group living, total group productivity should decrease as group size increase (Fig. 1.1a) and the per capita productivity would also decrease as group size increase (Fig.1.1b) because of the “ill effect of overcrowding” (Allee 1938). Also, the total group productivity and per capita productivity with good quality resources should be higher than with poor quality resources. Formally, based on inequality (1), resource benefit is defined as

$$R(n, E_G, r) > \sum_{i=1}^n R(1, E_i) \quad (2).$$

The left-hand side of the inequality (2) is the group productivity, $R(n, E_G, r)$ (R represents **R**esource), which is a function of group size, n , resource quality as the key **E**cological factor, E_G , and relatedness, r , between group members. Note that group

productivity only decreases as group size, n , increases. The right-hand side of the inequality (2) is the sum of each individual's direct fitness of being solitary ($n=1$), which is influenced by the quality of the resource the i^{th} individual can obtain, indicating by E_i . In other words, when sharing of good quality resources has a higher payoff than being solitary in a poor resource context, social groups could form because of mutual tolerance. Mutual tolerance is considered the first step toward sociality because individuals have to be together for more advanced types of group benefit to evolve (Allee 1938).

In the context of cooperative breeding, this type of group formation mechanism is usually referred to as extrinsic constraints or habitat saturation (Brown 1974; Emlen 1982a; Koenig et al. 1992). By this explanation, offspring forgo solitary breeding and delay dispersal because high quality resources, usually territories, are not available. Therefore, delayed dispersal is considered to be a 'best-of-a-bad-job' strategy since solitary breeding pairs usually have the highest per capita productivity (Koenig 1981). However, the concept of resource benefit is more general than extrinsic constraints because it is not based on explaining delayed offspring dispersal. For example, in burying beetles, joint breeding on large carcasses between unrelated females might be caused by the high cost of excluding co-breeders (Eggert & Muller 1997). In other words, group members breed jointly, not because co-breeders can bring any benefit, but simply because they are unable to exclude other individuals from sharing high quality resources, i.e. large carcasses, and thus 'tolerate' each other. Similarly, the high quality natal territory has been experimentally proven to be the key resource benefit for offspring to stay and become helpers in western bluebirds (Dickinson & McGowan 2005) and carrion crows (Baglione et al. 2006).

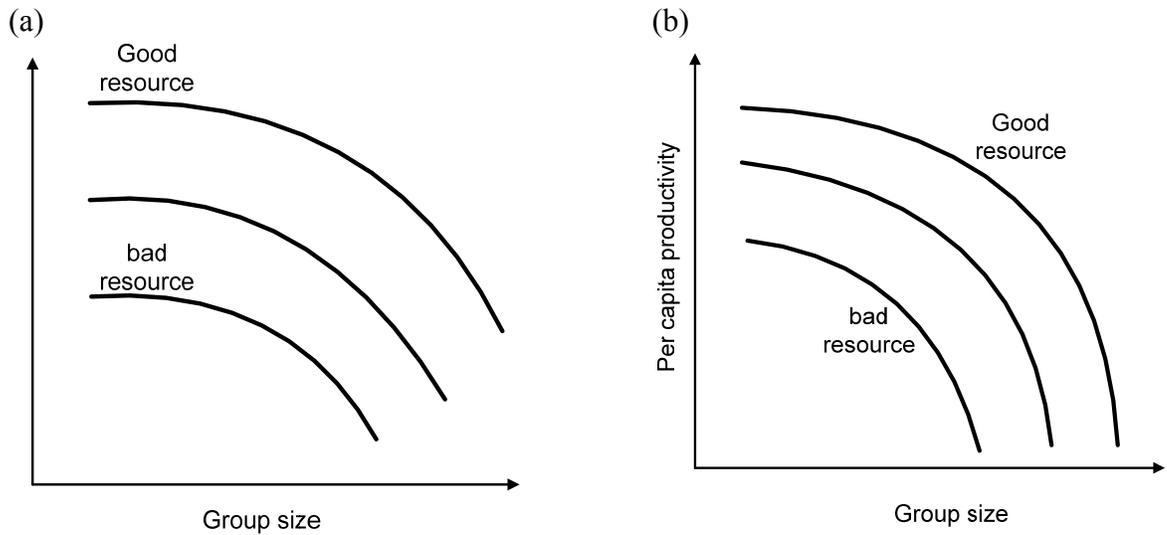


Figure 1.1 (a) Effects group size and resource quality on group productivity, $R(n, E_G, r)$, in a resource benefit type of social group. Group productivity of this type is determined by the resource quality and only decreases as group size increases because ill effect of crowding, such as competition between group members. (b) Effects group size and resource quality on per capita group productivity, $\frac{R(n, E_G, r)}{n}$, in a resource benefit type of social group.

Social benefit

Social benefit is defined as any group benefit generated by social coordination, such as reproductive, protective, and foraging benefits (Krause & Ruxton 2002; Whitehouse & Lubin 2005). By this definition, we exclude passive grouping effects such as lower predation rates in larger colonies. If a social benefit is more important for group formation, group productivity and per capita productivity usually increase as group size increases until they reach an optimum point and then decrease as group size increases (Fig. 1.1c,1.1d). The social benefit is defined mathematically as follows:

$$S(n, E_G, r) > \sum_{i=1}^n S(1, E_i) \quad (3)$$

Again, the left-hand side of the inequality (3) is the group productivity, $S(n, E_G, r)$ (S represents Social), which is a function of group size, n , Ecological factors, E_G , and relatedness, r , between group members. The right-hand side of the inequality (3) is the sum of each individual's direct fitness from breeding solitarily ($n=1$), which is influenced by the resource quality i^{th} individual can obtain, indicated by E_i .

The magnitude of group benefit is generally affected by ecological factors, such as food abundance and predation risk. For example, in the colonial-breeding sociable weaver, experimental supplementation of food decreases the average group size and increases the percentage of breeders in the manipulated colonies (Covas et al. 2004). This experiment clearly shows that food supplementation decreases the cost of foraging and thus decreases the social benefits created by group cooperation. In other words, the social benefit derived from group provisioning of young is more important when ecological conditions are poor (Fig. 1.1c and 1.1d).

Again, intrinsic benefits in the cooperative breeding literature belong to this social benefit category. Social benefit is more general than the intrinsic benefits or benefit of philopatry hypothesis because it is not based on explaining delayed offspring

dispersal. For example, some ant foundress associations consist of unrelated queens, which are clearly not formed through delayed offspring dispersal (Bernasconi & Strassmann 1999). The main reason that these non-kin groups form is because multiple-queen colonies can produce more workers to defend the nest and therefore can survive brood-raiding attacks better. Similarly, the social benefit of improved between-group competitive ability for resources is viewed as an important selective force for the formation of non-kin human social groups as well as kin social insect groups (Reeve & Hölldobler 2007; West et al. 2006).

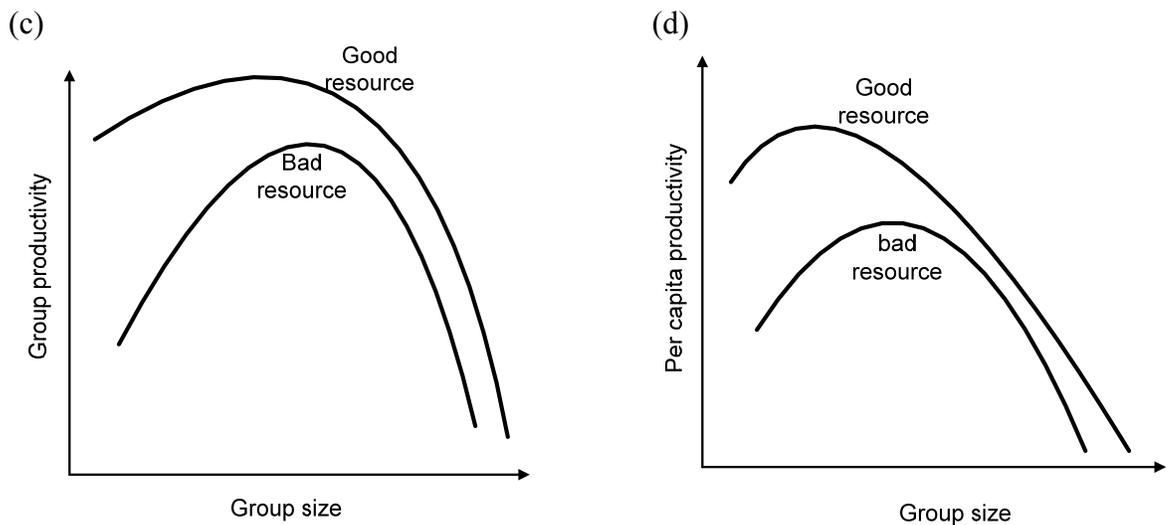


Figure 1.1 (c) Effects group size and resource quality on group productivity, $S(n, E_G, r)$, in a social benefit type of social group. The group productivity is increased through cooperation between group members. Thus, it increases as group size increases until it reach a point and then decreases as group size increases because the ill effect of crowding out weight the benefit created by group cooperation. (d) Effects group size and resource quality on per capita group productivity, $\frac{S(n, E_G, r)}{n}$, in a social benefit type of social group.

INTERGRATING SOCIAL AND RESOURCE BENEFITS WITH ECOLOGICAL CONSTRAINTS

We have emphasized the importance of separating social and resource benefits. However, social and resource benefits can both influence the evolution of cooperative breeding in a species. A more complete expression of the group benefit is

$$G(n, E_G, r) = S(n, E_G, r) + \alpha R(n, E_G, r) \quad (4),$$

where the influence of social benefit to group productivity is standardized to 1 and the influence of resource benefit is represented by α . When individuals are solitary, their direct fitnesses are not affected by group size and relatedness, but determined by the quality of the resources. This means that

$$S(1, E_i) = R(1, E_i) = L(E_i), \quad (5)$$

As a result, substituting inequality (4) and (5) into inequality (1), we obtain the explicitly necessary condition for a group to form and be stable, as follows

$$S(n, E_G, r) + \alpha R(n, E_G, r) > \sum_{i=1}^n L(E_i) \quad (6)$$

We believe that the important issue is to determine the relative importance of resource versus social benefits and their effect on the stability and size of the group. The best way to test the relative importance of social and resource benefits is through manipulation experiments. For example, in an excellent study of banded killifish, food and predation risk were manipulated separately. Predator scent was used to increase the benefit of group foraging and food scent modulated the perceived amount of resource. Killifish formed larger groups when predator scent was presented and were solitary or formed smaller groups when food scent was added. However, the group size is intermediate when both food and predator scent are presented (Hoare et al. 2004). Several other excellent experiments in cooperatively breeding species have shown the importance of social or resource benefits (Baglione et al. 2006; Dickinson

& McGowan 2005; Heg et al. 2004; Pruett-Jones & Lewis 1990). It would be even better to manipulate both social and resource benefits in the same species to determine the relative importance of each, although it might be empirically challenging to so.

TYPES OF GROUP BENEFIT AND THE GROUP COMPOSITION

The development of cooperative breeding theory has been largely influenced by avian studies and the helper-at-the-nest type of cooperative breeding system, in which “helpers” perform seemingly altruistic behavior such as foregoing personal reproduction and helping their parents. As a consequence, studies of cooperative breeding mainly focus on why offspring delay dispersal and why offspring help (but see Brown & Brown 1984; Cockburn 1996; Ekman et al. 2000; Emlen 1982b; Vehrencamp 1983). However, to develop a general theory of cooperative breeding, it is important to understand the costs and benefits of living in groups from the perspective of all group members.

The elegant concept of insider-outsider conflict constitutes the basic framework for studying group membership and group size in group-living species (Gaston 1978; Giraldeau & Caraco 1993; Higashi & Yamamura 1993). Insider-outsider conflict describes the tension between potential joiners, the outsiders, and the current group members, the insiders. For the insiders, it is often in their common interest to maintain the most productive group size. However, as long as joining the group yields higher inclusive fitness than being solitary, the outsiders would prefer to join the group and thus could drive the group size much larger than its most productive group size. If insiders have control of group membership, the observed group size is expected to be closer to the optimal size (Giraldeau & Caraco 2000). Following the logic of the insider-outsider conflict model, the parallel question to why offspring stay and help is

why insiders, the parents, accept or even facilitate, rather than evict, the delayed dispersal offspring.

If resource benefit is the key factor favoring group formation and the insiders have control over group membership, only kin groups are expected to form and the more closely related the group members are, the larger the group size (Fig. 1.2a). Non-kin groups can only form when insiders cannot control group membership. Also, groups with high quality resources are expected to have larger groups. However, if the social benefit is critical for living in a group, both relatives and non-relatives will be accepted by group members if the group size is smaller than the most productive size. Similarly, only kin groups are expected when the group size is larger than the most productive size (Fig. 1.2b). Consequently, studies of cooperative breeding can be integrated into a more general framework of social evolution.

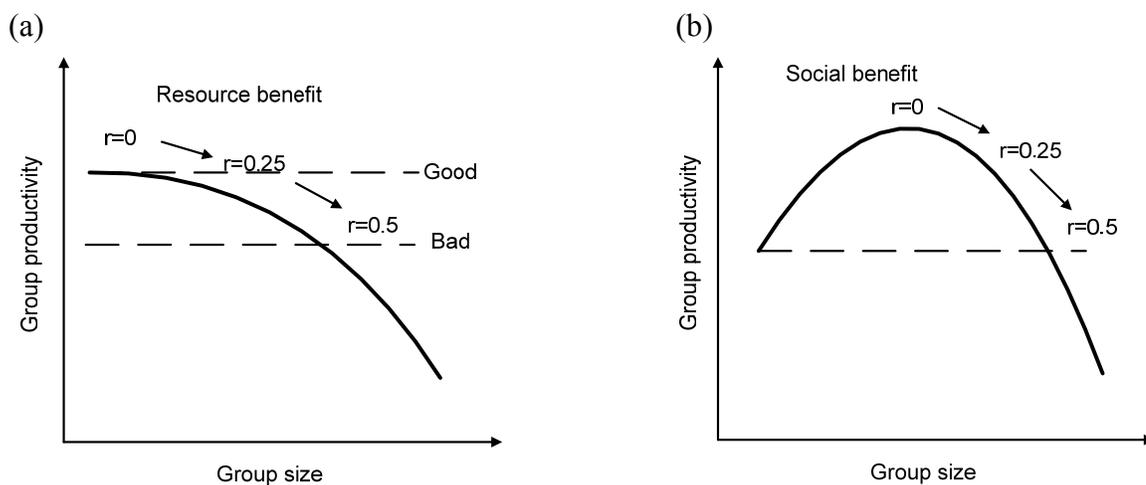


Figure 1.2 Group control version of insider-outsider conflict model. (a) Effect of relatedness on group size in (a) resource benefit type of group, and (b) social benefit type of group. Dash line indicates the payoff of solitary breeding.

BENEFITS, CONSTRAINTS, DELAYED DISPERSAL AND COOPERATIVE BREEDING

As we will show in the following sections, we believe that many of the problems related to the ecological constraint theory can be clarified by applying the resource and social benefit concepts.

1. *The ecological constraint hypothesis lacks predictive power because most species face some sort of ecological constraint but do not delay dispersal.* (Brockmann 1997; Covas & Griesser 2007; Hatchwell & Komdeur 2000; Koenig et al. 1992; Kokko 2007; Smith 1990).

This problem can be addressed by separating ecological constraints into resource and social benefits. It is apparent that this statement only works if the ecological constraint is a resource benefit because, by definition, if it is a social benefit, there will be strong selective forces favoring social living. Therefore, the question can be restated as, if resources are limited in many species, e.g. habitat saturation, why don't they all delay dispersal? Based on our previous analysis (Fig. 1.1, inequality (2)), limited resources in the environment does not automatically lead to a resource benefit and this is why the ecological constraint is considered to lack predictive ability because the resource benefit is key selection factor favoring group living. The insider-outsider conflict model also demonstrates that both the variation in resource quality and kinship are important for insiders to accept a potential joiner if the resource benefit is the key for a group to form. On the other hand, it has been shown both theoretically and empirically that given sufficient social benefits, groups can be stable even in the complete absence of constraints (Bull & Schwarz 1996; Kokko et al. 2001; Perrin & Lehmann 2001). Therefore, strong ecological constraints would not necessarily lead to cooperative breeding if the resource benefit is lacking, and

cooperative breeding could be stable under weak ecological constraints if the social benefit is high. Together, this shows that the ecological constraint hypothesis alone is overly generous and lacks predictive power, and that the social and resource benefit concept can help resolve this problem.

2. Stability of a social group

Based on the ecological constraints concept, cooperatively breeding groups are considered to be “inherently unstable” (Emlen 1995; Emlen 1997). This view has been supported by several excellent empirical studies (Dickinson & McGowan 2005; Komdeur 1992; Pruett-Jones & Lewis 1990; Walters et al. 1992). However, this view is clearly based on the resource benefits type of cooperative breeding groups. Similarly, delayed dispersal is often described as a “best-of-a-bad-job” strategy because of the fact that solitary breeders generally have the highest reproductive success, but this is only true for the resource benefit type of groups, as mentioned before. As a result, when high-quality resource becomes available, these delayed dispersal offspring would disperse and social groups are unstable.

Nevertheless, cooperatively breeding groups can be stable for many generations if social benefits are important for the formation of family groups. For example, in hunter-gather human societies, large extended families may be very stable for generations because large groups can defend themselves better and hunt more efficiently, without any limitation of resources (Alexander 1990). In pre-industrial human societies, the greater productivity of intensive cultivation results from more sophisticated technology, such as irrigation, and from intensification of labor, so family members are important working forces (Nanda 1991). These ideas all suggest that social benefits can lead to stable families and are supported by empirical data (e.g. Davis & Daly 1997).

3. *Bridging the gap between theories based on delayed dispersal and non-delayed dispersal.* As mentioned above, the development of cooperative breeding theories has been strongly influenced by avian studies. Since most cooperative breeding avian societies form through delayed offspring dispersal, the evolution of delayed dispersal has been the central focus for theories of the evolution of cooperative breeding (see Emlen & Vehrencamp 1983 for a notable exception). However, many cooperatively breeding groups are formed without delayed dispersal. Most researchers tend to treat these two types of breeding systems as having distinct selective forces. However, the distinction between the two might sometimes be difficult and artificial (Cockburn 1998). We believe that distinguishing social and resource benefit mechanisms of group formation helps bridge the gap between theories based on delayed dispersal and non-delayed dispersal types of cooperative breeding. This is also why we do not use the original terms of intrinsic benefit and extrinsic constraints, proposed in the context of explaining delayed dispersal, because social and resource benefit concepts work both with and without delayed dispersal. As a consequence, this theoretical framework will also help to integrate studies on different taxa and different types of cooperative breeding societies.

4. *Constraints, benefits, and delayed dispersal.*

Most studies on cooperative breeding have focused their attention on delayed dispersal by addressing two stepwise questions: “(1) why do offspring remain with their parents rather than disperse and attempt to breed independently on their own? And (2) why do such grown offspring help, rather than ignore, the breeding efforts of other adults in their group?” (Emlen 1997). If we apply the resource and social benefit framework, it is clear that if offspring only stay in the natal territory because of the resource benefit, the separation between “why stay” and “why help” is meaningful.

This is because if the main reason for staying is to gain a social benefit, e.g. increasing provisioning ability in poor years, delayed dispersal in such a scenario is linked with helping. This can help further clarify and shed new light on the old controversy between the ecological constraints hypothesis and the benefit of philopatry hypothesis. This disagreement has been settled by general consensus that the two hypotheses just look at different sides of the same coin: the benefit of staying and the cost of dispersal (but see Ligon 1999). However, we believe that there are deeper problems caused by the logical inconsistencies of both hypotheses. Stacey and Ligon (1991) listed the different predictions for the benefit of philopatry and ecological constraints hypotheses. Their benefit of philopatry hypothesis predictions are, in fact, based on social benefits and their ecological constraint hypothesis predictions are based on resource benefits. However, they include “access to critical resources”, which is a resource benefit, in the benefit of philopatry hypothesis, which is apparently equivalent to the ecological constraints hypothesis in stable environments (Stacey & Ligon 1987; Stacey & Ligon 1991). On the other hand, the original ecological constraints hypothesis emphasizes resource benefits when the environment is stable and social benefits when the environment is unpredictable (Emlen 1982a) . Therefore, the benefit of philopatry hypothesis provides the first hypothesis that social benefits alone, i.e. without habitat saturation or resource benefits, can favor the formation of stable social groups in stable environments. Unfortunately, the role of social benefits has been overlooked under the big umbrella of ecological constraints.

5. Inter-specific comparative studies on cooperative breeding

We believe that the resource and social benefit concept might also help explain why inter-specific comparative studies in birds have difficulty finding a clear relationship between the incidence of cooperative breeding and any environmental

factors (Brown 1987; Colwell 1974; Dow 1980; Duplessis et al. 1995; Ekman & Ericson 2006). It might simply be because those cooperative-breeding behaviors evolve through two distinctive routes, social versus resource benefits. For example, the life history hypothesis states that low annual mortality is the key factor that predisposes avian lineages to breed cooperatively, rather than any particular feature of their breeding ecology (Arnold 1998; Russell 1989). Extensions of the life history hypothesis further explain the link between life history traits, habitat saturation, and delayed dispersal in a stable environment, which are resource-benefit types of mechanisms (Covas & Griesser 2007; Hatchwell & Komdeur 2000; Kokko & Ekman 2002). On the other hand, a recent nice comparative study on Africa starlings shows that temporal environmental variability is correlated with cooperative breeding (Rubenstein & Lovette 2007). In this case, coping with the fluctuating insect abundances caused by unpredictable rain fall in different years might be the most important social benefit of grouping (Emlen 1982a). Therefore, distinguishing cooperative breeding species that have evolved via resource versus social benefits in comparative studies could give a better resolution for finding the relationship between ecological factors, life history characteristics and cooperative breeding in various taxa.

