Reproductive skew and the evolution of group dissolution tactics: a synthesis of concession and restraint models

P. M. BUSTON*, H. K. REEVE†, M. A. CANT‡, S. L. VEHRENCAMP† & S. T. EMLEN†

*National Center for Ecological Analysis and Synthesis, University of California, U.S.A.
†Department of Neurobiology and Behavior, Cornell University
‡Department of Zoology, University of Cambridge

Reproductive skew theory provides a compelling explanation for the partitioning of reproduction among individuals within animal societies. One constructive criticism of the theory is that there are too many models, all of which have different assumptions and predictions, which makes it difficult to know what to test. Here we begin the process of tackling this problem, by re-examining the assumptions and predictions of basic concession and restraint models, two transactional models that are often tested as alternatives. Concession models assume that the dominant has complete control over the allocation of reproduction but may yield some of the group's reproduction to prevent the subordinate from voluntarily departing. Restraint models assume that the subordinate has complete control over the allocation of reproduction but may not claim all of the group's reproduction to prevent the dominant from forcibly evicting it. We show that the group dissolution tactics that individuals use (forcible eviction or voluntary departure) need not be an assumption of the model, but rather they can be predicted using Hamilton's rule and the standard variables of skew models. We reveal that the assumption that one individual (dominant or subordinate) has complete control over the allocation of reproduction is an idea common to both models, and we resolve this semantic difference by calling this individual 'the allocator'. We show that, regardless of the group dissolution tactics that individuals adopt, the allocator's share of the reproduction always increases as relatedness increases, as group productivity increases, and as constraints on leaving to breed elsewhere intensify. We conclude that concession and restraint type models make qualitatively similar predictions, and should not be tested as alternatives. In summary, this study makes the transactional framework of reproductive skew more general, by eliminating restrictive assumptions, and more amenable to testing in the field, by clarifying assumptions and predictions.

The formation of animal societies is one of the most dramatic transitions in evolution (Maynard Smith & Szathmary 1995). During this transition, independently reproducing individuals began to reproduce as part of a group. In all such groups, there will be conflict between genetically selfish individuals over the allocation of reproduction. All things being equal, these conflicts will be more extreme when there is greater disparity in the amount of reproduction each individual receives, that is, when there is greater reproductive skew (Keller & Reeve 1994; Sherman et al. 1995). These reproductive conflicts must be resolved for the society to be stable. Thus, the key to understand these societies lies in understanding how and why reproductive conflicts among individuals within the society are resolved.

Reproductive skew theory provides a compelling explanation for how and why reproductive conflict is resolved (Keller & Reeve 1994; Johnstone 2000). The theory combines evolutionary game theory and kin selection theory

Correspondence and present address: P. M. Buston, Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Avda. María Luisa s/n Pabellón de Perú, 41013 Sevilla, España (email: buston@ebd.csic.es). H. K. Reeve, S. L. Vehrencamp and S. T. Emlen are at the Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, U.S.A. M. A. Cant is at the Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.

(Hamilton 1964; Maynard Smith 1982). The basic reproductive skew models predict the partitioning of reproduction among individuals within groups and the conditions under which groups will be stable (Vehrencamp 1979, 1983; Emlen 1982; Stacey 1982; Reeve & Ratnieks 1993; Johnstone & Cant 1999). Extensions of basic models provide insight into many other features of animal societies: group foraging (Hamilton 2000); group size (Reeve & Emlen 2000); lekking (Widemo & Owens 1995); manipulation (Crespi & Ragsdale 2000); origin of sterile castes (Jeon & Choe 2003); sex change (Buston 2002; Muñoz & Warner 2003); and social queuing (Kokko & Johnstone 1999; Ragsdale 1999).

The simplicity of skew models, in conjunction with the breadth of their predictions, has led some to suggest that reproductive skew theory might represent a unified theory of social evolution (sensu Wilson 1975; Keller & Reeve 1994; Sherman et al. 1995; Emlen 1997; Johnstone 2000). In spite of its potential, or perhaps because of its potential, reproductive skew theory has its constructive critics and its problems have been laid bare (Clutton-Brock 1998; Johnstone 2000; Magrath & Heinsohn 2000; Kokko 2003). The most serious problem is that there is a bewildering array of skew models, all of which have slightly different assumptions and predictions, and this makes it difficult to know what to test (Magrath & Heinsohn 2000). Here we begin the process of tackling this problem, by reducing the number of assumptions and clarifying the predictions of one of the two major classes of reproductive skew models: the transactional models.