REFERENCES

- Alexander, R. D. 1990 *How did humans evolve? Reflections on the uniquely unique species*. Ann Arbor: Museum of Zoology, University of Michigan Special Publication NO. 1.
- Allee, W. C. 1938 *The Social Life of Animals*. New York: Norton.
- Arnold, K. E. 1998 Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society B: Biological Sciences* **265**, 739-745.
- Baglione, V., Canestrari, D., Marcos, J. M. & Ekman, J. 2006 Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding carrion crows. *Proceedings of the Royal Society B-Biological Sciences* **273**, 1529-1535.
- Bernasconi, G. & Strassmann, J. E. 1999 Cooperation among unrelated individuals: the ant foundress case. *Trends in Ecology & Evolution* **14**, 477-482.
- Brockmann, H. J. 1997 Cooperative breeding in wasps and vertebrates: the role of ecological constraints. In *The Evolution of Social Behavior in Insects and Arachnids* (ed. j. C. Choe & B. J. Crespi), pp. 347-371. Cambridge: Cambridge University Press.
- Brown, J. L. 1974 Alternate routes to sociality in jays-with a theory for the evolution of altruism and communal breeding. *American zoologist* **14**, 63-80.
- Brown, J. L. 1987 *Helping and communal breeding in birds*. Princeton: Princeton University Press.
- Brown, J. L. & Brown, E. R. 1984 Parental facilitation: parent-offspring relations in communally breeding birds. *Behavioral Ecology and Sociobiology* **14**, 203-209.

- Bull, N. J. & Schwarz, M. P. 1996 The habitat saturation hypothesis and sociality in an allodapine bee: cooperative nesting is not "making the best of a bad situation". *Behavioral Ecology and Sociobiology* **39**, 267-274.
- Buston, P. M., Bogdanowicz, S. M., Wong, A. & Harrison, R. G. 2007 Are clownfish groups composed of close relatives? An analysis of microsatellite DNA variation in *Amphiprion percula*. *Molecular Ecology* **16**, 3671-3678.
- Cockburn, A. 1996 Why do so many Australian birds cooperate: social evolution in the Corvidae. In *Frontiers of Population Ecology* (ed. R. B. Floyd, A. W. Sheppard & P. J. Barro), pp. 451–472. Melbourne: CSIRO Publishing.
- Cockburn, A. 1998 Evolution of Helping Behavior in Cooperatively Breeding Birds. **29**, 141-177.
- Colwell, R. K. 1974 Predictability, constancy, and contingency of periodic phenomena. *Ecology* **55**, 1148-1153.
- Costa, J. T. 2006 *The other insect societies*. Cambridge, Mass.: Belknap Press of Harvard University Press.
- Covas, R., Doutrelant, C. & du Plessis, M. A. 2004 Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. *Proceedings of the Royal Society B: Biological Sciences* **271**, 827-832.
- Covas, R. & Griesser, M. 2007 Life history and the evolution of family living in birds. **274**, 1349-1357.
- Davis, J. N. & Daly, M. 1997 Evolutionary theory and the human family. *Quarterly Review of Biology* **72**, 407-435.
- Dickinson, J. L. & Hatchwell, B. J. 2004 Fitness consequences of helping. In *Ecology and Evolution of Cooperative Breeding in Birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 48–66. Cambridge: Cambridge University Press.

- Dickinson, J. L. & McGowan, A. 2005 Winter resource wealth drive's delayed dispersal and family-group living in western bluebirds. *Proceedings of the Royal Society B-Biological Sciences* **272**, 2423-2428.
- Dow, D. D. 1980 Communally breeding Australian birds with an analysis of distributional and environmental-factors. *Emu* **80**, 121-140.
- Duplessis, M. A., Siegfried, W. R. & Armstrong, A. J. 1995 Ecological and life-history correlates of cooperative breeding in south-African birds. *Oecologia* **102**, 180-188.
- Eggert, A. K. & Muller, J. K. 1997 Biparental care and social evolution in burying beetles: lessons from the larder. In *The Evolution of Social Behavior in Insects and Arachnids* (ed. j. C. Choe & B. J. Crespi), pp. 216-236. Cambridge: Cambridge University Press.
- Ekman, J., Bylin, A. & Tegelstrom, H. 2000 Parental nepotism enhances survival of retained offspring in the Siberian jay. *Behavioral Ecology* **11**, 416-420.
- Ekman, J. & Ericson, P. G. P. 2006 Out of Gondwanaland; the evolutionary history of cooperative breeding and social behaviour among crows, magpies, jays and allies. *Proceedings of the Royal Society B-Biological Sciences* **273**, 1117-1125.
- Emlen, S. T. 1982a The evolution of helping I: An ecological constraints model. *American Naturalist* **119**, 29-39.
- Emlen, S. T. 1982b The evolution of helping. II: The role of behavioral conflict. *American Naturalist* **119**, 40-53.
- Emlen, S. T. 1994 Benefits, constraints and the evolution of the family. *Trends in Ecology & Evolution* **9**, 282-284.
- Emlen, S. T. 1995 An Evolutionary Theory of the Family. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 8092-8099.

- Emlen, S. T. 1997 Predicting family dynamics in social vertebrates. In *Behavioural Ecology: An Evolutionary Approach*, vol. 4 (ed. J. R. Krebs & N. B. Davies), pp. 228-253. Oxford: Blackwell Science.
- Emlen, S. T. & Vehrencamp, S. L. 1983 Cooperative breeding strategies among birds. In *Perspectives in ornithology* (ed. A. H. Brush & G. A. Clark). Cambridge Cambridge University Press.
- Gaston, A. J. 1978 The evolution of group territorial behavior and cooperative breeding. *American Naturalist* **41**: , 1097-1100.
- Giraldeau, L. A. & Caraco, T. 1993 Genetic Relatedness and Group-Size in an Aggregation Economy. *Evolutionary Ecology* **7**, 429-438.
- Giraldeau, L. A. & Caraco, T. 2000 *Social Foraging Theory*. Princeton, NJ: Princeton University Press.
- Hatchwell, B. J. & Komdeur, J. 2000 Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal behaviour* **59**, 1079-1086.
- Heg, D., Bachar, Z., Brouwer, L. & Taborsky, M. 2004 Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**, 2367-2374.
- Higashi, M. & Yamamura, N. 1993 What Determines Animal Group-Size - Insider-Outsider Conflict and Its Resolution. *American Naturalist* **142**, 553-563.
- Hoare, D. J., Couzin, I. D., Godin, J. G. J. & Krause, J. 2004 Context-dependent group size choice in fish. *Animal Behaviour* **67**, 155-164.
- Johnson, D. D. P., Kays, R., Blackwell, P. G. & Macdonald, D. W. 2002 Does the resource dispersion hypothesis explain group living? *Trends in Ecology & Evolution* **17**, 563-570.

- Koenig, W. D. 1981 Reproductive Success, Group Size, and the Evolution of Cooperative Breeding in the Acorn Woodpecker. *American Naturalist* **117**, 421-443.
- Koenig, W. D. & Pitelka, F. A. 1981 Ecological factors and kin selection in the evolution of cooperative breeding in birds. In *Natural Selection and Social Behavior: Recent Research and New Theory*. (ed. R. D. Alexander & D. W. Tinkle), pp. 261-280. New York.: Chiron Press.
- Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L. & Stanback, M. T. 1992 The Evolution of Delayed Dispersal in Cooperative Breeders, vol. 67, pp. 111-150: JSTOR.
- Kokko, H. 2007 Cooperative behaviour and cooperative breeding: What constitutes an explanation? *Behavioural Processes* **76**, 81-85.
- Kokko, H. & Ekman, J. 2002 Delayed Dispersal as a Route to Breeding: Territorial Inheritance, Safe Havens, and Ecological Constraints. *American Naturalist* **160**, 468-484.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society B-Biological Sciences* **268**, 187-196.
- Komdeur, J. 1992 Importance of Habitat Saturation and Territory Quality for Evolution of Cooperative Breeding in the Seychelles Warbler. *Nature* **358**, 493-495.
- Krause, J. & Ruxton, G. 2002 *Living in Groups*. Oxford: Oxford University Press.
- Ligon, J. D. 1999 *The evolution of avian breeding systems*. New York: Oxford University Press
- Nanda, S. 1991 *Cultural Anthropology*. Belmont: Wadsworth Publishing Company.

- Pen, I. & Weissing, F. J. 2000 Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. *Proceedings of the Royal Society B-Biological Sciences* **267**, 2411-2418.
- Perrin, N. & Lehmann, L. 2001 Is Sociality Driven by the Costs of Dispersal or the Benefits of Philopatry? A Role for Kin-Discrimination Mechanisms. *American Naturalist* **158**, 471-483.
- Pruett-Jones, S. G. & Lewis, M. J. 1990 Sex-Ratio and Habitat Limitation Promote Delayed Dispersal in Superb Fairy-Wrens. *Nature* **348**, 541-542.
- Rankin, D. J., Bargum, K. & Kokko, H. 2007 The tragedy of the commons in evolutionary biology. *Trends in Ecology & Evolution* **22**, 643-651.
- Reeve, H. K. & Hölldobler, B. 2007 The emergence of a superorganism through intergroup competition. *Proceedings of the National Academy of Sciences* **104**, 9736.
- Rubenstein, D. R. & Lovette, I. J. 2007 Temporal environmental variability drives the evolution of cooperative breeding in birds. *Current Biology* **17**, 1414-1419.
- Russell, E. M. 1989 Cooperative breeding-a Gondwanan perspective. *Emu* **89**, 61-62.
- Selander, R. K. 1964 Speciation in wrens of the genus *Campylorhynchus*. *University of California publications in zoology* **74**, 1-224.
- Smith, J. N. M. 1990 Summary. In *Cooperative Breeding in Birds: long-term studies of ecology and behavior* (ed. P. B. Stacey & W. D. Koenig), pp. 593-611. Cambridge: Cambridge University Press.
- Stacey, P. B. & Ligon, J. D. 1987 The benefits-of-philopatry hypothesis for the evolution of cooperative breeding variation in territory quality and group size effects. *American Naturalist* **130**: 654-676. **130**, 654-676.

- Stacey, P. B. & Ligon, J. D. 1991 Territory quality and dispersal options in the acorn woodpecker and a challenge to the habitat-saturation model of cooperative breeding. *American Naturalist* **137**, 831-846.
- Vehrencamp, S. L. 1983 A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour* **31**, 667-682.
- Walters, J. R., Doerr, P. D. & Iii, J. H. C. 1992 Delayed Dispersal and Reproduction as a Life-History Tactic in Cooperative Breeders: Fitness Calculations from Red-Cockaded Woodpeckers. *American Naturalist* **139**, 623-643.
- West, S. A., Gardner, A., Shuker, D. M., Reynolds, T., Burton-Chellow, M., Sykes, E. M., Guinnee, M. A. & Griffin, A. S. 2006 Cooperation and the Scale of Competition in Humans. *Current Biology* **16**, 1103-1106.
- Whitehouse, M. E. A. & Lubin, Y. 2005 The functions of societies and the evolution of group living: spider societies as a test case. *Biological Reviews* **80**, 347-361.

CHAPTER 2

REPRODUCTIVE SKEW THEORY UNIFIED:

THE GENERAL BORDERED TUG-OF-WAR MODEL

ABSTRACT

Reproductive skew has been identified as a major dimension along which animal societies vary. Two major kinds of reproductive skew models are transactional models, in which explain the distribution of reproduction within animal societies as the result of reproductive payments exchanged among group members with differential leverage, and tug-of-war models, in which the reproductive shares are determined by costly 'tugs-of-war'. These two models have recently been synthesized to yield the mutual-pay, bordered tug-of-war model. In this paper, we extend the latter and demonstrate that the generalized model yields four sub-models, namely the mutual-pay, alpha-pay, beta-pay, and pure tug-of-war. The alpha-pay sub-model turns out to closely resemble the original “concessions” transactional skew model, and the beta-pay sub-model turns out to have properties similar to the “restraint” transactional skew model. Thus, the general model unifies the four major models of reproductive skew and is rich in its predictions, as each sub-model exhibits different qualitative and quantitative relationships between reproductive skew or intra-group conflict and the ecological and genetic factors that determine skew and conflict. The conditions favoring transitions among these sub-models also are precisely predicted by the general model. The general model accommodates the data from acorn woodpeckers and primitively eusocial bees and potentially can account for many of the highly varied empirical findings on reproductive skew. We suggest further research that focuses on (1) determining which model is suitable for certain species and (2) understanding why and how various social animals resolve their breeding conflict by different conflict resolution mechanisms.

INTRODUCTION

Reproductive skew refers to the partitioning of reproduction among same sex individuals within social groups and has been identified as a major dimension along which animal societies vary (Sherman et al., 1995). In high-skew societies, reproduction is monopolized by one or a few group members; in low-skew societies, reproduction is shared more evenly. Two major kinds of reproductive skew models are the transactional models and the tug-of-war models. Transactional models of social evolution explain the distribution of reproduction within animal societies as the result of reproductive payments exchanged among group members one of whom has complete control over reproductive shares (Buston et al., 2007; Emlen, 1982; Johnstone, 2000; Reeve and Keller, 2001; Reeve and Ratnieks, 1993; Vehrencamp, 1983). In contrast, tug-of-war models assume that no individual may have complete control of the reproductive partitioning, and the reproductive skew may be determined instead by costly 'tugs-of-war' in which it is assumed that effort allocated to increasing one's own selfish share results in decreased overall group productivity (Reeve et al., 1998).

The fact that the applicability of the transactional models is limited by the assumption that someone has complete reproductive control and that tug-of-war models do not take group stability into account stimulated Reeve and Shen (2006) to develop the "mutual-pay bordered tug-of-war" model (or, the incomplete-control transactional model), which has elements of both the transactional model and the tug-of-war model. In particular, the dominant and subordinate may yield some reproduction to each other to maintain group stability (i.e., there are mutual payments), as in a transactional model, but the dominant and subordinate might enter into a tug-of-war over the non-ceded part of reproduction. This model is more biologically realistic with predictions different from either the transactional or tug-of-

war models (Reeve and Shen, 2006). Nonacs (2006; 2007) criticized this model on the grounds that the mutual payment bordered-tug-of-war will collapse to a pure tug-of-war, but below we show why this conclusion is mistaken. Instead, we show that a natural generalization of the mutual-payment, bordered tug-of-war immediately generates four special case skew models: (1) the mutual-pay bordered tug-of-war, (2) the original pure tug-of-war, (3) a bordered tug-of-war in which the subordinate pays the dominant but not vice versa (a “beta-pay” bordered tug-of-war), and (4) a bordered tug-of-war in which the dominant pays the subordinate but not vice versa (an “alpha-pay” bordered tug-of-war). The alpha-pay sub-model turns out to closely resemble the original “concessions” model of transactional skew theory, and the beta-pay sub-model turns out to have properties similar to the “restraint” model of transactional skew theory. In short, the general model unifies the four major models of reproductive skew. Moreover, by relaxing the restrictive “complete control” assumption of the original transactional theory, we argue that the skew theories are now more biologically realistic and potentially applicable to more animal societies.

As we show below, the general model is rich in its predictions, as each sub-model exhibits different qualitative and quantitative relationships between reproductive skew and the ecological and genetic factors that determine skew. We derive the ecological and genetic conditions that determine which sub-model applies in a given case. The hope is that the general model is rich enough to account for many or most of the varied and puzzling patterns of reproductive partitioning encountered in recent empirical studies of skew. Moreover, the theoretical generalization presented here cleans up and unifies models that previously seemed disconnected. The fast proliferation of the seemingly different skew models and the complex predictions of these models have raised empiricists’ concern of the difficulty to testing these models in the field (e.g. Magrath et al., 2004), so theoretical unification would be highly

welcome to empiricists: Unification will greatly facilitate the testing of alternative models because we now have a theory of which sub-model should apply in specified ecological and genetic conditions.

We begin by extending the “mutual-pay bordered tug-of-war”, which describes the situation that both group members need to yield reproduction to its partner to maintain cooperation (Reeve and Shen, 2006), to allow for the possibility that the only one or neither individual needs to yield reproduction to its partner to keep the latter in the group.

THE BASIC MODEL

We consider a simple group of two individuals, a dominant and a subordinate. Following Reeve et al. (1998), dominance is assumed to be determined by resource-holding power. The dominant can decide how much fraction x , and the subordinate can decide how much fraction y , of the group’s output to invest in the tug-of-war. The fraction of non-ceded part of group resources going to the dominant is $x/(x + by)$ and to the subordinate is $by/(x + by)$, where the constant b (ranging from 0 to 1) represents the subordinate’s smaller resource holding power (RHP) or competitive efficiency compared to the dominant. The actual group output becomes $G(1 - x - y)$, where G is the total group resource. Therefore, the x and y are the selfish efforts because the more effort, x or y , put into a tug-of-war, the greater the individual’s relative reproductive share but the smaller the group output. The total group resource that is “spent” in the competition to increase personal shares (i.e., $G(x+y)$) measures the degree of within-group conflict. In addition, individuals may have to yield some reproduction as an “incentive” to keep its partner in the group. However, unlike in previous transactional models with the complete control assumption, in our model, both the dominant and the subordinate must yield a fraction p and q , respectively, of the group resource

remaining after the tug-of-war ($G(1-x-y)$) to each other to prevent each other from pursuing non-cooperative options, i.e., to maintain group stability. The best available non-cooperative option will depend on the species and ecology, but for simplicity, we assume that it is to fight for sole possession of the group's resource, with a reproductive output L going to the winner and the solitary breeding payoff S going to the loser, whose is forced to disperse. (Therefore, the group output (k) in previous versions of transaction models is equivalent to $G(1-x-y)/L$ in this version.) The proportion of realized group output that is yielded by the other member to a focal individual could be viewed as the focal individual's "protected share" because it is exempt from the costly tug-of-war process. As a consequence, the total share of direct reproduction that the subordinate obtains is

$p + (1-p-q)\left(\frac{by}{x+by}\right)$ and the share that the dominant obtains is $q + (1-p-q)\left(\frac{x}{x+by}\right)$. In this simple dyadic group case, an individual's inclusive fitness (Hamilton, 1964) associated with a certain strategy is

$$I_i = P_i + rK_i, \quad (1)$$

where P_i is the focal individual's personal reproduction associated with i strategy, K_i is the other party's reproduction if strategy i is performed, and r is the genetic relatedness between the two parties. The subordinate's overall inclusive fitness when staying in the group is thus

$$I_{g_s} = G(1-x-y)\left\{ \left[p + (1-p-q)\frac{by}{x+by} \right] + r \left[q + (1-p-q)\frac{x}{x+by} \right] \right\}, \quad (2)$$

and the dominant's inclusive fitness when staying in the group is

$$I_{g_d} = G(1-x-y)\left\{ \left[q + (1-p-q)\frac{x}{x+by} \right] + r \left[p + (1-p-q)\frac{by}{x+by} \right] \right\}. \quad (3)$$

However, both the dominant and the subordinate may choose the non-cooperative option, where f is the probability of the subordinate's winning the fight for the group's resource. We further assume that the probability f of winning a fight is an increasing

function of the subordinate's relative resource holding power b , i.e., $f = b/(1+b)$. Therefore, the reproductive output for the subordinate's non-cooperative option, i.e. fighting for the territory, is $fL + (1-f)S$ and $fS + (1-f)L$ is that for the dominant. Using Equation (1) and substituting $f = b/(1+b)$ to obtain the subordinate's inclusive fitness associated with the non-cooperative option, we get

$$I_{S_s} = \frac{L(b+r) + S(1+br)}{1+b}, \quad (4)$$

and for the dominant

$$I_{S_d} = \frac{L(1+br) + S(b+r)}{1+b}. \quad (5)$$

The group will be stable if

$$I_{g_s} > I_{S_s}; \text{ and } I_{g_d} > I_{S_d}. \quad (6a, 6b)$$

We use the Inequalities (6a and 6b) to find the minimum incentives, p^* and q^* , that the dominant and the subordinate need to yield to the other party to maintain the group's stability. We seek the Nash equilibrium (x^*, y^*, p^*, q^*) with the fitness function from Equations (2), (3) and Inequality (9) (Mesterton-Gibbons, 1992). The Nash equilibrium in this case is obtained by finding the positive values x^* , y^* , p^* and q^* simultaneously satisfying

$$\partial I_{g_d} / \partial x = 0; \partial I_{g_s} / \partial y = 0; I_{g_s} = I_{S_s}; \text{ and } I_{g_d} = I_{S_d}$$

at $x = x^*$; $y = y^*$; $p = p^*$ and $q = q^*$. This is a constrained optimization problem, in that the evolutionarily stable selfish efforts and incentives depend on the constraints that each party must end up with at least as high a fitness by being in the group as by taking the non-cooperative option. (Nonacs (2007) was puzzled at how Reeve and Shen's bordered tug-of-war model could yield different conclusions from those of Johnstone (2000) since both used the same formulae for inclusive fitnesses for cooperation- the answer is that the form of the constraint, which differs in the two

approaches, sensitively affects the fitness-maximizing strategies as is generally the case in constrained optimization.)

The solutions are

$$\begin{aligned}
p^* &= \frac{1}{(1+b)^2(r^2-1)(L+S)^3} \{G[L(b+r)+s+brs][L+bLr+S(b+r)] \\
&+ b(G-L-S)[L+bLr+(b+r)s]^2 - (L+S)[(1+r-r^2)(bL+S)^2 \\
&+ 2(bL+S)(L+bS)+r(L+bS)^2]\} \\
q^* &= \frac{1}{b(1+b)^3(r^2-1)(S+L)^3} \{(1+b)(G-L-S)[L(b+r)+S+brS]^2 + b\{r(G+bg-bL-S) \\
&(bL+S)^2 + [r(r-1)-1](L+bS)^3 + (b+1)(bL+S)(L+bS)[G(1+r^2) - \frac{(2+r)(bL+S)}{1+b}] \\
&+ (1+b)(L+bS)[Gr + \frac{(bL+S)[r(r-1)]-3}{1+b}]\} \\
x^* &= \frac{(G-S-L)[L(b+r)+S+brS]}{G(1+b)(1+r)(S+L)}, \text{ and} \\
y^* &= \frac{(G-S-L)[L+S(b+r)+bLr]}{G(1+b)(1+r)(S+L)}. \tag{7}
\end{aligned}$$

Inspection of Equation (7) immediately reveals that for $x^* > 0$ and $y^* > 0$ to be true, the inequality

$$G > (S+L) \tag{8}$$

must be true. Inequality (8) also is derived from the inequality

$$(1-p^*-q^*) > 0 \tag{9}$$

which must be satisfied if the group is to be stable (if p^* and q^* sum to greater than 1, then it would not be possible for both parties to give incentives large enough to keep its partner cooperating in the group). In other words, Inequality (8) must be true for the group to be stable, and, if it is stable, then the evolutionarily stable selfish efforts will be positive.

The solutions in (7) assume that the ecological parameters G , L , and S , the competition parameter b , and the genetic relatedness r are such that $p^* > 0$ and $q^* > 0$. Nonacs (2007) criticized the mutual-pay bordered tug-of-war model because situations

can arise for which p^* or q^* or both can be less than zero. However, the proper conclusion is that the mutual-pay bordered tug-of-war model simply does not apply to such cases, not that it is flawed. The correct procedure to follow if p^* or $q^* < 0$ is to set the variables with negative values to zero and then again solve $\partial I g_d / \partial x = 0$; $\partial I g_s / \partial y = 0$; $I g_s = I s_s$; and $I g_d = I s_d$ for the selfish efforts and for the incentives that did not initially come out negative. We show that doing the latter generates the four sub-models together constituting the general bordered tug-of-war: the mutual-pay tug-of-war, the pure tug-of-war, the alpha-pay tug-of-war, and the beta-pay tug-of-war. Before doing this, we first need to note the dynamics of the decision process assumed by the general bordered tug-of-war model.

DYNAMICS OF DECISION-MAKING IN THE GENERAL TUG-OF-WAR

Considerable confusion exists over the dynamics of the decision-making process assumed in the transactional models and general BTOW model (Nonacs 2006, 2007). It has long been acknowledged that some kind of cheater prevention mechanism is necessary for *all* transactions to be evolutionarily stable (Reeve and Keller, 1997; Reeve and Nonacs, 1992). The intuitive explanation is that individuals would always benefit by yielding a lesser reproductive share to her partner unless she would respond by leaving the group or otherwise punishing her. Therefore, the conceded share is determined by the boundary conditions for group stability. This is also why transactions can be evolutionarily stable only if individuals can respond to partner's cheating behavior on behavioral time scales (Kokko, 2003). Thus, cheater prevention mechanisms, such as punishment and differential partner choice, are implicitly assumed in all transactional models of reproductive skew.

Since the bordered tug-of-war model is an incomplete control transactional model, cheater prevention mechanisms also are assumed in this model. Incorporating the

latter assumption, we clarify the decision-making process here to show that some recent criticisms of the BTOW approach are incorrect. The assumed decision dynamics are pictured in Fig. 2.1a. At an initial time, the dominant (Dom) and subordinate (Sub) each choose their incentives (p^* and q^* , respectively) and selfish efforts (x^* and y^* , respectively) based on their assessments of all input parameters. Each chooses values that maximize its inclusive fitness given that its partner chooses values that maximize its own inclusive fitness. Thus, the partner's fitness-maximizing choices are computed by both individuals (since all input variables, including relative fighting ability, are assumed assessable by both individuals), and each individual plays its "sealed bids" simultaneously, these bids (i.e., incentives and selfish efforts) determine the group production and reproductive shares in a small time interval Δt (the interval is "small" compared to the full duration of the cooperative association, not necessarily small in absolute duration). After Δt , each individual repeats its assessments and decisions, altering its computation of its own optima if the latter did not behave as computed in the previous time interval. In particular, the observed partner's effort and incentives would be plugged into the focal individual's new optimization procedure. (If the input variables have the same value in this next time interval, the evolutionary stable decisions will remain unaltered as well.) In sum, we assume that each player plays according to the rule: (1) Initially, choose the selfish effort and incentive that maximizes the inclusive fitness of cooperation given that the partner does the same, and cooperate if this maximal inclusive fitness exceeds that for non-cooperation; otherwise, take the non-cooperative option. (2) Thereafter, repeat (1) except use the partner's previously observed efforts and incentives in the calculation of one's own optimal selfish effort and incentive for cooperation.

In this process, the selfish efforts and incentives in (7) are evolutionarily stable for the case of $p^* > 0$ and $q^* > 0$. For example, suppose that one individual decreases

the conceded incentive to its partner below that specified in (7). Then the partner would be favored to take its non-cooperative option in the next small time interval, and the focal individual would necessarily experience reduced inclusive fitness (if $G > S+L$) because of the loss of cooperation of its partner. Thus, by not taking into account the subsequent, immediate damage-inflicting behavior of its partner, an individual skimming the incentives would be behaving sub-optimally. The individual cheated upon would have minimal losses in inclusive fitness, because of the small time interval involved. (Note: The inclusive fitness expressions in [2] and [3] always increase as a partner's incentive decreases, but this does not mean that incentives should not be given, because a decrease in the partner's incentive causes the inclusive fitnesses [2] and [3] to no longer apply, the inclusive fitnesses instead becoming equal to the lower values in (4) and (5). Unfortunately, Nonacs (2007) missed this point in erroneous arguments that the bordered tug-of-war reverts to a pure-tug-of-war without incentives). Similarly, any elevation in selfish efforts above or below those in (7) would trigger subsequent changes in the partner's selfish efforts that would necessarily inflict inclusive fitness losses on the focal individual. It might be thought that reducing both incentives and selfish effort simultaneously below the solutions in (7) might yield an inclusive fitness advantage while retaining the partner, but this leads to the subordinate or dominant responding with increasing selfish effort. After a few steps, both group members eventually choose the non-cooperative options because the payoffs for both group members are lower than the payoffs obtained by the solutions in (7) (Fig. 2.1b). In sum, the solutions in (7) are stable for $p^* > 0$ and $q^* > 0$.

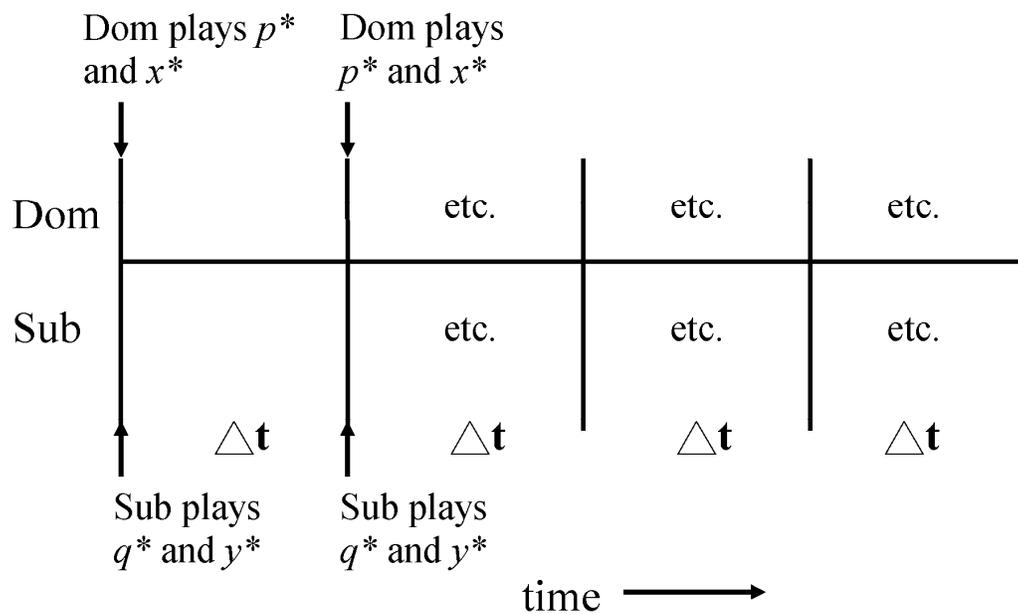


Figure 2.1 (a) Dynamics of decision-making in the synthetic model. At an initial time, the dominant (Dom) and subordinate (Sub) each choose their conceded shares (p^* and q^* , respectively) and selfish efforts (x^* and y^* , respectively) based on their assessments of all input parameters; each chooses values that maximize its inclusive fitness given that its partner chooses values that maximize its own inclusive fitness (the partner's fitness-maximizing choice is computed by both individuals). After a short time Δt , each individual repeats its assessments and decisions.

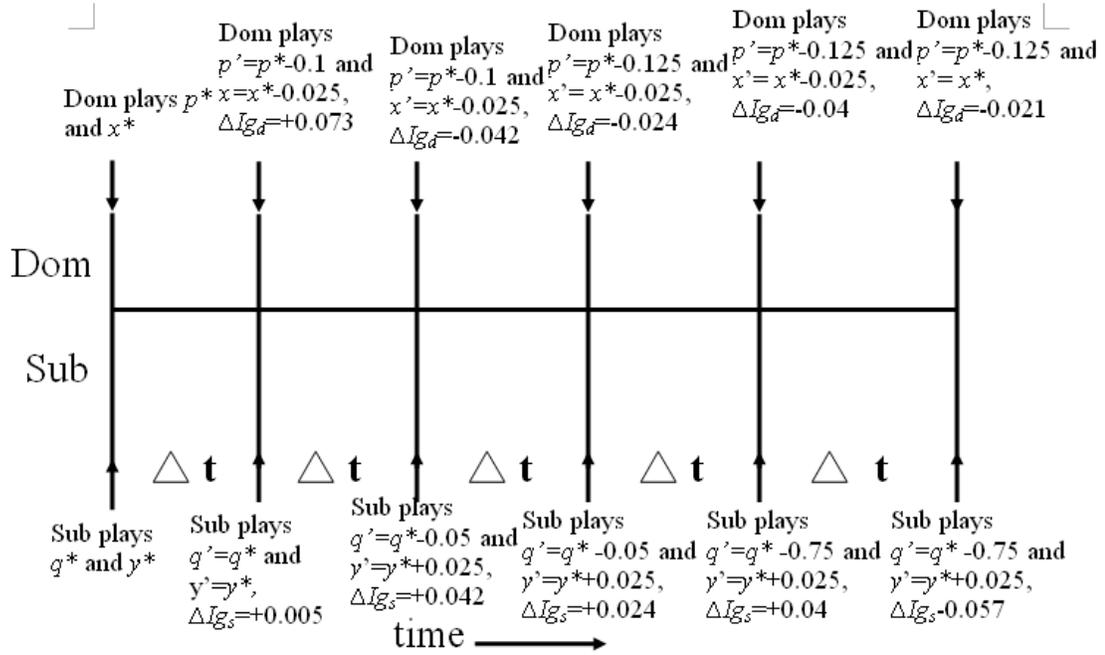


Figure 2.1 (b) A numerical example shows that a mutant strategy of simultaneously decreasing selfish effort, from x^* to $x^* - 0.025$, and conceded share, from p^* to $p^* - 0.1$, is not stable. This is because if one individual decreases her selfish effort, her partner would always gain by increasing its own selfish effort, at the cost of the first individual. After a few steps, both group members eventually choose the non-cooperative options because the payoffs for both group members are lower than the payoffs obtained by the solutions in (7). ΔI_{gd} and ΔI_{gs} represent the inclusive fitness differences between the mutant strategy (p', q', x', y') and the strategy corresponding to our original solutions $(p^*, q^*, x^*, y^*, \text{equation 7})$. Parameter values used in the figure are $L=1, r=0.25, S=0.8, b=0.6, G=2.5$.

TRANSITIONS BETWEEN DIFFERENT SUB-MODELS

In the parameter space in which both p^* and q^* are greater than zero, both the dominant and the subordinate benefit by yielding a certain fraction of the group's resource to each other. Therefore, we call this region the “*mutual-pay bordered tug-of-war*”, or mutual-pay BTOW (Fig. 2.2 and 2.3; see Reeve and Shen 2006). We can also view $p^* > 0$ (or $q^* > 0$) as occurring when the subordinate (or dominant) requires a non-zero fraction of reproduction to no longer be favored to choose the non-cooperative option. As a result, in the mutual-pay BTOW, both the dominant and the subordinate achieve almost the same inclusive fitness by staying in the group as they would have by choosing their non-cooperative options (Fig. 2.4a and 2.4b).

Similarly, when $p^* = 0$ (or $q^* = 0$), the subordinate (or dominant) prefers staying in the group even without the other party yielding any fraction of reproduction to it (Fig. 2.4a and 2.4b). For example, when $p^* > 0$ but $q^* = 0$, the subordinate will not choose to stay in the group without the dominant's incentive but the dominant will prefer to stay regardless of whether the subordinate yields reproduction or not (Fig. 2.4a and 2.4b). Because $q < 0$ is not biologically meaningful, when ecological or genetic parameters are such that $q^* \leq 0$ in (7), we substitute zero for q in Equations (1) and (2) to obtain the dominant's and the subordinate's inclusive fitness for cooperation as follows

$$I_{g_s} = G(1-x-y) \left\{ \left[p + (1-p) \frac{by}{x+by} \right] + r \left[(1-p) \frac{x}{x+by} \right] \right\} \quad (10)$$

$$I_{g_d} = G(1-x-y) \left\{ \left[(1-p) \frac{x}{x+by} \right] + r \left[p + (1-p) \frac{by}{x+by} \right] \right\}. \quad (11)$$

The procedure in (7) is then applied to (10) and (11) to solve for p^* , x^* , and y^* , with $q^* = 0$. Unfortunately, the solutions are very cumbersome, so we will examine this sub-model numerically below. We term this subset of the model as “ *α -pay bordered tug-of-war*”, or α -pay BTOW. Since in α -pay BTOW, only the dominant yields

reproduction to keep the subordinate staying in the group, this sub-model is conceptually similar to the original concession transactional model (Emlen, 1982; Reeve and Ratnieks, 1993; Vehrencamp, 1983). However, the complete control assumption is relaxed. As we will show later, the properties of the α -pay BTOW are similar to those of the concession model as well.

Similarly, we can obtain the “ β -pay bordered tug-of-war”, or β -pay BTOW when $q^* \leq 0$ but $p^* \geq 0$ in (7). The procedure in (7) is now applied to solve for q^* , x^* , and y^* , with $p^* = 0$. Unfortunately, the solutions are very cumbersome, so we will examine this sub-model numerically below. The β -pay BTOW model is similar to the restraint model (Johnstone and Cant, 1999), in which only the subordinates yields reproduction the dominant. Again, unlike in restraint model, we do not assume the subordinate has complete control over reproduction.

Interestingly, if both $q^* \leq 0$, and $p^* \leq 0$ in (7), the inclusive fitnesses for the dominant and the subordinate become

$$I_{g_s} = G(1 - x - y) \left[\frac{by}{x + by} + r \frac{x}{x + by} \right] \quad (12)$$

$$I_{g_d} = G(1 - x - y) \left[\frac{x}{x + by} + r \frac{by}{x + by} \right], \quad (13)$$

which are the same as those of the original tug-of-war (TOW) model developed by Reeve et al. (1998) except that we add G to describe the total group resource in this model. We solve for just x^* and y^* as in Reeve et al. (1998). All of the transitions between sub-models are summarized in Table 2.1.

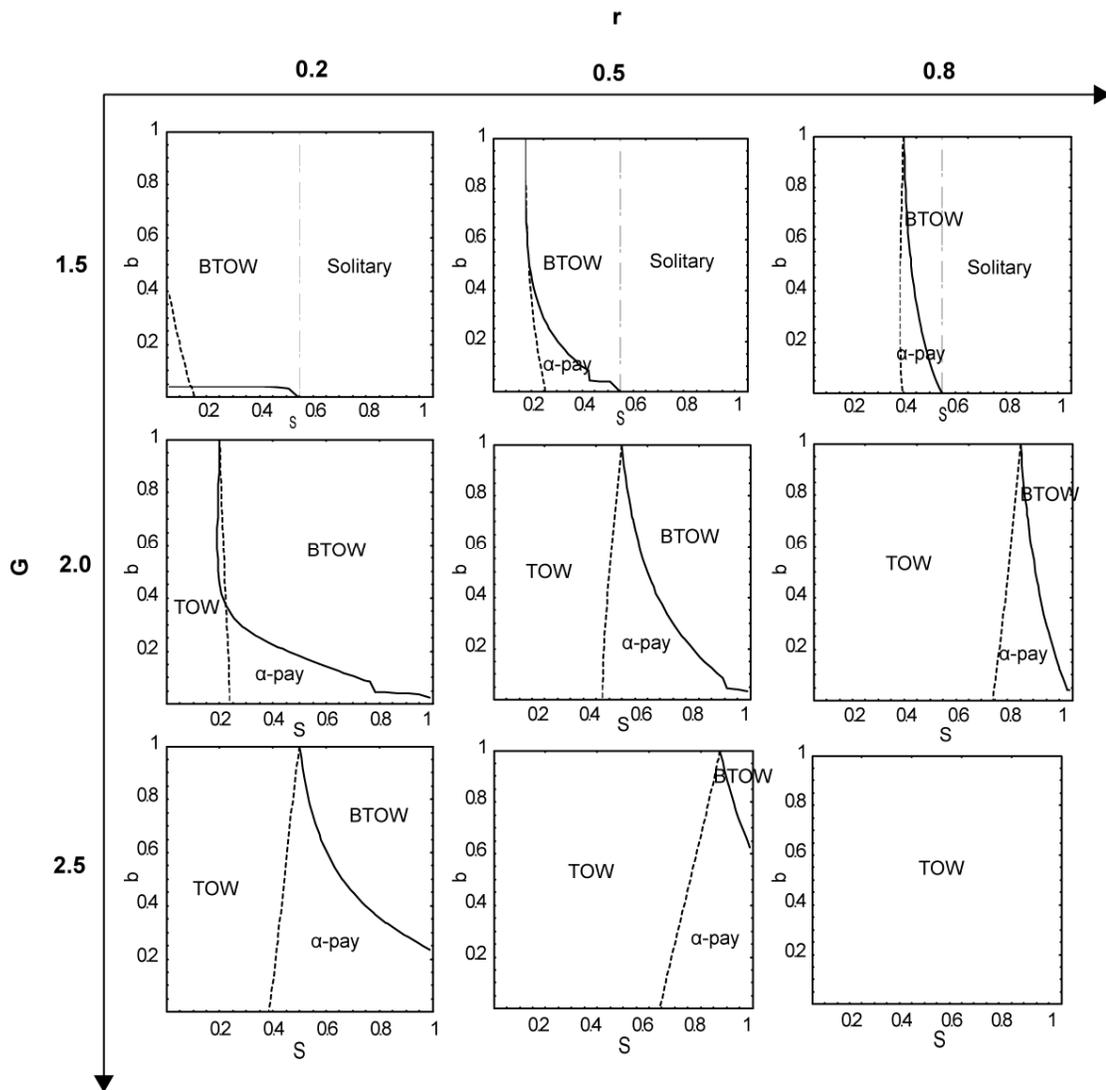


Figure 2.2 Transitions of different sub-models in relation to group resource (G) and genetic relatedness (r). The dash lines represent isoclines where $p=0$ and solid lines indicate parameter space where $q=0$ and the dash-and-dot lines show the group stability threshold ($G > S+L$).