TRANSACTIONAL MODELS

Basic reproductive skew models can be assigned to one of two major classes, transactional or tug of war, based on fundamental differences in their assumptions regarding the mechanism by which reproduction is distributed among group members (Johnstone 2000; Reeve & Keller 2001). In the transactional models it is assumed that there is a cost-free negotiated settlement over reproductive shares within societies. In these models, it is assumed that one individual has complete control over the allocation of reproduction, but this individual yields reproduction to other group members to retain the benefits of group cohesion (Vehrencamp 1979, 1983; Reeve & Ratnieks 1993; Johnstone & Cant 1999). In tug-of-war models, it is assumed that there is costly competition over reproductive shares within societies. In these models, it is assumed that no individual has complete control over the allocation of reproduction, and all individuals exert effort to obtain reproduction at the expense of total group reproductive output (Reeve et al. 1998; Johnstone 2000; Reeve & Shen 2006). Regardless of one's preconceived notion of whether the assumptions of transactional or tug-of-war models are more commonly fulfilled in nature, the transactional framework will be useful for predicting the tactics of individuals in animal societies when individuals have mechanisms in place that allow them to negotiate and resolve conflict without entering into costly competition.

Within the transactional framework itself there have been two views on how reproduction is allocated within groups

and on how group dissolution occurs: concession and restraint (Reeve & Ratnieks 1993; Clutton-Brock 1998; Johnstone & Cant 1999; Johnstone 2000). Concession models assume that (a) the dominant has complete control over the allocation of reproduction, but (b) it may yield a share of the reproduction, that is, it may provide a concession to (c) prevent the subordinate from voluntarily departing (Vehrencamp 1979, 1983; Emlen 1982; Reeve & Ratnieks 1993; Reeve & Keller 1997). Restraint models assume that (a) the subordinate has complete control over the allocation of reproduction, but (b) it may not claim all of the reproduction, that is, it may show restraint to (c) prevent the dominant from forcibly evicting it (Johnstone & Cant 1999). Laying out the assumptions of concession and restraint models side by side, like this, suggests that there are six different assumptions (concession a–c and restraint a–c) underlying the models. We believe that the existence of multiple different assumptions, and the vagueness associated with terms like yield or claim and concession or restraint, has contributed significantly to difficulties associated with understanding and testing reproductive skew theory.

In this study, we focus on reducing the number of assumptions underlying concession and restraint models of reproductive skew. Using a combination of modelling and a review of the semantics, we show that the number of assumptions underlying the models can be reduced from six to two, and show that the predictions of the models are nearly identical. This clarification should be useful because the predictions of these models are often pitted against each other (Reeve & Keller 2001; Haydock & Koenig 2003; Langer et al. 2004; Heg et al. 2006). Our hope is that this study makes the transactional framework of reproductive skew more general and more amenable to testing in the field.

EVOLUTION OF GROUP DISSOLUTION TACTICS

Previous transactional models of reproductive skew assumed that only one individual could dissolve the group, and that it could do it in only one way (Table 1): the subordinate could voluntarily depart in the concession models (Reeve & Ratnieks 1993); the dominant could forcibly evict the subordinate in the restraint model (Johnstone & Cant 1999). This difference in assumptions set up an arbitrary association of voluntary departure with the concession models and forcible eviction with the restraint model. Yet, in nature, all individuals in a group will have the potential to dissolve the group, either by voluntary departure or by forcible eviction (Buston 2003a). Furthermore, it is widely recognized that group dissolution strategies will themselves evolve in response to selection (Danchin & Wagner 1997; Clutton-Brock et al. 1998; Buston 2003a; Young et al. 2006). Here we show that the group dissolution tactic that each individual uses can be predicted using Hamilton's rule and the standard variables of skew models.

Model

We consider a simple group of two individuals, A and B. We use parameters consistent with the original

Table 1. Summary of the assumptions of the concession model (Reeve & Ratnieks 1993), the restraint model (Johnstone & Cant 1999), and the three models presented here

	Model				
Assumption*	Concession	Model (1)	Restraint	Model (2)	Model (3)
Control of reproduction†	Dominant	Allocator	Subordinate	Allocator	Allocator
Forcible eviction‡**	[Dominant]	**Allocator**	Dominant	**Partner**	**Both**
Voluntarily departure§**	Subordinate	**Partner**	[Subordinate]	**Allocator**	**Neither**

*All transactional models assume that there is a cost-free negotiated settlement over reproductive shares. This is the fundamental difference between transactional and tug-of-war models, since tug-of-war models assume that there is costly competition over reproductive shares.