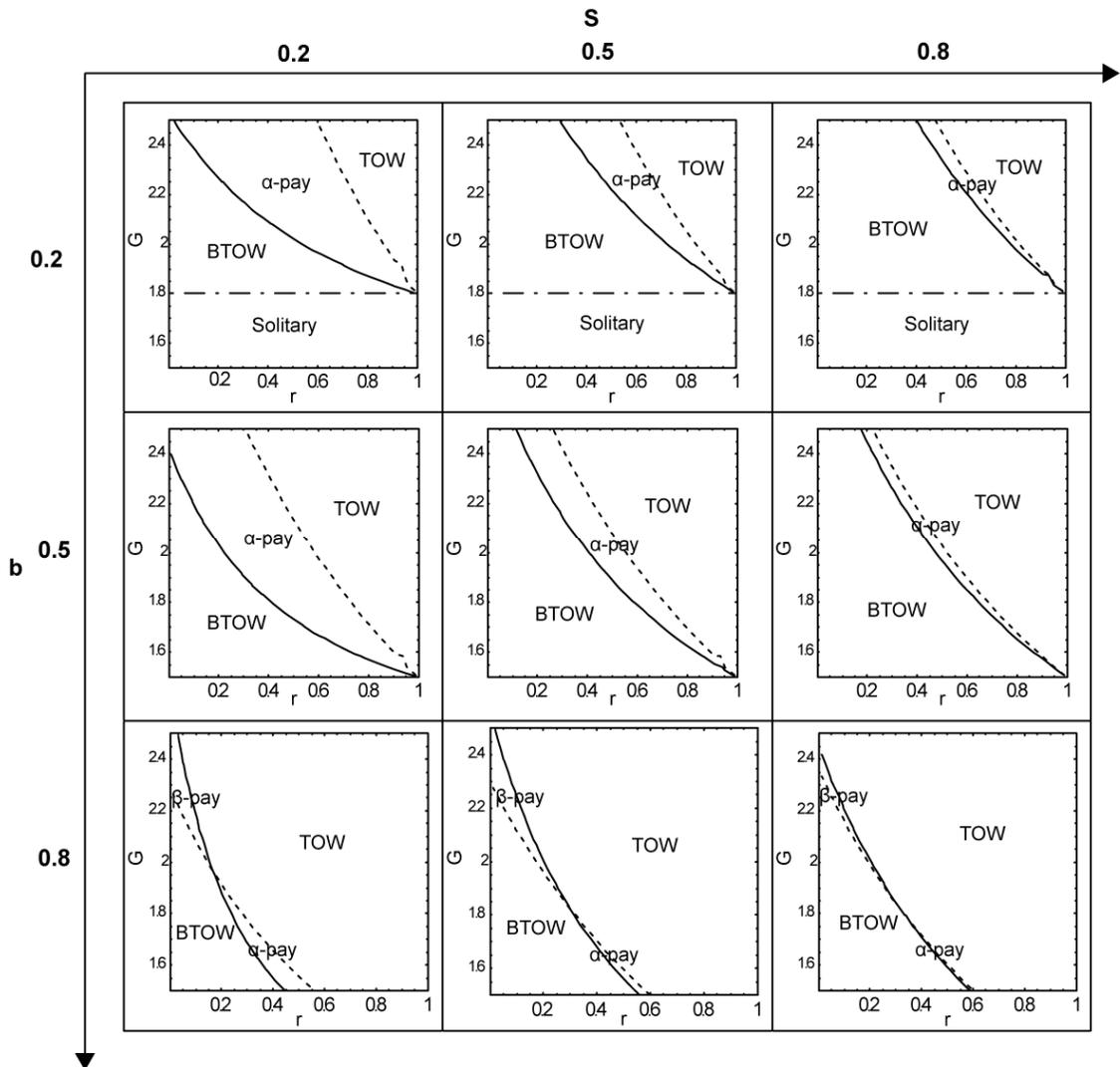
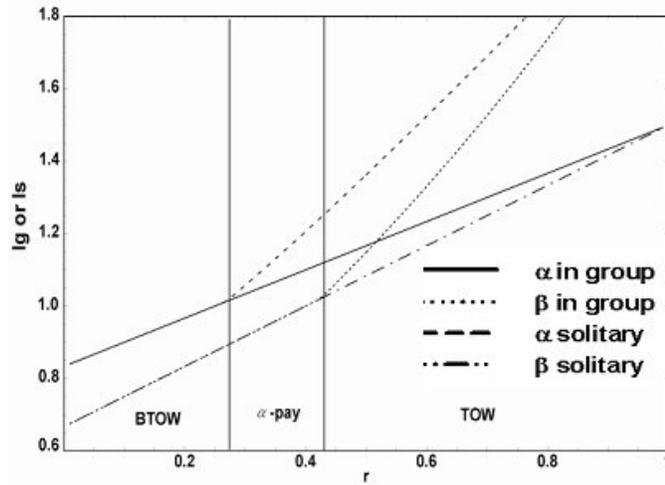


Figure 2.3 Transitions of different sub-models in relation to the subordinate are relative competitive efficiency of the subordinate (b) and direct fitness of leaving the group (S). The dash lines represent isoclines where $p^*=0$ and solid lines indicate parameter space where $q^*=0$ and the dash-and-dot lines show the group stability threshold ($G>S+L$).

(a)



(b)

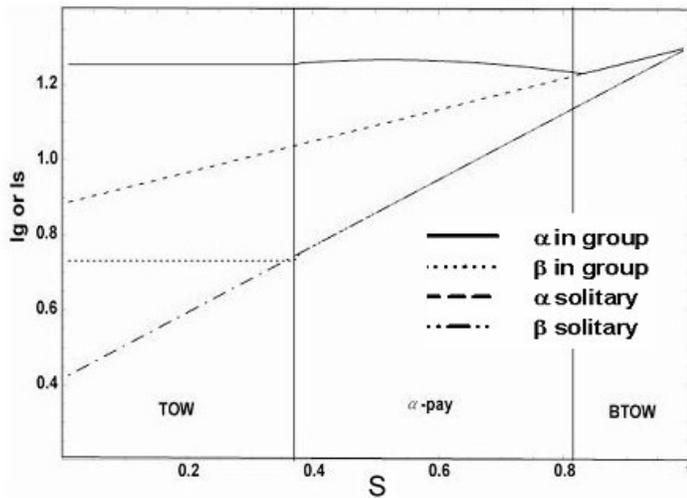


Figure 2.4 The inclusive fitness of the dominant and the subordinate compared to their non-cooperative option in relation to (a) genetic relatedness (r) at $G=2.2, L=1, S=0.5, b=0.5$ and (b) direct fitness of leaving the group (S) at $G=2.2, r=0.3, b=0.2, L=1$.

Table 2.1. Summary of skew predictions of different sub-models.

	BTOW	β -pay	α -pay	TOW
	$p^*>0, q^*>0$	$p^*\leq 0, q^*>0$	$p^*>0, q^*\leq 0$	$p^*\leq 0, q^*\leq 0$
Inclusive fitness compare to non-cooperative option	Both the same	β higher, α the same	α higher, β the same	Both higher
skew versus r	None	Negative	Positive	None or Negative
skew versus G	None	Negative	Positive	None
skew versus L	Positive	Negative	Positive	None
skew versus S	Negative	Positive	Negative	None
skew versus b	None	Negative	Negative	Negative
skew versus aggression	Negative	Positive	Negative	None or Negative

PARAMETER SPACES THAT APPLY TO EACH SUB-MODEL

As described above, whether an individual must yield group resources as an incentive to keep the other member in the group is the key feature to determining the transitions between different sub-models (Table 2.1). We can now investigate the parameter space that applies to each model (Fig. 2.2 and 2.3).

The pure TOW is the case in which both individuals are better off staying in the group even without any protected share ($p^* = 0$, and $q^* = 0$), which is exactly the original tug-of-war model (Reeve et al. 1998). The pure TOW is favored by selection when relatedness r between group members is high because within-group conflict is lower and therefore no protected share is needed for either party. The pure TOW is also favored when (i) group productivity G is high, because leaving the group is unattractive in such cases (making incentives unnecessary) and (ii) the direct fitness L

of winning a territory fight is low or the losing payoff S is low because incentives are again less likely when the non-cooperative option provides a lesser payoff.

In the mutual-pay BTOW, both parties require some “protected share” ($p^* > 0$, $q^* > 0$), with the result that this sub-model applies primarily to situations opposite to that favoring the pure TOW, i.e., when relatedness r is low, group productivity G is lower, and L and S are higher. The relative competitive efficiency b has little effect on the relative favorability of the mutual-pay BTOW or the pure TOW. This is a somewhat counter-intuitive result. Although smaller b lowers the payoff a subordinate gets in a pure tug-of-war, it also reduces the subordinate’s chances of winning the fight if the non-cooperative option is taken, leading to a lower payment by the dominant. Such counter-acting effects of b explains why b has such little effect on whether the mutual-pay BTOW or pure TOW is more likely to apply.

The remaining two cases, β -pay BTOW and α -pay BTOW, are cases in which only one individual needs to yield group resources to keep the other party cooperating in the group (i.e., $p^* > 0$ and $q^* = 0$, or vice versa). The key question here is why (in the case of α -pay BTOW) only the subordinate should require a protected share, not alpha (or vice versa). By definition, the only difference between alpha and beta is their relative fighting efficiency (b). This difference in competitive efficiency will cause them to have different payoffs for the non-cooperative options (see Equation 3 and 4), which are also determined by the reproductive outputs for losing (S) or winning (L) a fight. An alpha-pay BTOW is favored over a pure TOW when G is high, r is low, b is low and S is high (Fig. 2.2 and 2.3). Under these conditions, low b means that the dominant will capture much more reproduction than will the subordinate in a tug-of-war, so much so that the dominant will be favored to stay even without any additional incentives provided by the subordinate. However, the subordinate does so poorly in the tug-of-war that it requires a non-zero protected share to be favored to stay within

the group versus take the non-cooperative option. These factors together explain the why the dominant often needs to pay the subordinate to keep him or her in the group but not the reverse.

The β -pay BTOW is rarely favored in our model, as a consequence of the above reasoning. If the subordinate is competitively similar to the dominant (b near 1), then there is nothing to distinguish either, and they will either both be favored to pay (mutual BTOW) or both be favored not to pay the other (pure TOW). However, if the subordinate is substantially weaker (b low), then it is more likely to demand payment when the dominant is not (alpha-pay BTOW), as explained in the previous paragraph.

REPRODUCTIVE SKEW

The “phase-transition” property of the global BTOW model can be clearly seen in that the different sub-models have quite distinctive predictions (Fig. 2.5, 2.6, 2.7, summarized in Table 2.1). To better show this numerically, all figures in which the group productivity (G) and relatedness (r) are varied use the same values for the other parameters ($b = 0.5$ and $S = 0.5$). Similarly, all figures in which the payoff of losing territory fight (S) and relative competitive efficiency (b) are varied use the same values for the other parameters.

Numerical results indicate that the subordinate’s reproductive share in the mutual-pay BTOW increases (i.e., skew decreases) with an increase in the subordinate’s relative competitive efficiency b , group productivity G , and the payoff for leaving S , but is not affected by relatedness r (Fig. 2.5 a, 2.5b). In the mutual-pay BTOW, the reproductive share of each party is sensitively determined by the payoff of the non-cooperative option. Increases in G and S and f through increases in b all increase the payoff for the subordinate’s non-cooperative option and thus the incentive paid to the subordinate by the dominant (Reeve and Shen, 2006). However, increasing relatedness

has no effect on the skew because it affects the intensity of the internal tug-of-war and the magnitudes of the incentives oppositely.

The α -pay BTOW is conceptually similar to the concession model and has similar properties and predictions as does the concession model (Reeve and Ratnieks, 1993), i.e. the subordinate's share will increase as group productivity and the payoff for leaving increase but decreases as relatedness decreases (Fig. 2.5 a, 2.5b). In addition, the subordinate's reproductive share increases with the increase of her competitive efficiency because (i) she will do better in the tug-of-war and (ii) an increase in her competitive efficiency increases the payoff for the non-cooperative option by increasing her probability of winning a fight. In contrast, β -pay BTOW has properties similar to those of the original restraint transactional model (Johnstone and Cant 1999). Its predictions are opposite to those of the α -pay BTOW except that the subordinate with higher competitive efficiency will still have a higher overall reproductive share than the weaker one (owing to the former's better performance in the tug-of-war).

In the pure TOW, the subordinate's share is not affected by group productivity and the payoff for leaving, and it increases as the subordinate's relative fighting ability increases. The relatedness has either no effect or a negative effect on the subordinate's share, as described by Reeve et al. (1998).

DEGREE OF WITHIN-GROUP CONFLICT

We distinguish between *destruction*, the fraction of maximal group output used up in the tug-of-war, and *aggression*. Destruction is the same as an individual's selfish effort in the tug-of-war (x and y for dominant and subordinate, respectively). Aggression, on the other hand, is the degree of actual behavioral conflict that directly determines reproductive share in a tug-of-war: Aggression takes both competitive

efficiency and selfish effort into account (x and by are the aggression levels for dominant and subordinate, respectively) and represents the observed conflict level. Overall aggression and selfish effort in the general BTOW model are determined by the disparities between potential group resources and the payoffs of the individuals' non-cooperative options. In other words, the greater such disparity, the more each individual gains by conflict (Table 2.2). This explains the similar predictions of mutual-pay BTOW, α -pay BTOW, and β -pay BTOW: aggression and destruction increase as group resources G increase and decrease as the direct fitness of losing (S) or winning (L) a fight increases (Fig. 2.6 a, 2.6c). Intriguingly, then, the general model predicts higher levels of conflict within groups that are increasingly stable. The same logic could also be used to explain why these three factors don't affect the degree of conflict in a pure TOW: When the pure TOW is favored, the payoffs for both parties cooperating in the group without incentives are still higher than the payoffs for their non-cooperative options. Therefore, the non-cooperative option does not affect levels of destruction and aggression.

When genetic relatedness is high, both parties' genetic interests are aligned. Thus, the total amount of destruction and aggression is low in the alpha-pay BTOW, beta-pay BTOW and pure TOW (Fig. 2.6b, 2.6d). However, relatedness doesn't affect the degree of conflict in the mutual-pay BTOW. In the mutual-pay BTOW higher relatedness reduces the incentives, widening the tug-of-war zone, but also increases the indirect fitness losses for engaging in a tug-of-war with a relative, and these two effects exactly cancel.

Table 2.2. Summary of level-of-conflict predictions of different sub-models.

	BTOW	β -pay BTOW	α -pay BTOW	TOW
Level of conflict versus r	None	Negative	Negative	Negative
Level of conflict versus G	Positive	Positive	Positive	None
Level of conflict versus L	Negative	Negative	Negative	None
Level of conflict versus S	Negative	Negative	Negative	None
Level of conflict versus b	Positive	Negative	Positive	Positive

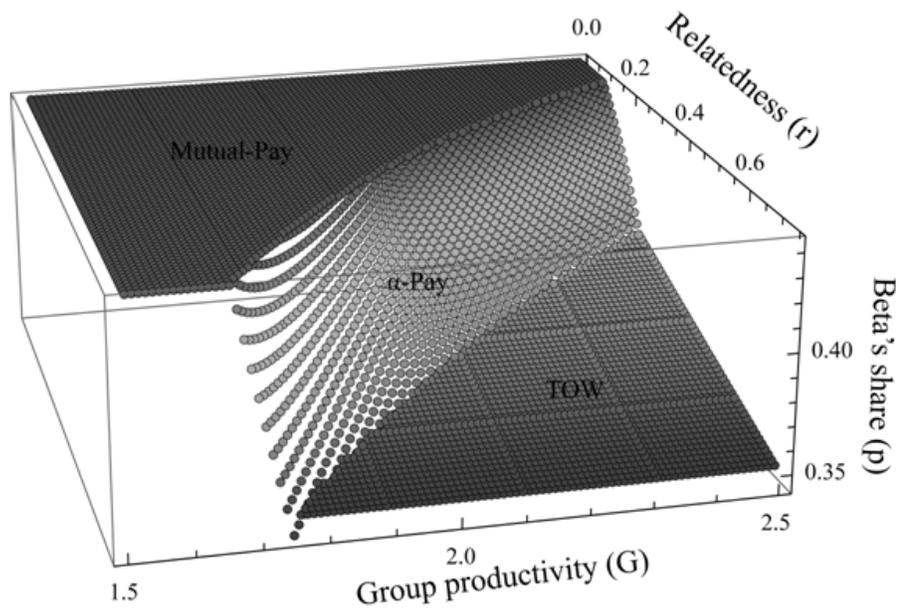


Figure 2.5a. The reproductive skew in relation to group productivity (G) and relatedness (r) at $s=0.5$, $b=0.5$, which correspond to the middle figure of figure 3.

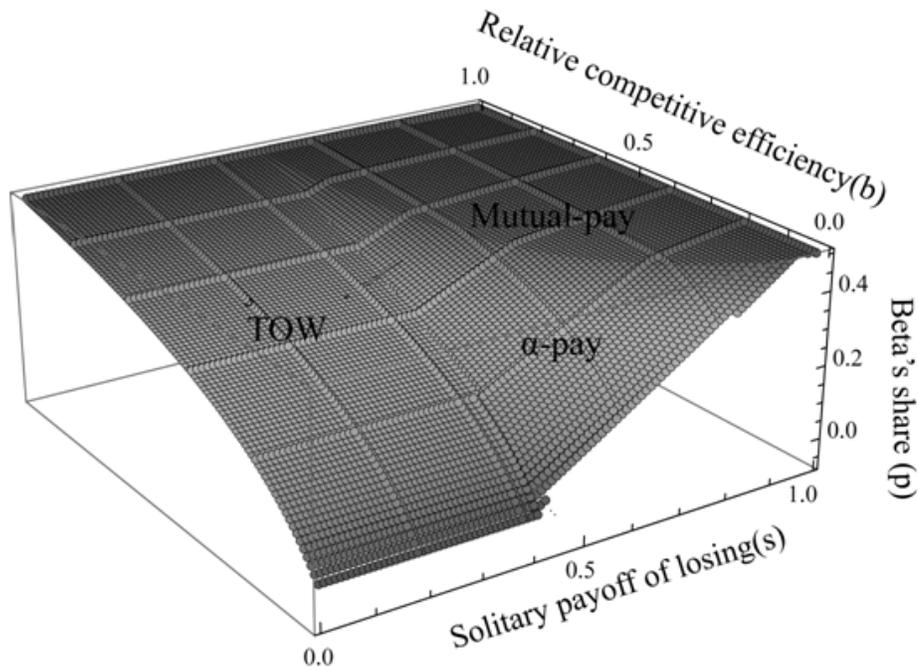


Figure 2.5b The reproductive skew in relation to solitary payoff of losing (S) and relative competitive efficiency of the subordinate (b) at $r=0.5$, $G=2$, which correspond to the middle figure of figure 2.

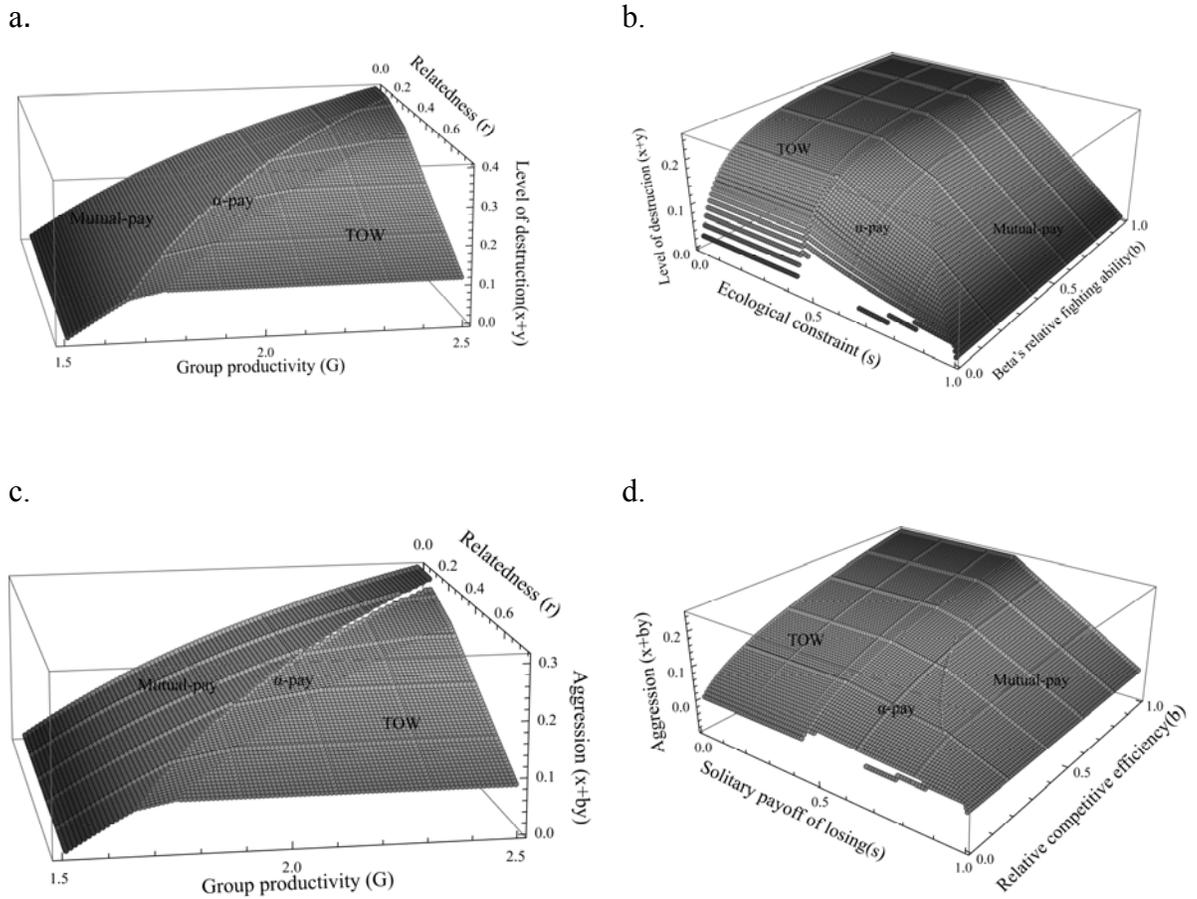


Figure 2.6 The level of destruction in relation to (a) group productivity (G) and relatedness (r) at $S=0.5$, $b=0.5$; and (b) solitary payoff of losing (S) and relative competitive efficiency of the subordinate (b) at $r=0.5$, $G=2$; and the level of aggression in relation to (c) group productivity (G) and relatedness (r); and (d) solitary payoff of losing (S) and relative competitive efficiency of the subordinate (b) at the same parameter spaces as 5(a) and 5(b)

COMPARISON OF DOMINANT'S AND SUBORDINATE'S SELFISH EFFORTS AND AGGRESSION

In most of the investigated parameter space, the subordinate has higher level of selfish effort than does the dominant (Fig. 2.7a, 2.7b). This occurs because the dominant has a greater share of the group output and thus is harmed more by using up a fixed fraction of that output in the tug-of-war. In the alpha-pay BTOW region, the disparity between the dominant's and subordinate's selfishish efforts increases as the relatedness decreases. As the relatedness decreases, the subordinate is less harmed by indirect fitness losses by using up group-output in the tug-of-war. When solitary payoff for losing a territory fight S is lower, the subordinate also tends to have a relatively higher selfish effort. The latter occurs because low S means that its likely payoff for non-cooperation is especially poor and therefore it will receive a small incentive, reducing its direct fitness loss for using up group output in the tug-of-war.

In contrast, the dominant has a higher aggression level than the subordinate in most of the parameter space, except when the subordinate's competitive efficiency is very low (Fig. 2.7c, 2.7d). This is because the subordinate's competitive efficiency is lower, which usually more than compensates for its higher selfish effort.

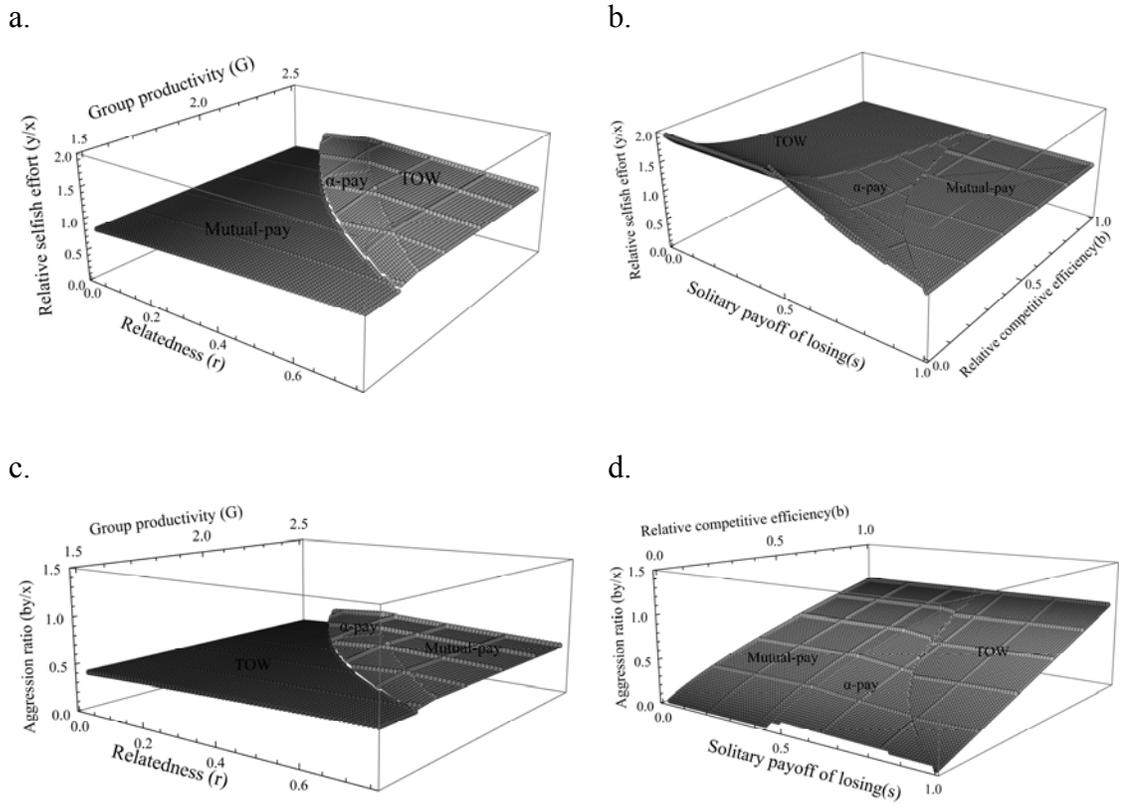


Figure 2.7 The relative level of destruction in relation to (a) group productivity (G) and relatedness (r) at $s=0.5$, $b=0.5$; and (b) solitary payoff of losing (S) and relative competitive efficiency (b) at $r=0.5$, $G=2$; and the relative level of aggression in relation to (c) group productivity (G) and relatedness (r); and (d) solitary payoff of losing (S) and relative competitive efficiency of the subordinate (b) at the same parameter spaces as 5(a) and 5(b)

DISCUSSION

The model described here fully unifies transactional and tug-of-war models of reproductive skew. This unification potentially will help to resolve several raging controversies and expand the applicability of reproductive skew theories. These controversies include the realism of theoretical assumptions of the models and the difficulties of empirical tests among the myriad models. Among the assumptions, the one that legitimately raises the most concern is the “complete control assumption”, which assumes that dominant individuals have complete control over breeding so that the reproductive share of each party can be solved (Vehrencamp 1983, Reeve and Ratnieks 1993). Our model relaxes this by allowing both the dominant and the subordinate to have partial control over reproduction and to allocate selfish effort to fight for personal reproduction. The results suggest that dominants are very unlikely to have complete control over reproduction, as assumed by previous transactional models, even when dominants are vastly more efficient than subordinates. It is almost inevitable for the subordinate to put at least some selfish effort into a costly fight, to which the dominant responds with his or her own selfish effort. Thus, complete control should probably not ever be assumed.

In addition, the unified model presented here indicates that four major reproductive skew models with strikingly different assumptions and predictions can actually be viewed as flowing from a general over-arching model. For instance, the original concession transactional model assumes that the dominant has complete control over both reproduction and group membership and doles out reproductive shares, whereas the eviction model assumes that the dominant is in control of group membership but the subordinate has full control over reproduction and doles out the reproductive shares (Buston et al., 2007; Johnstone and Cant, 1999; Reeve and Ratnieks, 1993). Therefore, these two models are analogous to the α -pay BTOW and

β -pay BTOW, which have parallel predictions to the concession and eviction models. However, in the BTOW model the subordinate by definition will have lower RHP to compete for group resources, and therefore, will never have a higher share of reproduction than the dominant. Moreover, the alpha-pay and beta-pay BTOW models, unlike the concession and restraint models, make precise predictions about the levels of conflict within-groups and how these levels of conflict will be affected by genetic and ecological factors.

By unifying the models into one synthetic framework, our model makes testing alternative models empirically more feasible. The results suggest that β -pay BTOW is unlikely in most of the parameter spaces, at least when the subordinate's probability of winning the fight in the non-cooperative option parallels its relative competitive efficiency. Thus, in general, empirical tests should probably focus on mutual-pay BTOW, α -pay BTOW, and pure TOW models. We suggest that testing a suite of predictions will generally be the most conclusive way to distinguish alternative models (Langer et al. 2004). For example, when these three models have different predictions regarding relatedness and skew, such relatedness versus skew data are informative. However, it would be more conclusive if at least one other (preferably distinctive) prediction could also be tested so that the possibility of a false support could be decreased. Therefore, if we obtain evidence that the dominant has higher inclusive fitness in the group and the subordinate has similar fitness in the group compared to her non-cooperative options, *and* reproductive skew increases as relatedness increases, this would be clear support for the α -pay BTOW. The problem of confounding effects could also be minimized in this way (Clutton-Brock, 1998; Emlen, 1996; Magrath and Heinsohn, 2000; Magrath et al., 2004).

Another approach to evaluating which models are potentially relevant to a particular system is to measure the values for at least two model input variables and

then determine which models are most applicable for this parameter space. For example, consider the acorn woodpecker, in which both males and females often co-breed (Haydock and Koenig, 2002, 2003). Estimates for r among cobreeders have been estimated to be 0.46 for males and 0.41 for females and relative group productivity is 1.529 for males and 1.472 for females. Since G is the total group resource, some of which may be spent in costly competition, the value of G must be greater than or equal to relative group productivity. These values indicate that the most appropriate parameter space for both sexes is represented by the first and second rows in the middle column in Fig. 2.3. In the case of females, the relative competitive ability of cobreeders is almost certainly very similar ($b = 1$), as indicated by the potential reciprocal nature of egg destruction (W. Koenig, pers. comm.). For males, this parameter is not as obvious, but b is likely to be fairly high. Meanwhile, S , the relative fitness payoff to an individual who fights and loses, is probably low for both sexes, given the difficulty of successful dispersal. This places both sexes in the parameter space where the pure TOW or mutual-pay BTOW are likely to be applicable, with a small chance that α -pay BTOW is applicable to cobreeder males. For females, there appears to be no relationship between skew and relatedness, and egg destruction occurs regardless of whether cobreeders are related (W. Koenig, pers. comm.), results that are consistent only with the BTOW model (Table 2.1 and 2.2). For males, skew decreases when the direct fitness of dispersing (S) increases and when relatedness increases, results that are consistent only with the α -pay BTOW. Additional work will be required to confirm the appropriateness of the models in these cases. Another example is from primitively eusocial bees, in which the group productivity is very high in rich floral habitat (3.4 to 5.3, Hogendoorn and Zammit, 2001; Langer et al., 2004). Our model predicts that the pure TOW is favored in all

possible parameter spaces, as found in a series of elegant experiments (Langer et al., 2004).

We point out that even within the same population of the same species, it is possible that multiple mechanisms of resolving breeding conflict (and thus different models) could be applied. For instance, different relatednesses between group members in different groups and different group productivity in relation to habitat quality, seasonality or other ecological factors might result in different conflict resolution mechanisms within different groups of the same species. This possibility provides another powerful way to test different models' predictions. For example, it would be interesting to see whether primitively eusocial bees will shift to using a mutual-pay BTOW to resolve their breeding conflict in high-quality habitats (Langer et al., 2004).

In conclusion, we unify seemingly different models into a general theoretical framework. The concession, eviction, pure tug-of-war, and mutual pay, bordered tug-of-war models now should be considered as sub-models of a general model. The most controversial "complete control" assumption of transactional skew models has been relaxed. The result is a theory rich in specific predictions, perhaps rich enough to accommodate much of the substantial variation in patterns of skew observed across vertebrates and invertebrates.

We suggest further research that in addition to determining which model is suitable for certain species, more effort should focus on understanding why and how various social animals resolve their breeding conflict by different conflict resolution mechanisms. These results could potentially shed the light for the development of a general theory of social evolution.

REFERENCES

- Buston PM, Reeve HK, Cant MA, Vehrencamp SL, Emlen ST, 2007. Reproductive skew and the evolution of group dissolution tactics: a synthesis of concession and restraint models. *Animal Behaviour* 74:1643-1654.
- Clutton-Brock TH, 1998. Reproductive skew, concessions and limited control. *Trends in Ecology & Evolution* 13:288-292.
- Emlen ST, 1982. The evolution of helping II: the role of behavioral conflict. *American Naturalist* 119:40-53.
- Emlen ST, 1996. Reproductive sharing in different types of kin associations. *American Naturalist* 148:756-763.
- Haydock J, Koenig WD, 2002. Reproductive skew in the polygynandrous acorn woodpecker. *Proceedings of the National Academy of Sciences of the United States of America* 99:7178-7183.
- Haydock J, Koenig WD, 2003. Patterns of reproductive skew in the polygynandrous acorn woodpecker. *American Naturalist* 162:277-289.
- Hogendoorn K, Zammit J, 2001. Benefits of cooperative breeding through increased colony survival in an allodapine bee. *Insectes Sociaux* 48:392-397.
- Johnstone RA, 2000. Models of reproductive skew: A review and synthesis (invited article). *Ethology* 106:5-26.
- Johnstone RA, Cant MA, 1999. Reproductive skew and the threat of eviction: a new perspective. *Proceedings of the Royal Society of London Series B-Biological Sciences* 266:275-279.
- Kokko H, 2003. Are reproductive skew models evolutionarily stable? *Proceedings of the Royal Society of London Series B-Biological Sciences* 270:265-270.
- Langer P, Hogendoorn K, Keller L, 2004. Tug-of-war over reproduction in a social bee. *Nature* 428:844-847.

- Magrath RD, Heinsohn RG, 2000. Reproductive skew in birds: models, problems and prospects. *Journal of Avian Biology* 31:247-258.
- Magrath RD, Heinsohn RG, Johnstone RA, 2004. Reproductive skew. In: *Ecology and Evolution of Cooperative Breeding in Birds* (Koenig WD, Dickinson JL, eds). Cambridge: Cambridge University Press; 157-176.
- Mesterton-Gibbons M, 1992. *An introduction to game-theoretic modelling*. Redwood City, California: Addison-Wesley.
- Nonacs P, 2006. The rise and fall of transactional skew theory in the model genus *Polistes*. *Annales Zoologici Fennici* 43:443-455.
- Nonacs P, 2007. Tug-of-war has no borders: It is the missing model in reproductive skew theory. *Evolution* 61:1244-1250.
- Reeve HK, Emlen ST, Keller L, 1998. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behavioral Ecology* 9:267-278.
- Reeve HK, Keller L, 1997. Reproductive bribing and policing evolutionary mechanisms for the suppression of within-group selfishness. *American Naturalist* 150:S42-S58.
- Reeve HK, Keller L, 2001. Tests of reproductive-skew models in social insects. *Annual Review of Entomology* 46:347-385.
- Reeve HK, Nonacs P, 1992. Social contracts in wasp societies. *Nature* 359:823-825.
- Reeve HK, Ratnieks FLW, 1993. Queen-queen conflict in polygynous societies: mutual tolerance and reproductive skew. In: *Queen, Number, and Sociality in Insects* (Keller L, ed). Oxford: Oxford University Press; 45-85.
- Reeve HK, Shen SF, 2006. A missing model in reproductive skew theory: The bordered tug-of-war. *Proceedings of the National Academy of Sciences of the United States of America* 103:8430-8434.

Sherman PW, Lacey EA, Reeve HK, Keller L, 1995. The eusociality continuum.

Behavioral Ecology 6:102-108.

Vehrencamp SL, 1983. A model for the evolution of despotic versus egalitarian

societies. Animal Behaviour 31:667-682.

CHAPTER 3

PARENTAL CARE, COSTLY YOUNG AND REPRODUCTIVE SKEW: A GENERAL MODEL OF PARENTAL INVESTMENT IN COOPERATIVELY BREEDING SOCIETIES

ABSTRACT

Understanding the mechanisms by which animals resolve conflicts of interest is the key to understanding the basis of cooperation in social species. Conflict over reproductive shares is the critical type of conflict among cooperative breeders. The costly young model represents an important, but underappreciated, idea about how an individual's intrinsic condition and cost of reproduction should affect the resolution of conflict over the distribution of reproduction within a cooperatively breeding group. However, dominant control in various forms is assumed in previous versions of costly young models. In this paper, we first relax the control assumption of costly young models, and then develop a general model of cost of reproduction by relaxing the fixed parental care assumption of the original costly young model. After relaxing the control assumption, we found that relatedness has little effect on the subordinate's reproductive share, which is different from the "beneficial sharing" effect in previous costly young models where the subordinate's share increases as relatedness increases. We further relax the fixed group productivity assumption of the costly young model and allow individuals to adjust their parental effort and offspring production. This parental investment model predicts that the total group output increases as relatedness increases and reproductive share is insensitive to changes in relatedness between group members; these results are similar to the tug-of-war models. However, the underlying mechanisms explaining the group productivity predictions are different. Group productivity is modulated by within-group conflict in the tug-of-war model but

is determined by parental effort in our parental investment model. Nonetheless, reproductive share is predicted to be insensitive to relatedness in both models because group members are predicted to decrease their competitive effort in both cases. These results, we believe, help identify the similarities and key differences between different models and simplify the seemingly divergent predictions of different reproductive skew models.

INTRODUCTION

Reproductive skew refers to the partitioning of reproduction among same sex individuals within social groups and has been identified as a major dimension along which animal societies vary (Sherman et al. 1995). The development of the simple modeling framework of skew theories with their general predictions has stimulated many theoretical and empirical studies in diverse taxa (reviews in Reeve and Keller 2001, Johnstone 2000, Magrath et al. 2004). Two major kinds of reproductive skew models, based on different conflict resolution mechanisms, are transactional models and tug-of-war models. In transactional models (Emlen 1982; Keller & Reeve 1994; Reeve & Ratnieks 1993; Vehrencamp 1980; Vehrencamp 1983), a single dominant individual is assumed to fully control both group membership and the fraction of total group reproduction obtained by the subordinate breeder. The dominant breeder maximizes its own fraction of reproduction at the expense of the subordinate, but yields just enough reproduction to the subordinate to make it favorable for the subordinate to stay in the group. In tug-of-war models, on the other hand, no individual may have complete control of the reproductive partitioning, and the reproductive skew may be determined instead by competitive 'tugs-of-war' among group members (Reeve et al. 1998). Each group member is assumed to decide what fraction of the group's resources to expend in increasing its share of the group reproduction, and the share each group member receives depends on the ratio of these selfish investments.

Many empirical studies have been focused on distinguishing the transactional and tug-of-war models, especially on testing the "complete-control" assumption of the transactional model (Cant 2000; Clutton-Brock 1998; Haydock & Koenig 2002; Packer et al. 2001). These authors have argued that it is unlikely for a dominant individual to exert complete control over others' reproduction and therefore have

embraced the tug-of-war model as being more applicable to their findings. The recent develop of the bordered tug-of-war model (or incomplete-control transactional model) has relaxed the complete- control assumption of the transactional model (Reeve & Shen 2006; Shen & Reeve in review). This theoretical advance shows that the complete-control assumption is not necessary for the transactional type of conflict resolution mechanism to occur and that evidence of incomplete control does not automatically prove the pure tug-of-war to be operating. For example, in subsocial beetles *Parastizopus armaticeps*, no overt aggression was observed between communally laying females, which does not fit the tug-of-war model unless the competition is non-aggressive, i.e. exploitative. Reproduction was shared between closely related females, but reproductive share was closely correlated with individual body condition and not determined by social suppression. Therefore, the transactional model also does not seem to apply (Heg et al. 2006). It is clear that additional conflict resolution mechanisms besides the transactional and tug-of-war mechanisms should be incorporated into skew theory.

The costly young model represents another important, but overlooked, idea of how an individual's intrinsic condition and cost of reproduction could affect the distribution of reproduction within social groups (Cant 1998; Cant & Johnstone 1999). However, various forms of dominant control are assumed in different versions of costly young models. In addition, parental care is assumed to be fixed in the original costly young model. Here, we first relax the assumption of complete control of the costly young model, and secondly, we develop a general parental investment model to include the elements of cost of reproduction and parental care. Our results show that (1) in relaxing the complete-control assumption, the costly young model behaves very differently from the original model and (2) in relaxing the fixed parental care assumption, the general parental investment model displays similar predictions to the

tug-of-war model, although the underlying mechanisms causing these similar patterns are different. These results, we believe, help identify the similarities and key differences between different models and simplify the seemingly divergent predictions of different reproductive skew models.

THE MODEL

The modified costly young model with simultaneous solution

We consider a two-person model without dominance. For ease of comparison with previous models, two group members, referred to as Alpha and Beta, both contribute to a communal brood, and we ask how reproduction will be partitioned between them. Alpha produces n offspring and Beta produces f offspring. The total clutch size is denoted $t (=n+f)$. Following Cant and Johnstone (1999), we assume that an individual offspring's fitness, $s(t)$, declines linearly with brood size, t , so that $s(t)=1-kt$, where k is a measure of the sensitivity of offspring to increasing clutch size. The total productivity of a clutch of size t is

$$T(t) = t(1 - kt). \quad (1)$$

We also assume that the cost of producing n young is equal to en^2 , where e is a constant describing the degree of current reproductive effort affecting future reproduction. The conclusions of the model are not affected by different power values of the cost functions. We can find the optimum clutch size for a single breeder by maximizing $F(n)$, the net benefit of producing n young. $F(n)$ is given by

$$F(n) = n(1 - kn) - en^2 \quad (2)$$

Solving for n , a single female's optimum clutch size, we obtain

$$\hat{n} = \frac{1}{2(k + e)} \quad (3)$$

The direct fitness $F(n)$ of a female breeding solitarily can be obtained by substituting equation (3) into (2), which is

$$F(n) = \frac{1}{4}(e+k)[2-(e+k)^2] \quad (4)$$

Next, we consider what happens when two females contribute to a joint clutch by finding expressions for the inclusive fitness payoff to Alpha and Beta as functions of n and f . The cost of producing n and f young are $ae n^2$ and ef^2 for Alpha and Beta, respectively, where a is a constant between 0 and 1 to express the greater efficiency, or lower cost, of reproduction for Alpha relative to Beta, which may be caused by differences in body condition, experience, or resource access. Combining all above factors, we can write Alpha's direct fitness function, w_α , and Beta's, w_β , as follows:

$$w_\alpha = T(n+f) \frac{n}{n+f} - aen^2, \quad (5a)$$

$$w_\beta = T(n+f) \frac{f}{n+f} - ef^2 \quad (5b)$$

(note: $T(n+f)$ is the same function as equation 1)

The inclusive fitnesses of Alpha and Beta are

$$W_\alpha = w_\alpha + r w_\beta, W_\beta = w_\beta + r w_\alpha \quad (6)$$

Unlike the original costly young model (Cant 1998, Cant and Johnstone 1999), we do not assume that Alpha has full control over the distribution of reproduction, i.e. where both Alpha and Beta maximize Alpha's inclusive fitness. Thus, we seek the Nash equilibrium at which neither player can gain by altering its level of investment with the payoffs being calculated from equation 3a and 3b. The best level of investment for Alpha and Beta are considered simultaneously by finding the positive values $\{n^*, f^*\}$ satisfying

$$\partial W_\alpha / \partial n = 0, \quad \partial W_\beta / \partial f = 0, \quad \text{at } n=n^*, f=f^*.$$

The solutions are

$$n^* = \frac{2e+k(1-r)}{4ce(e+k)+k[4e-k(r-1)(3+r)]} \quad (7a)$$

$$f^* = \frac{2ce+k(1-r)}{4ce(e+k)+k[4e-k(r-1)(3+r)]} \quad (7b)$$

and they are fitness maxima ($\partial W_\alpha / \partial^2 n < 0$, $\partial W_\beta / \partial^2 f < 0$). This solution is biologically meaningful only if $f^* \geq 0$ and $n^* \geq 0$. For $f^* \geq 0$ and $n^* \geq 0$ to be true, the inequality

$$r < 1 + \frac{2ce}{k}$$

must be satisfied. Since r is always smaller than 1, $f^* \geq 0$ and $n^* \geq 0$ are always true.

Results of the modified costly young model

When we relax the assumption that Alpha has complete control over Beta's reproduction, we find that both Alpha and Beta's clutch sizes (n^* and f^*) decrease as the relative cost of young (e) increases (Fig. 3.1a), whereas in the complete-control version of the costly young model, only Alpha's clutch size decreases with an increase in the relative cost of young. Beta's clutch size either increases or stays constant (Fig. 2 in Cant and Johnstone 1999). This happens because if Alpha has complete control, Alpha's clutch size is mainly limited by her own tradeoff between current and further reproduction. Therefore, as the cost of young increases, Alpha's clutch size decreases and if Alpha's clutch size does not reach the most productive clutch size of the brood (see equation 1), Alpha's would benefit by letting Beta reproduce if Beta is her relative. This is also why the "beneficial sharing" effect, in which Beta's share increases as relatedness increases, is observed in the complete-control costly young model but disappears in our no-control model. Beta's share is constant regardless of relatedness (Fig. 3.1b). Also, both Alpha and Beta's clutch sizes decrease when relatedness increases in our model (fig 3.1c), which is caused by the assumption that offspring survival is lower as number of offspring increases in the no-control costly young model (see equation 1). Therefore, when Alpha and Beta are more closely related to each other, both Alpha and Beta's clutch size decrease so that the joint clutch size (n^*+f^*) is closer to the most productive size. This also explains why the total group output, $(n^*+f^*)(1-k(n^*+f^*))$, stays unchanged as relatedness increases in the

no-control costly young model but increases with the increase of relatedness in the complete-control model (Fig. 3.1d). In the no-control costly young model, individuals decrease their own clutch sizes as relatedness increases, and hence the survival of each offspring increases. The cancellation of these two effects results in constant brood productivity with smaller clutch sizes as relatedness increases. However, in the complete-control costly young model, Alpha lets Beta produce more offspring when Beta is more closely related. This happens because the negative survival effect on Alpha's offspring, as Beta produces more offspring, can be compensated by the increase in total productivity of the joint clutch. Nonetheless, the total group output is higher when no one has control than when Alpha has complete control over reproduction (Fig. 3.1d).

Parental investment model

In this section, we develop a more general costly young model by allowing individuals to freely adjust their parental effort instead of assuming a fixed clutch size-productivity function. Again, we consider a two-person model without dominance. The two group members are still referred to as Alpha and Beta, and both contribute to a communal clutch. Alpha produces n offspring and Beta produces f offspring. As before, the cost of producing n and f young are $ae n^2$ and ef^2 for Alpha and Beta, where a is still the constant indicating the greater efficiency of reproduction for Alpha relative to Beta. However, in this model, instead of assuming that offspring survival decreases with the increase in total number of offspring, we model a more general scenario of how parental care affects the reproductive value of offspring (Fisher 1930). The more parental care an offspring receives, the higher its reproductive value or expected future reproduction. Therefore, offspring production is limited by the cost of

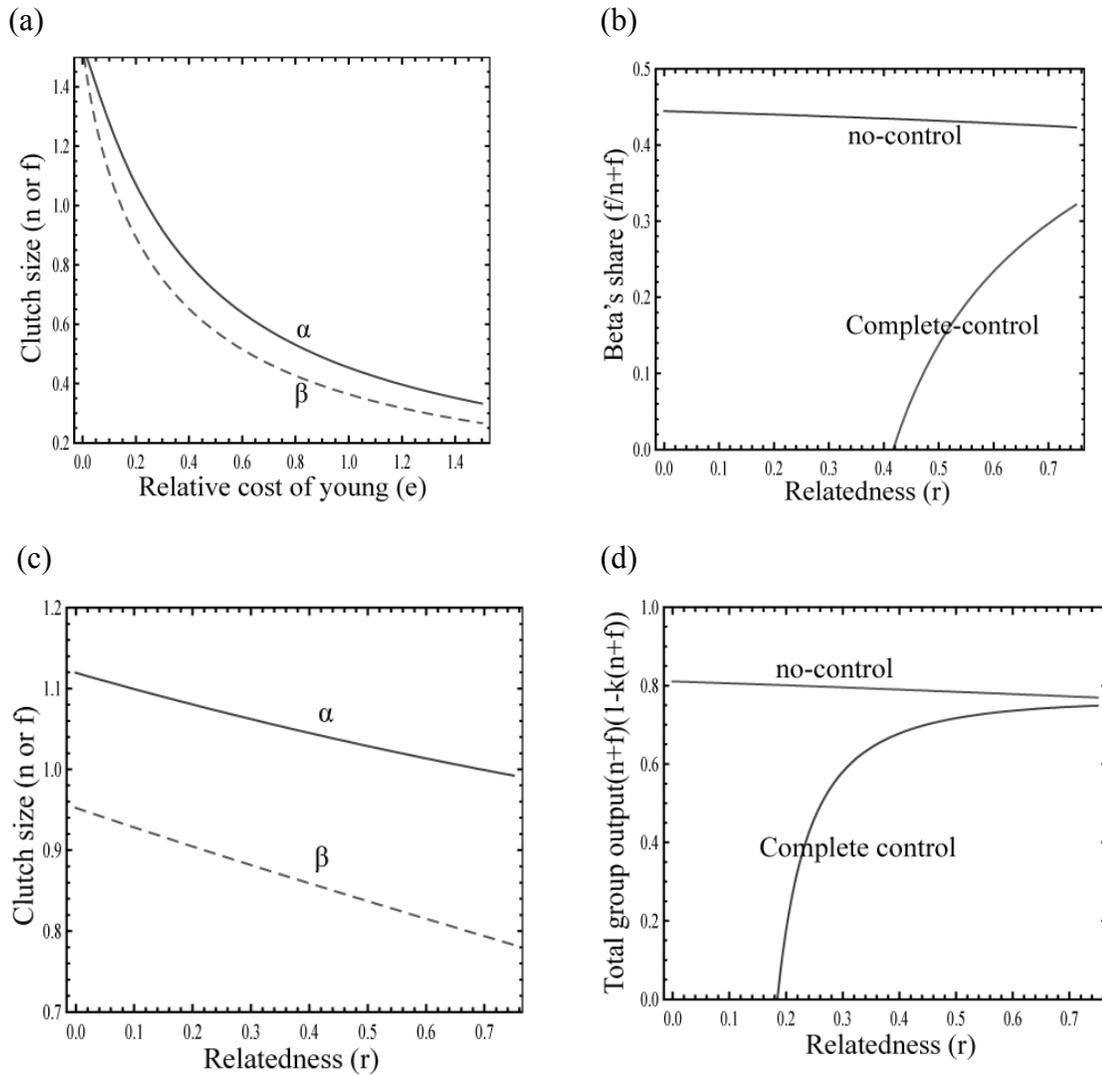


Figure 3.1 Results of the incomplete-control costly young model. (a) clutch size in relation to relative cost of young; The effect of relatedness on (b) Beta's reproductive share, (c) clutch size and (d) total group output. Relaxing the complete-control assumption changes the properties of the costly young models.

producing young *and* the cost of parental care. Specifically, Alpha invests d in parental care and Beta invests s in parental care in the current breeding attempt and the cost of parental care is avd^2 and vs^2 for Alpha and Beta, respectively, where v (for investment) is the scaling factor for relative cost of parental care. Again, the conclusions of the model are not affected by different power values of the cost functions. Since the general power functions, vd^m , vs^m and en^z , ef^z , do not yield analytic solutions, we use the squared cost functions here for simplicity. Alpha and Beta's direct fitness functions are summarized as follows:

$$w_\alpha = (d + s) \frac{n}{n + f} - a(vd^2 + en^2) \quad (8a)$$

$$w_\beta = (d + s) \frac{f}{n + f} - vs^2 - ef^2 \quad (8b).$$

We use equations (8) and (6) to obtain Alpha and Beta's inclusive fitness functions, W_α and W_β and seek the Nash equilibrium $\{n^*, f^*, d^*, s^*\}$ by simultaneously finding positive values $\{n^*, f^*, d^*, s^*\}$ satisfying

$\partial W_\alpha / \partial n = 0$, $\partial W_\beta / \partial f = 0$, $\partial W_\alpha / \partial d = 0$, $\partial W_\beta / \partial s = 0$, at $n=n^*$, $f=f^*$, $d=d^*$, and $s=s^*$. The solutions are

$$n^* = - \frac{\sqrt{\frac{-2ad^*e + 2ad^*er - 2aes^* + 2aers^* + \sqrt{a(1+a)^2e^2(r-1)^2(d^*+s^*)^2}}{(a-1)^2ae^2}}}{\sqrt{2}} \quad (9a),$$

$$f^* = - \frac{a(1+a)e(r-1)(d^*+s^*) \sqrt{\frac{-2ad^*e + 2ad^*er - 2aes^* + 2aers^* + \sqrt{a(1+a)^2e^2(d^*+s^*)^2}}{(a-1)^2ae^2}}}{\sqrt{2} \sqrt{a(1+a)^2e^2(r-1)^2(d^*+s^*)^2}} \quad (9b),$$

$$d^* = - \frac{\sqrt{a^3v^2(r-1)^2 + av(ar-1)}}{2(a-1)a^2v^2} \quad (9c), \text{ and}$$

$$s^* = - \frac{\sqrt{a^3v^2(r-1)^2 + av(r-a)}}{2(a-1)av^2} \quad (9d)$$

(note: d^* =eq.9c and s^* =eq. 9d in equation 9a and 9b).

Results of the parental investment model

In this model, we assume that individuals do not discriminate their own offspring from other group members' offspring, and that parental care (d and s) is necessary for increasing offspring reproductive value. Therefore, parental care can be viewed as investing in the creation of common group resources. Offspring production (n and f), on the other hand, is a means of competing for group resources, because as one group member increases her offspring production it lowers her collaborator's share of the group resources. Therefore, as relatedness increases, both Alpha and Beta's clutch sizes decrease (Fig. 3.2a) and levels of parental care increase (Fig. 3.2b). The simultaneous adjusting of parental care and offspring production also leads to the result that reproductive share is insensitive to differences in relatedness (Fig. 3.2c). This also explains why the total group output, $(d+s)(n+f)$, increases as relatedness increases (Fig. 3.2d), mainly because individual parental care levels increase as relatedness increases. This result is different from the no-control costly young model, in which the total group output is unchanged as relatedness increases. This is because in the original costly young model, the clutch size-group productivity relationship is assumed to be fixed and parental care is also implicitly fixed, regardless of the relatedness between group members. Note that the slight decrease in total group output when relatedness is very high (>0.5) is caused by a faster rate of decreasing clutch size than parental care. In this case, individuals still have higher inclusive fitness when breeding with more closely related group members but save more energy for future reproduction. Different power values of the cost functions give different quantitative results, but the qualitative relationship between total group output and relatedness is similar.

Table 3.1. Predictions of the effect of relatedness on different phenomena in different models. The effect of relatedness assumes that other parameters and group size are held constant.

Skew model's predicted association of relatedness with different phenomena					
	costly young		investment	pure tug-of-war	
	complete control	no-control			
Skew	negative	none*	none*	none*	
Within-group conflict	-	-	-	negative	
Parental effort	-	-	positive	-	
Total group output	positive	none	positive	positive	
Clutch size	positive	negative	negative	-	
	α	β			
Lifetime direct fitness	- [#]	+ [#]	Positive	Positive	Positive
Lifetime inclusive fitness	-	+	Positive	Positive	Positive

*Skew slightly increases as relatedness increases when b is very small.

[#] "+" indicates "positive"; "-" represents negative relationship.

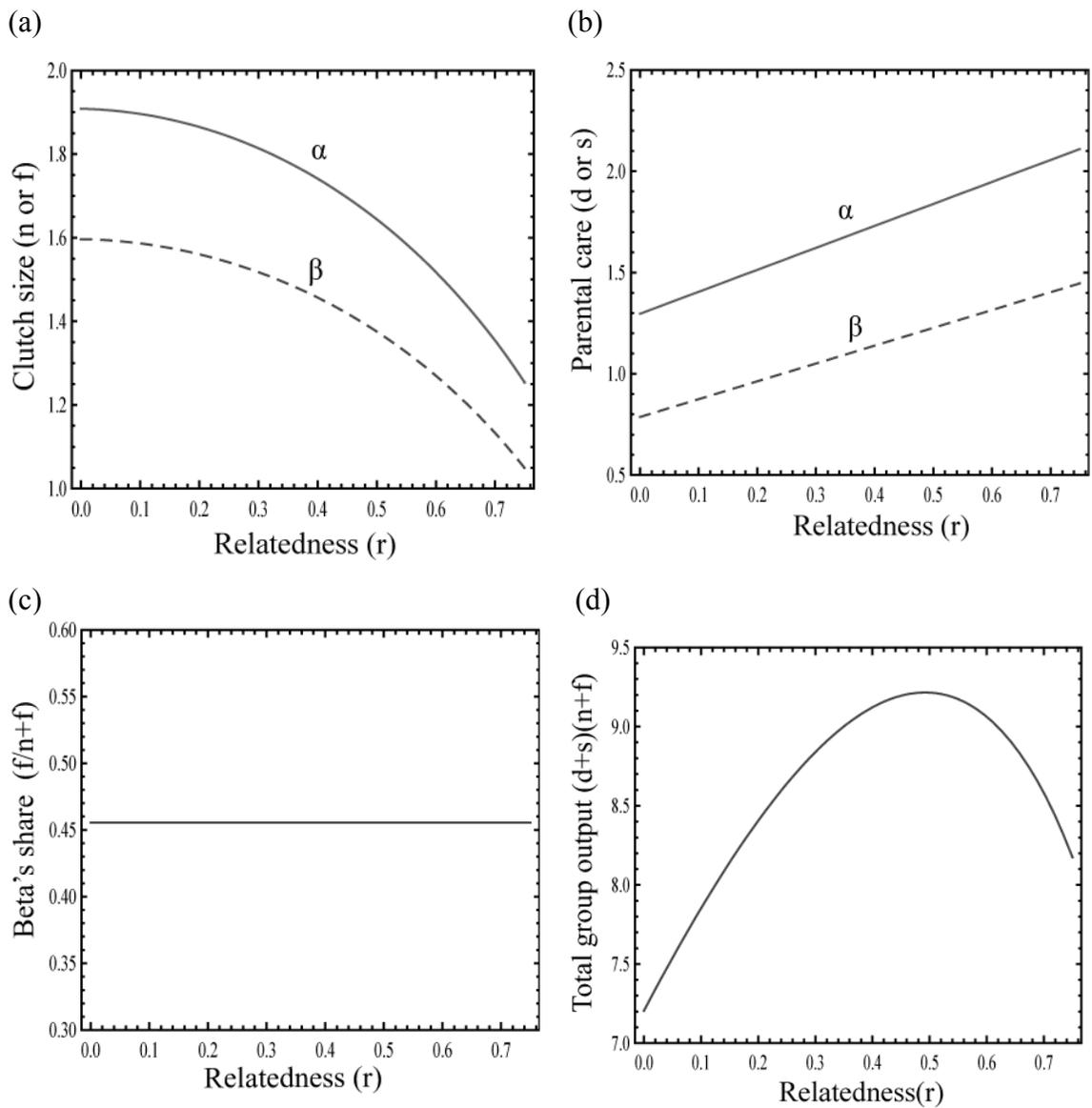


Figure 3.2 The effect of relatedness on (a) clutch size, (b) level of parental care, (c) Beta's reproductive share, and (d) total group output in the parental investment models of reproductive skew, which relaxes the fixed group productivity of costly young models (see text).

DISCUSSION

Our modified costly young model describes how the cost of reproduction affects the distribution of reproduction in a cooperative breeding group in the absence of social suppression. Various forms of social suppression are assumed in previous versions of costly young models. In Cant's (1998) original model, Alpha sets her optimal clutch size first and then adjusts again after Beta makes her decision according to Alpha's first move. As the author correctly points out, this gives Alpha an advantage and imposes constraints on Beta for seeking her own optimal production of young. In the subsequent model (Cant and Johnstone 1999), Alpha is assumed to have complete control over the distribution of reproduction, such that both Alpha and Beta produce the clutch sizes that maximize Alpha's inclusive fitness; or Alpha yields a minimum proportion of reproduction to retain Beta in the group, as assumed in the standard transactional model (Vehrencamp 1983, Reeve and Ratnieks 1993). However, the complete-control assumption is not realistic (Clutton-Brock 1998; Reeve & Shen 2006). Our model relaxes these assumptions by seeking the Nash equilibrium of Alpha's and Beta's clutch sizes. Our modification of the costly young models allows us to examine how different cost functions affect individual reproductive shares. Interestingly, our model predicts that relatedness has either no effect or a negative effect on Beta's reproductive share. The "beneficial sharing" effect discovered in previous costly young models, where Beta has a larger share while the number of young produced by Alpha decreases with an increase in relatedness, disappears in our model. This makes sense, because without the complete-control assumption, the different clutch sizes that Alpha and Beta produce are due to the different costs of producing young. Therefore, Alpha's and Beta's clutch size functions (n^* and f^*) have similar dependences on the other variables in the model. In the subsocial beetle *Parastizopus armaticeps*, no overt female-female aggression was seen and the higher

share of reproduction obtained by a communally breeding female was considered to be the result of good condition instead of social suppression (Heg et al. 2006). This finding provides some preliminary support for our modified costly young model. In a comparative study of cooperatively breeding carnivores, Creel and Creel (1991) found that skew is highest among those carnivores with the highest costs of breeding. They hypothesized that as energetic costs increase, subordinates are more likely to have a fitness cost that exceeds the expected fitness benefit of breeding directly. However, our model shows that the high cost of reproduction alone is not sufficient to explain high skew (see also Russell 2004). One possible explanation, based on our model, is that body condition of dominants in those species with a high cost of reproduction is much better than the subordinates (helpers). Nevertheless, mechanisms such as active dominant suppression of subordinate reproduction in order to get subordinates' help in parental care when energetic cost of breeding is high (e.g. Scantlebury et al. 2002), are not implicitly included in our model. Further modeling effort is needed.

In addition to the complete-control assumption, the original costly young model also assumed a fixed clutch size-productivity function. In other words, it was implicitly assumed that individuals do not adjust their parental effort to the number of offspring they have in the current brood. This assumption is similar to the classic skew models which also assumed automatic group benefit (Keller & Reeve 1994; Reeve & Ratnieks 1993), but as many authors have pointed out, the fixed group benefit assumption might not be biologically realistic (Johnstone 2000; Magrath & Heinsohn 2000; Magrath et al. 2004). We also relaxed this fixed productivity assumption and in Table 3.1 compare the predictions of this general parental investment model with other models, including the complete-control costly model (Cant & Johnstone 1999), the no-control costly young model (this paper) and pure tug-of-war model (Reeve et al. 1998).

Interestingly, after relaxing the assumption of complete control and fixed parental care, the general parental investment model has predictions similar to the pure tug-of-war model. Both models predict that reproductive share is insensitive to the relatedness between group members and that group productivity increases as relatedness increases. Selfish effort in the tug-of-war model and offspring production in the costly young model are both group members' competitive strategies, which increase personal direct fitness and decrease the other group member's direct fitness. This explains why reproductive share is predicted to be insensitive to the change of relatedness in both models, because as relatedness increases, the conflict of genetic interests between group members decreases. Therefore, Alpha and Beta are both predicted to decrease their selfish effort and offspring production by each model, which causes the prediction of insensitivity of reproductive share to differences in relatedness in both models (Reeve et al. 1998). However, selfish effort and offspring production are different in the sense that a higher level of selfish effort always decreases total group output and decreases other group members' inclusive fitness. But production of offspring could either increase or decrease total group output and the partner's inclusive fitness, depending on the cost of offspring production and parental care.

Although both tug-of-war and parental investment models predict that total group output increases as relatedness increases, the underlying mechanisms causing this similar prediction are different. In the pure tug-of-war model, group members engage in costly competition at the expense of group resources. Group members can freely decide their level of selfish effort, which decreases total group output but increases an individual's personal share of group resources. Group members' selfish efforts decrease as relatedness increases, and therefore the total group output increases with an increase in relatedness because of lowered within-group conflict. However, in

the parental investment model, the tradeoff between current and further reproduction is considered. Current reproductive investment is further divided into parental care and offspring production. As relatedness increases, individuals invest more in current reproduction, which causes the increase in total group output.

The tug-of-war model is a broad framework describing “the tragedy of the commons” phenomenon (Hardin 1968; Rankin et al. 2007). Many conflicts related to reproduction, such as aggressive suppression of subordinates (Young et al. 2006), infanticide (Koenig et al. 1995; Vehrencamp 1977; Young & Clutton-Brock 2006) or even non-aggressive exploitative types of competition can be considered in this framework, as long as they increase personal share at the expense of group output. The parental investment model, on the other hand, has a property similar to the “paradox of collective action” (Brown 1999; Olson 1965; Sandler 1992): if group benefits are created by group members’ contributions at their own costs and the group benefits are available to all group members, individuals could gain by not investing or investing less to the creation of the group benefits. Since we do not assume discriminate parental care, parental care provided by group members creates common group resources, which are available to every group member. However, in our model, group members could simultaneously adjust their parental care and offspring production, which might explain the stable level of investment observed in many animal societies.

We believe our clarification between tug-of-war and investment models also helps resolve the difficulties of testing the tug-of-war model empirically. Cant (2006) argues that “rigorous testing of the tug-of-war model is difficult because of the nondiscriminating nature of its predictions”: skew is predicted to be insensitive to relatedness and the prediction of greater group productivity in more closely related groups is also predicted by the complete-control costly young model (Cant & Johnstone 1999) and the helping effort model based on kin selection (Cant & Field

2001; Kokko et al. 2001). However, as we have pointed out above, although the increase in total group output with increasing relatedness is predicted by several models, different underlying mechanisms (higher level of parental care or low within-group conflict) cause this similar prediction. It is empirically feasible to distinguish the two (see Table 3.1). For example, in their elegant experiment in primitively social bees, reproductive share was not affected by relatedness and group productivity increased as relatedness increased because within-group conflict decreased (Langer et al. 2004, Langer P. personal communication), which provided very strong support for the tug-of-war model.

In conclusion, by relaxing the complete-control and fixed-productivity assumptions of the original costly young model, we identified the similarities and the key differences between different reproductive skew models. These findings simplify the seemingly divergent predictions between costly young and the tug-of-war models and could potentially help researchers to focus on how animals resolve their conflict and why different animal societies employing same or different conflict resolution mechanisms. Different reproductive skew models are based on different conflict resolution mechanisms (Cant 2006). Identifying the key properties of these alternative conflict resolution mechanisms and individual strategies in both theoretical and empirical studies would help us better understand the nature of social evolution.

REFERENCES

- Brown, S. P. 1999 Cooperation and conflict in host-manipulating parasites. *Proceedings: Biological Sciences* **266**, 1899-1899.
- Cant, M. A. 1998 A model for the evolution of reproductive skew without reproductive suppression. *Animal Behaviour* **55**, 163-169.
- Cant, M. A. 2000 Social control of reproduction in banded mongooses. *Animal Behaviour* **59**, 147-158.
- Cant, M. A. 2006 A Tale of two theories: parent-offspring conflict and reproductive skew. *Animal Behaviour* **71**, 255-263.
- Cant, M. A. & Field, J. 2001 Helping effort and future fitness in cooperative animal societies. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268**, 1959-1964.
- Cant, M. A. & Johnstone, R. A. 1999 Costly young and reproductive skew in animal societies. *Behavioral Ecology* **10**, 178-184.
- Clutton-Brock, T. H. 1998 Reproductive skew, concessions and limited control. *Trends in Ecology & Evolution* **13**, 288-292.
- Creel, S. R. & Creel, N. M. 1991 Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behavioral Ecology and Sociobiology* **28**, 263-270.
- Emlen, S. T. 1982 The Evolution of Helping II. the Role of Behavioral Conflict. *American Naturalist* **119**, 40-53.
- Fisher, R. A. 1930 *The Genetical Theory of Natural Selection*. Oxford: Oxford University Press.
- Hardin, G. 1968 The Tragedy of the Commons. *Science* **162**, 1243-1248.

- Haydock, J. & Koenig, W. D. 2002 Reproductive skew in the polygynandrous acorn woodpecker. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 7178-7183.
- Heg, D., Heyl, S., Rasa, O. A. E. & Peschke, K. 2006 Reproductive skew and communal breeding in the subsocial beetle *Parastizopus armaticeps*. *Animal Behaviour* **71**, 427-437.
- Johnstone, R. A. 2000 Models of reproductive skew: A review and synthesis (invited article). *Ethology* **106**, 5-26.
- Keller, L. & Reeve, H. K. 1994 Partitioning of Reproduction in Animal Societies. *Trends in Ecology & Evolution* **9**, 98-102.
- Koenig, W. D., Mumme, R. L., Stanback, M. T. & Pitelka, F. A. 1995 Patterns and Consequences of Egg Destruction among Joint-Nesting Acorn Woodpeckers. *Animal Behaviour* **50**, 607-621.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268**, 187-196.
- Langer, P., Hogendoorn, K. & Keller, L. 2004 Tug-of-war over reproduction in a social bee. *Nature* **428**, 844-847.
- Magrath, R. D. & Heinsohn, R. G. 2000 Reproductive skew in birds: models, problems and prospects. *Journal of Avian Biology* **31**, 247-258.
- Magrath, R. D., Heinsohn, R. G. & Johnstone, R. A. 2004 Reproductive skew. In *Ecology and Evolution of Cooperative Breeding in Birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 157-176. Cambridge: Cambridge University Press.
- Olson, M. 1965 *The Logic of Collective Action*. Cambridge, MA: Harvard University Press.

- Packer, C., Pusey, A. E. & Eberly, L. E. 2001 Egalitarianism in female African lions. *Science* **293**, 690-693.
- Rankin, D. J., Bargum, K. & Kokko, H. 2007 The tragedy of the commons in evolutionary biology. *Trends in Ecology & Evolution* **22**, 643-651.
- Reeve, H. K., Emlen, S. T. & Keller, L. 1998 Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behavioral Ecology* **9**, 267-278.
- Reeve, H. K. & Keller, L. 2001 Tests of reproductive-skew models in social insects. *Annual Review of Entomology* **46**, 347-385.
- Reeve, H. K. & Ratnieks, F. L. W. 1993 Queen-queen conflict in polygynous societies: mutual tolerance and reproductive skew. In *Queen, Number, and Sociality in Insects* (ed. L. Keller), pp. 45-85. Oxford: Oxford University Press.
- Reeve, H. K. & Shen, S. F. 2006 A missing model in reproductive skew theory: The bordered tug-of-war. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 8430-8434.
- Russell, A. F. 2004 Mammals: comparisons and contrasts. In *Ecology and evolution of cooperative breeding in birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 210-227. Cambridge: Cambridge University Press.
- Sandler, T. 1992 *Collective Action: Theory and Applications*. Ann Arbor: University of Michigan Press.
- Scantlebury, M., Russell, A. F., McIlrath, G. M., Speakman, J. R. & Clutton-Brock, T. H. 2002 The energetics of lactation in cooperatively breeding meerkats *Suricata suricatta*. *Proceedings of the Royal Society of London Series B-Biological Sciences* **269**, 2147-2153.
- Shen, S. F. & Reeve, H. K. in review The synthesis of reproductive skew theory: The bordered tug-of-war model.

- Sherman, P. W., Lacey, E. A., Reeve, H. K. & Keller, L. 1995 The Eusociality Continuum. *Behavioral Ecology* **6**, 102-108.
- Vehrencamp, S. L. 1977 Relative Fecundity and Parental Effort in Communally Nesting Anis, *Crotophaga sulcirostris*. *Science* **197**, 403-405.
- Vehrencamp, S. L. 1980 To skew or not to skew? *Proceedings of the 17nd International Ornithology Congress* **17**, 869-874.
- Vehrencamp, S. L. 1983 A Model for the Evolution of Despotic Versus Egalitarian Societies. *Animal Behaviour* **31**, 667-682.
- Young, A. J., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennett, N. C. & Clutton-Brock, T. 2006 Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 12005-12010.
- Young, A. J. & Clutton-Brock, T. 2006 Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. *Biology Letters* **2**, 385-387.

CHAPTER 4

WHY DO COOPERATIVELY BREEDING TAIWAN YUHINAS COOPERATE WITH NON-RELATIVES?

INTRODUCTION

Most social animals live with kin (Emlen 1995). Based on Hamilton's rule (Hamilton 1964), the threshold for selection to favor altruistic behavior is lower for closely related individuals than for non-kin. Most studies of non-kin cooperation have focused on the evolutionary stability of such groups (reviews in Dugatkin 2002; Gardner & Foster 2008; Nowak 2006). Again, based on Hamilton's rule, the answer is simply: cooperation between non-kin is stable only if the direct fitness of cooperative behavior is positive. For example, Vehrencamp (1983) found that non-kin groups are more likely to form when the group benefit is large and the payoff of solitary breeding is small. Nevertheless, these arguments are not enough to explain why animals cooperate with non-kin. Everything else being equal, cooperating with kin would still be a better option because the alignment of genetic interests between related individuals lowers the level of social conflict. Therefore, the reason why animals form non-kin groups, rather than cooperate with kin in the first place, is still largely unanswered.

Two crucial factors for understanding why some, but not all, social animals form groups with non-kin are 1) the availability of kin, and 2) the preference for cooperating with kin. Various hypotheses concerning the formation of non-kin groups can be summarized by these two factors. One straightforward reason for non-kin groups is simply that there are not enough kin available (Aviles et al. 2004; Reeve 1998; Vehrencamp 1983). In this scenario, non-kin groups form even though group

members prefer to cooperate with kin because larger group size is beneficial to every group member (Aviles et al. 2004; Reeve 1998).

Despite the intrinsic genetic benefit of cooperating with kin, everything else may not be equal, and other effects may modulate the preference for cooperating with kin versus non-kin. For example, local competition between relatives can potentially negate the benefits of kin cooperation (Queller 1994; West et al. 2002). In other words, forming kin groups might not be beneficial because low mobility of kin could increase local population density and increase local competition between relatives (Le Galliard et al. 2005). Another possibility is that the benefit of cooperating with non-kin is higher than cooperating with kin. For example, genetic diversity, and thus low relatedness, promotes colony stability and productivity in social insects (Cole & Wiernasz 1999; Jones et al. 2004; Mattila & Seeley 2007). In this case, queens actually prefer to create low relatedness groups through multiple mating (Oldroyd & Fewell 2007).

In addition to the preference and availability of kin, the control of group membership also affects the composition and size of social groups (Giraldeau & Caraco 1993; Giraldeau & Caraco 2000; Higashi & Yamamura 1993). The insider-outsider conflict model of group size, referred to as IOM hereafter, describes the tension between group members, the insiders, and potential joiners, the outsiders. Assuming that per capita fitness follows a hump-shaped curve as group size increases, there will be conflict between insiders and outsiders over accepting the joiners. A solitary outsider would prefer to join a group as long as the fitness of joining is larger than being solitary. However, if the group size is larger than optimal, the addition of an outsider decreases the fitness of insiders. Thus, the level of control exercised by group insiders affects group size and composition. If solitaries can join any group at no cost, the IOM predicts that groups larger than the optimal group size are more

likely to be comprised of non-kin. This is because an outsider can still gain by joining a group even though the per capita group productivity is decreased. However, if group members can repel or accept an intruding outsider, an unrelated individual is likely to be repelled when the group size is equal to or larger than the optimal size. In this case, larger groups are more likely to be composed of kin.

Here we investigate the formation of non-kin groups in joint-nesting Taiwan yuhinas (*Yuhina brunneiceps*). Elsewhere we have shown that most yuhinas live in cooperatively breeding groups comprised of non-kin (Zhong et al, unpublished ms), and that direct fitness benefits are responsible for social group formation (Shen 2002; Yuan et al. 2004). In this paper, we test three alternative, but not mutually exclusive, hypotheses for non-kin group formation: (1) the kin availability hypothesis, (2) the kin competition hypothesis and (3) the insider-outsider conflict model, IMO. If the availability of kin is a key constraint on the formation of non-kin group of yuhinas, unrelated group members should be more common in larger groups (Aviles et al. 2004). Also, as reproductive success increases and more fledglings are produced in a population or season, more related dyads should be found because more kin are available. However, if kin competition plays an important role in determining the formation of non-kin group in yuhinas, kin groups should be more likely to form when population density is low, such as when reproductive success is low and adult mortality is high. Also, related dyads should occur at random rates in different-sized groups. Finally, based on IOM, if insiders have control over group membership, related individuals are more likely to be accepted when the group size is larger than the most productive group size; but both related and unrelated outsiders will be accepted when group size is smaller than the most productive size. Therefore, the insider-outsider model predicts that kin dyads are more likely to occur in large groups than in small groups. Our results are consistent with the predictions of IOM, although

the availability of relatives is affected by parental-offspring conflict. We then examine the mechanisms of group formation by studying breeding vacancy replacements in yuhinas.

METHOD

Study site and population

We study Taiwan yuhina at the National Taiwan University Highlands Experiment Farm at MeiFeng in central Taiwan (24° 05'N, 121° 10'E, elevation 2150 m). The size of study area is 50 ha with a system of small roads so that activities of the breeding groups could be monitored. In total, 103 year-groups were studied during seven field seasons (March- September, 1997-2001, 2003-2007). A group-year is defined as the number of groups observed each year over the study period. There were 6, 7, 6, 8, 18, 9, 15, 15, 14, and 19 groups in 1997, 1998, 1999, 2000, 2001, 2003, 2004, 2005, 2006 and 2007, respectively. Additional details of the study site can be found in an earlier publication (Lee *et al.* 2005).

The yuhina breeding season extends from March/April to September, and yuhinas usually make multiple nesting attempts each breeding season. Most yuhinas live in joint-nesting groups, in which several monogamous pairs, sometime with unmated individuals, lay eggs in the same nest and shared the labor of nest-building, incubating and provisioning. Reproductive skew for females is low (0.19, Yuan *et al.* 2004). After the breeding season, the breeding groups disband and the yuhinas join larger 'feeding groups' comprised of more than 20 individuals. Yuhinas remain in feeding groups until the start of the next breeding season when smaller cooperative breeding groups form (Yuan *et al.* 2004).

Behavioral observation

Adult yuhinas were caught using mist nets. Each individual was banded on both legs with one metal ring and a unique combination of three colored plastic leg-rings. In total, 683 adults and 167 nestlings were banded. Group composition of yuhinas was based on censuses conducted on systematic nest watches at 1-3 day intervals during the breeding season. The linear dominance hierarchy of each gender was determined by the consistent patterns of displacement and chasing (Yuan *et al.* 2004). Higher-ranked individuals consistently chase and displace lower-ranked, same-gender members of the group. The data set for the 10 years consisted of 103 group-years. For individual pairs that participated in more than one breeding group in the same year, the paired data were calculated only once in order to prevent pseudo-replication. For analysis of reproductive vacancies, the group composition data were compiled and the outcomes of 159 vacancies, 85 by females and 74 by males over the 10-year study period, were noted.

Genetic structure analysis

For analysis of genetic relatedness, a total of 69 group-years and 198 different individuals, collected in 1998-2001 and 2004, were used in the analyses. We sex-typed individuals with 2550F and 2718R primers (Fridolfsson & Ellegren 1999). Each individual was genotyped at 6-9 microsatellite loci for kinship assignment and relatedness pattern analysis. We used KINGROUP V2 (Konovalov & Heg 2008) (<http://www.it.jcu.edu.au/kingroup>) to compare the relative likelihoods that a given pair of birds was closely related ($r > 0.25$) or unrelated ($r < 0.25$). This software uses the likelihood formulas proposed by Goodnight & Queller (1999). Given a specific hypothesis about particular pedigree relationships, KINGROUP V2 tested the hypothesis that alleles were identical by descent as a consequence of the primary

hypothesis (kin relationship, $r > 0.25$) or null hypothesis (e.g. unrelated kin relationship, $r < 0.25$). Additional details of the molecular method used here can be found in (Zhong et al.). The proportions of closely-related kin dyads of each sex within cooperatively breeding groups were compared with chi-square tests.

RESULTS

Most yuhina offspring dispersed from their natal territories soon after they fledged. Only 4.19% of fledglings ($n=167$), including six males and one female, remained in their natal territory in the next breeding season. The genetic data also showed that most yuhinas cooperated with non-kin group members. Only 7.58% of within-group dyads ($n=633$) were comprised of kin and the proportion of related dyads was not affected by breeding success or adult mortality rates. However, compared to random expectation, males were more likely to live in groups with kin than were females ($\chi^2=5.268$, $p=0.022$, Table 4.1).

To test the IOM predictions of group formation and understand the role of kinship in the formation of yuhina groups, kinship structures were compared for small (group size ≤ 4) and large (group size ≥ 5) groups. Individuals were more likely to live with kin in large groups than in small groups relative to random expectations (Fig. 4.1, $\chi^2=5.27$, $p=0.027$).

Local recruitment, percentage of fledglings remained in the study area, patterns were studied to address the key puzzle of why most yuhinas do not recruit kin when there are breeding vacancies. There was a significant effect of nest success rate – the percentage of local recruitment recruited decreased with an increase in nest success rate (Fig. 4.2, linear regression, slope $b=-2.924$, $t=-6.047$, $p=0.004$). There was a trend for the percentage of local recruitment to increase as adult mortality rate increased (linear regression, slope $b=1.213$, $t=2.502$, $p=0.067$). Fledgling date also has significant

effect on local recruitment, with more recruitment of late fledglings (Fig. 4.3, logistic regression, $p < 0.01$).

To understand the group formation mechanism, the breeding vacancy replacements of different sexes and ranks were examined. The breeding vacancies of alpha males were more likely to be filled by a lower-ranking male from the same group. Other breeding vacancies were mostly filled by individuals from outside the group. Specifically, 73% of alpha male vacancies were filled by within-group males (insiders), while only 44% of alpha female, 26% of beta female and 31% of beta male vacancies were filled by insiders (Table 4.2). However, several factors simultaneously affected the resolution of breeding vacancies. Since two-pair groups were most common in yuhinas (Fig. 4.4), it is obvious that there were significantly more insiders available to fill the alpha vacancies (95.7%, $n=69$) than the beta vacancies (56.5%, $n=69$, $\chi^2=18.28$, $p < 0.001$, Table 4.2). Thus, availability of insiders had a significant effect on the resolution of beta vacancies: beta vacancies were more likely to be filled by insiders (56.4%, $n=39$) if insiders were available compared to all beta vacancies (28.6%, $n=77$, Fisher exact test, $p=0.005$). Whether or not alpha females remained in the group significantly affected the resolution of alpha male vacancies: outsider males were more likely to obtain alpha male vacancies when the alpha female remained in the group (50%, $n=14$) than when the alpha female also disappeared (6.3%, $n=16$, Fisher exact test, $p=0.012$). However, whether opposite-sex breeders remained in the group did not affect the resolution of breeding vacancies for other breeding roles (Table 4.2). Most alpha and beta vacancies were filled (92.4%, $n=158$), while vacancies of lower ranking individuals, such as gamma and unpaired individuals, were significantly less likely to be replaced (8.6%, $n=70$, Fisher exact test, $p < 0.001$).

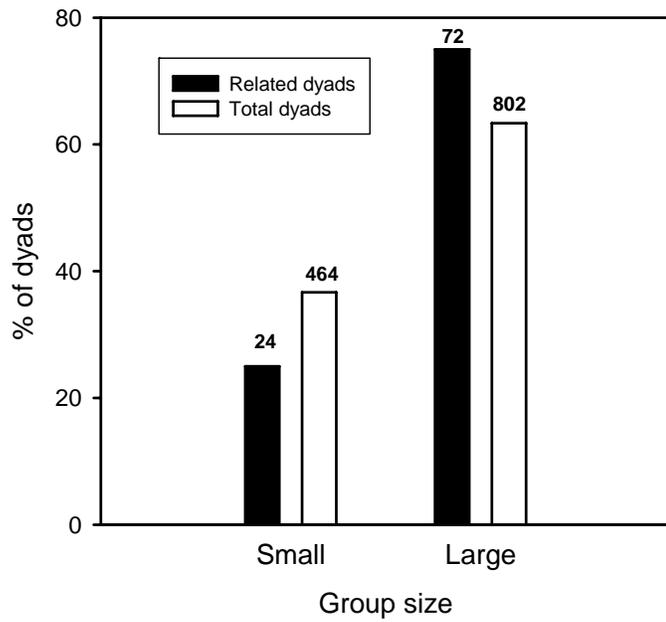


Figure 4.1 Percentage of related dyads in small (group size=3-4) and large (group size>4) compared to the distribution of all dyads.

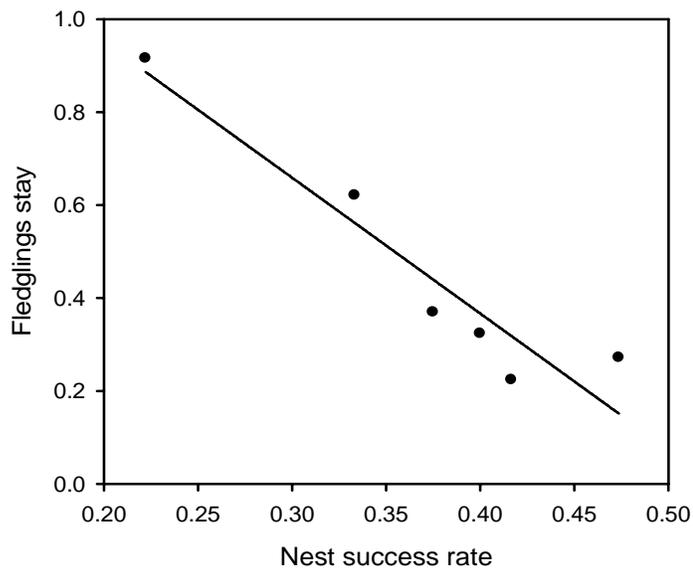


Figure 4.2 The relationship between proportion of fledglings staying in the study area in the following season and the nest success rate of the season.

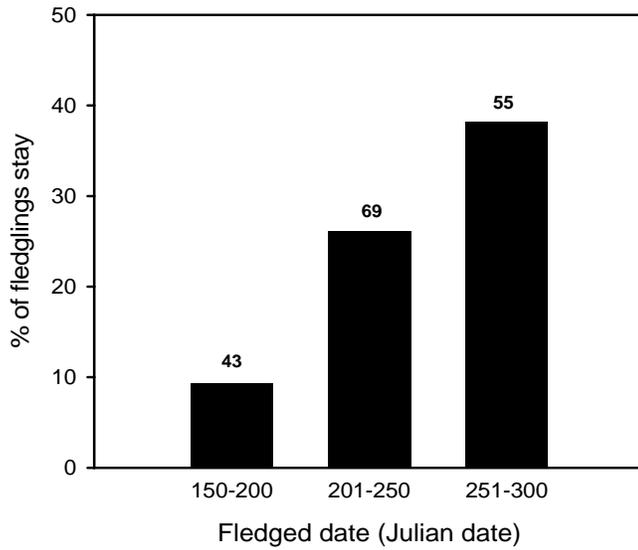


Figure 4.3 The relationship between percentage of fledglings staying in the study area in the following season and fledged date of the fledglings.

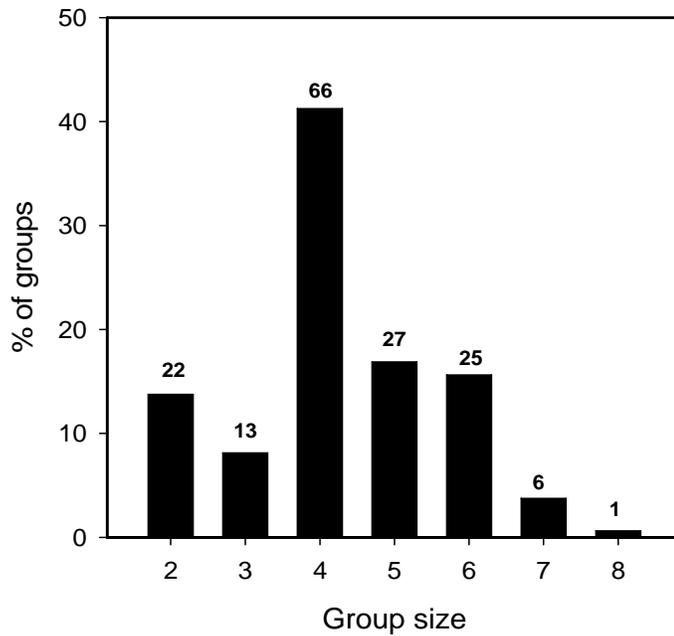


Figure 4.4 The group size distribution of Taiwan yuhinas groups.

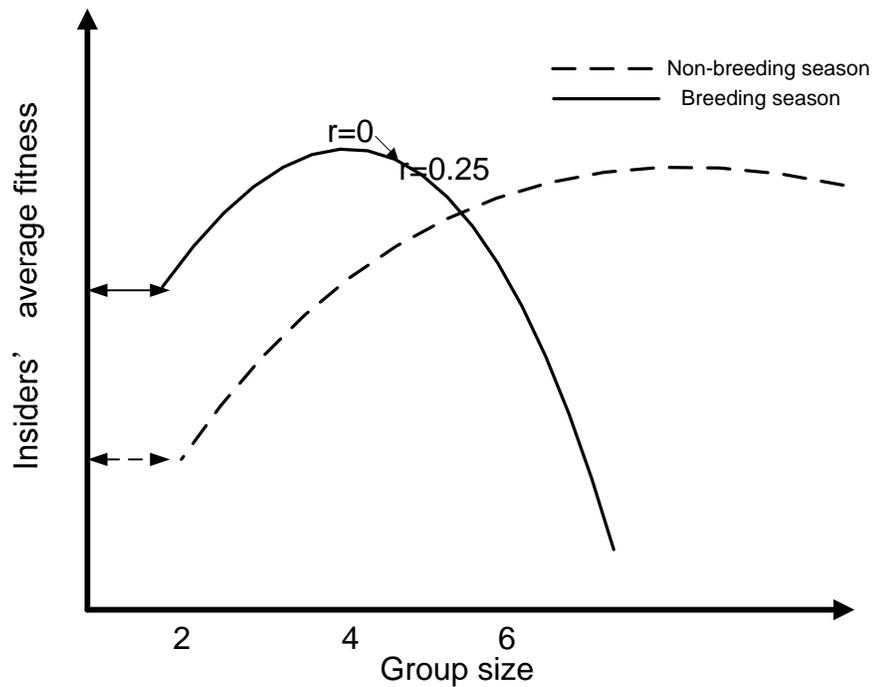


Figure 4.5 The hypothetical figure showing the relationship between insider yuhinas' average inclusive fitness and group size in breeding season and non-breeding season. r indicates average relatedness between group members.

DISCUSSION

Both our behavioral and genetic data show that most yuhinas cooperate with unrelated group members. Since the instances of offspring remaining in their natal territory were extremely rare, only seven cases in eight years of study, we focus our analysis of within-group kinship using the genetic data. One of the critical predictions distinguishing the availability hypothesis, kin competition hypothesis, and the insider-outsider models is the occurrence of within-group related dyads in different-sized groups. Our results show that related dyads occurred more frequently in large groups of yuhinas, which is predicted by the insider-outsider model (Giraldeau & Caraco 1993; Giraldeau & Caraco 2000; Higashi & Yamamura 1993) but is different from the predictions of the availability and kin competition hypotheses. Further support for the

IOM is provided by the good match between the most commonly observed group size (two pairs) and the most reproductively productive group size. In yuhinas, the most productive groups are the two-pair groups, which results from the balance between the group benefit of a bet-hedging strategy of coping with fluctuating environmental conditions and conflict over the sharing of reproduction (Shen 2002; Yuan et al. 2004).

Our results are clearly at odds with the kin availability hypothesis. This hypothesis predicts that larger groups are more likely to be comprised of non-kin, but we found larger groups to be composed of kin (Aviles et al. 2004; Lukas et al. 2005). Moreover, the percentage of fledglings breeding in the study area decreased as nest success rate increased, instead of increasing as the availability hypothesis would predict. Taken together, this evidence strongly suggests that a lack of available kin is not the reason why yuhinas breed with non-kin. We also did not find any evidence that reproductive success and adult mortality rate affected the probability of fledglings remaining in their natal territory in the next breeding season. Therefore, kin competition is also unlikely to be the key factor determining the formation of non-kin groups in yuhinas. In short, our results generally support the predictions of the IOM.

Since the IOM is based on Hamilton's rule, this means that if relatives are available, insiders are predicted to prefer to cooperate with kin by the IOM. In other words, unrelated outsiders would only be accepted when group size is smaller than the most productive size. Given that our result supports the IOM, this suggests that kinship still plays a role in the formation of yuhina cooperatively breeding groups. Why, then, are most of the yuhina groups comprised of non-kin? Again, applying the IOM, the prevalence of non-kin groups in yuhinas suggests that when there are breeding vacancies, relatives are not available to join the group. However, our result

also indicate that availability of kin is not the main reason for yuhinas to form non-kin group and there should be enough kin produced each season to fill the breeding vacancies. We believe that the key to resolving this seemingly inconsistent result is understanding why offspring do not stay in or near their natal territories.

Kin groups in most cooperatively breeding species are formed through delayed offspring dispersal (Brown 1987; Koenig & Dickinson 2004; Solomon & French 1997; Stacey & Koenig 1990, but see Hatchwell & Sharp 2006; Sharp et al. 2008). However, most yuhinas dispersed from their natal territories. Our results on local recruitment show that late fledglings were more likely to breed in the study area in the following breeding season. This result coincides with our observation that adults usually evicted the offspring soon after they fledged, unless it was their season's last nesting attempt. Fledglings from the last successful nesting attempt of the season usually wintered with their natal groups and dispersed from their natal territories in the following spring. This observation suggests that the conflict over the allocation of parental investment in different broods is the reason that parents evict their fledglings. In other words, the cost of keeping fledglings might be too high for insiders during the breeding season and/or fledglings could have higher fitness by dispersing during the breeding season. As a result, an adult's inclusive fitness of retaining fledglings in the group should increase as the end of the breeding season approaches because fewer breeding opportunities remain (Fig. 4.5). Because of the stochastic nature of nesting success in yuhinas, caused by typhoons and nest predation, many groups end up with no relatives around to fill the breeding vacancies in future breeding seasons (Shen 2002).

Our breeding vacancy replacement data helps us further understand the mechanism of group formation in yuhinas. In general, higher ranking vacancies, especially alpha male vacancies (73%), are more likely to be filled by lower ranking insiders, if lower

ranking individuals are available. Almost all alpha male vacancies were filled by insiders (15/16 cases) if their mates also disappeared from the group. This suggests that social queuing is an important route for male yuhinas to become alpha breeders. The social queuing observed in yuhinas also explains the result that most retained offspring are males (6/7 cases) and is consistent with the finding that male yuhinas are more likely to live with kin than females. However, the vast majority of fledglings, both males and females, still dispersed from their natal group before the coming breeding season. Only 32.7% of yuhina groups are larger than two pairs and therefore most beta vacancies, 74% of beta female and 69% of beta male vacancies, were filled by outsiders because lower ranking insiders were not available. The reason that yuhinas do not have relatives around to fill the breeding vacancies is because most of the fledglings do not stay. On the other hand, this result also suggests that dispersing offspring might have relatively good chances of being accepted by other unrelated groups, although this kind of dispersal data is extremely difficult to estimate precisely in yuhinas, as well as in most other species.

Table 4.1 Cases of individuals who lived with related group members.

	Alpha	Beta	Gamma or unpaired	Total
Male	20	18	24	62
Female	11	12	11	34
Total	31	30	35	96

Table 4.2 Resolutions of reproductive vacancies in Taiwan yuhinas.

Breeding vacancies	Mate remained in the group	Alpha	Beta	Gamma	Un-paired	Insider total	Insider available?			outsider total	No ²	Total
							M ¹	N	Y			
Alpha females	No	0	5	0	3	8	0	0	7	7	1	16
	Yes	0	9	0	0	9	0	1	14	15	2	26
Beta Females	No	1	0	0	1	2	3	8	6	17	1	20
	Yes	2	0	4	2	8	3	6	2	11	4	23
Total		3	14	4	6	27	6	15	29	50	8	85
Alpha males	No	0	9	4	2	15	0	0	1	1	1	17
	Yes	0	5	1	1	7	0	2	5	7	1	15
Beta males	No	1	1	1	4	7	1	6	5	12	1	20
	Yes	1	0	3	1	5	1	10	4	15	1	21
Total		2	15	9	8	34	2	18	15	35	4	74

1. whether insiders are available is unknown
2. instances of breeding vacancies were not resolved.

Most cooperatively breeding societies are formed by delayed offspring dispersal, and therefore most of the group members are closely related to each other (Emlen 1995). However, it has also long been acknowledged that the death, divorce or departure of a group member and its replacement from unrelated outsiders, will generate complex genetic structures within social groups (Emlen 1997). The different genetic relatednesses between group members in cooperatively breeding societies is often used to test the predictions, such as levels of conflict and helper efforts, of Hamilton's rule (Emlen & Wrege 1988; Griffin & West 2003; Komdeur 1994; Mumme 1992). Nonetheless, despite the conceptual elegance, the group membership prediction of

IOM has received little attention in studies of cooperative breeding (but see Ost et al. 2005). As we have shown in this study, the IOM can incorporate the factors of the availability and preference of kin and generate simple predictions, which can potentially help us understand the mechanisms affecting the group compositions of cooperative breeding societies. Furthermore, the occurrence of unrelated individuals in social groups are commonly found in broad range of other type of social groups such as some cooperative breeding species (Koford et al. 1990; Vehrencamp & Quinn 2004), fish shoals (Krause et al. 2000; Steck et al. 1999), lek (Knopp et al. 2008), and bat roosting (Metheny et al. 2008). Therefore, the IOM could server as the general framework for understanding the group membership and group size in these varieties of social groups, especially with the help of molecular tools.

REFERENCES

- Aviles, L., Fletcher, J. A. & Cutter, A. D. 2004 The kin composition of social groups: Trading group size for degree of altruism. *American Naturalist* **164**, 132-144.
- Brown, J. L. 1987 *Helping and communal breeding in birds*. Princeton: Princeton University Press.
- Cole, B. J. & Wiernasz, D. C. 1999 The Selective Advantage of Low Relatedness. *Science* **285**, 891.
- Dugatkin, L. 2002 Animal cooperation among unrelated individuals. *Naturwissenschaften* **89**, 533-541.
- Emlen, S. T. 1995 An evolutionary theory of the family. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 8092-8099.
- Emlen, S. T. 1997 Predicting family dynamics in social vertebrates. In *Behavioural Ecology: An Evolutionary Approach*, vol. 4 (ed. J. R. Krebs & N. B. Davies), pp. 228-253. Oxford: Blackwell Science.
- Emlen, S. T. & Wrege, P. H. 1988 The role of kinship in helping decisions among white-fronted bee-eaters. *Behavioral Ecology and Sociobiology* **23**, 305-315.
- Fridolfsson, A. K. & Ellegren, H. 1999 A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* **30**, 116-121.
- Gardner, A. & Foster, K. R. 2008 The evolution and ecology of cooperation: history and concepts. . In *Ecology of Social Evolution*. (ed. J. Korb & J. Heinz). Berlin: Springer.
- Giraldeau, L. A. & Caraco, T. 1993 Genetic relatedness and group size in an aggregation economy. *Evolutionary Ecology* **7**, 429-438.
- Giraldeau, L. A. & Caraco, T. 2000 *Social Foraging Theory*. Princeton, NJ: Princeton University Press.

- Goodnight, K. F. & Queller, D. C. 1999 Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Molecular Ecology* **8**, 1231-1234.
- Griffin, A. S. & West, S. A. 2003 Kin Discrimination and the Benefit of Helping in Cooperatively Breeding Vertebrates. *Science* **302**, 634-636.
- Hamilton, W. D. 1964 The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* **7**, 1-16.
- Hatchwell, B. J. & Sharp, S. P. 2006 Kin selection, constraints, and the evolution of cooperative breeding in long-tailed tits. *Advances in the Study of Behavior, Vol 36* **36**, 355-395.
- Higashi, M. & Yamamura, N. 1993 What Determines Animal Group-Size - Insider-Outsider Conflict and Its Resolution. *American Naturalist* **142**, 553-563.
- Jones, J. C., Myerscough, M. R., Graham, S. & Oldroyd, B. P. 2004 Honey Bee Nest Thermoregulation: Diversity Promotes Stability, vol. 305, pp. 402-404: American Association for the Advancement of Science.
- Knopp, T., Heimovirta, M., Kokko, H. & Merila, J. 2008 Do male moor frogs (*Rana arvalis*) lek with kin? *Molecular Ecology* **17**, 2522-2530.
- Koenig, W. D. & Dickinson, J. L. 2004 *Ecology and Evolution of Cooperative Breeding in Birds*: Cambridge University Press.
- Koford, R. R., Bowen, B. S. & Vehrencamp, S. L. 1990 Groove-billed Anis: joint-nesting in a tropical cuckoo. In *Cooperative Breeding in Birds: Long Term Studies of Ecology and Behaviour* (ed. P. B. Stacey & W. D. Koenig), pp. 335-355. Cambridge: Cambridge University Press.
- Komdeur, J. 1994 The effect of kinship on helping in the cooperative breeding seychelles warbler (*Acrocephalus-sechellensis*). *Proceedings of the Royal Society of London Series B-Biological Sciences* **256**, 47-52.

- Konovalov, D. A. & Heg, D. 2008 A maximum-likelihood relatedness estimator allowing for negative relatedness values. *Molecular Ecology Resources* **8**, 256-263.
- Krause, J., Butlin, R. K., Peuhkuri, N. & Pritchard, V. L. 2000 The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. *Biological Reviews* **75**, 477-501.
- Le Galliard, J. F., Ferriere, R. & Dieckmann, U. 2005 Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility. *American Naturalist* **165**, 206-224.
- Lukas, D., Reynolds, V., Boesch, C. & Vigilant, L. 2005 To what extent does living in a group mean living with kin? *Molecular Ecology* **14**, 2181-2196.
- Mattila, H. R. & Seeley, T. D. 2007 Genetic Diversity in Honey Bee Colonies Enhances Productivity and Fitness. *Science* **317**, 362.
- Metheny, J. D., Kalcounis-Rueppell, M. C., Willis, C. K. R., Kolar, K. A. & Brigham, R. M. 2008 Genetic relationships between roost-mates in a fission-fusion society of tree-roosting big brown bats (*Eptesicus fuscus*). *Behavioral Ecology and Sociobiology* **62**, 1043-1051.
- Mumme, R. L. 1992 Do helpers increase reproductive success - an experimental-analysis in the Florida scrub jay. *Behavioral Ecology and Sociobiology* **31**, 319-328.
- Nowak, M. A. 2006 Five rules for the evolution of cooperation. *Science* **314**, 1560-1563.
- Oldroyd, B. P. & Fewell, J. H. 2007 Genetic diversity promotes homeostasis in insect colonies. *Trends in Ecology & Evolution* **22**, 408-413.

- Ost, M., Vitikainen, E., Waldeck, P., Sundstrom, L., Lindstrom, K., Hollmen, T., Franson, J. C. & Kilpi, M. 2005 Eider females form non-kin brood-rearing coalitions. *Molecular Ecology* **14**, 3903-3908.
- Queller, D. C. 1994 Genetic relatedness in viscous populations. *Evolutionary Ecology* **8**, 70-73.
- Reeve, H. K. 1998 Game theory, reproductive skew, and nepotism. *Game Theory and Animal Behavior*, 118-145.
- Sharp, S. P., Simeoni, M. & Hatchwell, B. J. 2008 Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird. *Proceedings of the Royal Society B-Biological Sciences* **275**, 2125-2130.
- Shen, S. F. 2002 *The Ecology of Cooperative Breeding Taiwan Yuhinas (Yuhina brunneiceps) in Mayfeng Areas*. MSc. thesis, Department of Zoology. Taipei: National Taiwan University.
- Solomon, N. G. & French, J. A. 1997 *Cooperative Breeding in Mammals*: Cambridge University Press.
- Stacey, P. B. & Koenig, W. D. 1990 *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*. Cambridge: Cambridge University Press.
- Steck, N., Wedekind, C. & Milinski, M. 1999 No sibling odor preference in juvenile three-spined sticklebacks. *Behavioral Ecology* **10**, 493-497.
- Vehrencamp, S. L. 1983 A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour* **31**, 667-682.
- Vehrencamp, S. L. & Quinn, J. S. 2004 Joint laying systems. In *Ecology and Evolution of Cooperative Breeding in Birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 177-196. Cambridge: Cambridge University Press.
- West, S. A., Pen, I. & Griffin, A. S. 2002 Cooperation and competition between relatives. *Science* **296**, 72-75.

Yuan, H. W., Liu, M. & Shen, S. F. 2004 Joint nesting in Taiwan Yuhinas: A rare passerine case. *Condor* **106**, 862-872.

Zhong, Q.-D., Shen, S.-F., Li, S.-H., Lin, K.-Y., Pu, C.-E. & Yuan, H.-W. Genetic structure and relatedness in the joint-nesting Taiwan yuhina (unpublished ms).