†The concession model assumes that the dominant controls the allocation of reproduction while the restraint model assumes that the subordinate controls the allocation of reproduction. Models (1) and (2) resolve this discrepancy by calling the individual that controls reproduction the 'allocator' and calling the other individual the 'partner'.

‡Dominant may forcibly evict subordinate at some cost in the restraint model, and the dominant may indirectly evict the subordinate by withdrawing the staying incentive in the concession model. Models (1) and (2) clarify that there is no difference between forcible eviction and indirect eviction when the cost of eviction is negligible.

§Subordinate may voluntarily depart in the concession model, and the subordinate may indirectly depart by withdrawing dominant's share, thereby eliciting eviction, in the restraint model.

**In the concession and restraint model the group dissolution tactics adopted by each individual were assumptions of the model. The model developed here reveals that group dissolution tactics (Bold) can be predictions of Hamilton's rule and the standard variables of reproductive skew theory (see inequality (2)).

transactional models: the coefficient of relatedness between the two individuals is r (assumed symmetrical here); the group's expected reproductive output if the individuals remain together is equal to G; each individual's expected reproductive output if it leaves is equal to L; each individual's expected reproductive output if it stays alone is equal to S; and the probability of a focal individual winning a contest over eviction is c. We use the parameters G, L, and S, rather than the standard K, x, and l, because we believe that, in the long run, they will make the models easier to understand (see Discussion; Kokko 2003; Zink & Reeve 2005). To avoid confusion we make it clear how our results relate to the results of previous models.

In dyadic transactional models of reproductive skew, behaviours favoured by selection are determined by use of Hamilton's rule (Hamilton 1964). In particular, an action i is favoured over an action j if

$$X_i - X_j + r(Y_i - Y_j) > 0 \qquad (1)$$

where X_i (or X_j) is the personal reproductive output associated with the ith (or jth) action, Y_i (or Y_j) is the other individual's reproductive output.

Which group dissolution tactic will an individual adopt?

We assume that once one individual has left the territory the other remains in the territory, as commonly observed in nature and assumed in previous transactional models. By applying Hamilton's rule (inequality (1)) and the above variables to a focal individual's decision of whether to forcibly evict or voluntarily depart, we find that the inclusive fitness of an individual that attempts to forcibly evict will be greater than the inclusive fitness of an individual that voluntarily departs when

$$cS + (1-c)L - L + r[cL + (1-c)S - S] > 0$$

which yields the simple condition

$$S > L. \qquad (2)$$

Results

Inspection of this inequality reveals that an individual will be more likely to use the tactic of forcible eviction as the individual's reproductive output if it stays alone (S) increases and as the individual's reproductive output if it leaves (L) decreases. Conversely, an individual will be more likely to use the tactic of voluntary departure as L increases and S decreases. It is noteworthy that an individual's decision to forcibly evict or voluntarily depart does not depend on the coefficient of relatedness (r) or the individual's probability of winning the contest over eviction (c). This is intuitively appealing, since it indicates that, regardless of r and c, if conditions are better inside the territory than outside the territory, then individuals will adopt a forcible eviction tactic rather than a voluntary departure tactic.

For simplicity, we assumed that the cost of evicting (e, Johnstone & Cant 1999) is negligible within the model. This is equivalent to saying that the long-term fitness cost of evicting is negligible, while accepting that there may be a short-term energetic cost of evicting. This is logically consistent with the assumption that control of reproduction comes at negligible costs within transactional models (Reeve & Ratnieks 1993; Johnstone & Cant 1999). The implications of introducing a cost of evicting are fairly obvious; introducing a cost of evicting would change inequality (2) to $S - e > L$, and forcible eviction would be favoured over a smaller range of conditions.

From this short analysis, it is apparent that the group dissolution tactic adopted by each individual can be predicted using Hamilton's rule and the standard variables of reproductive skew models. It is unclear why this was not done before, because it removes a restrictive assumption

(that group dissolution tactics are fixed, assumption c) from reproductive skew models and thereby increases their generality. Further, since there are two group dissolution tactics and two individuals, this indicates that there might be four basic transactional models of reproductive skew: (1) A uses a forcible eviction tactic while B uses a voluntary departure tactic; (2) A uses a voluntary departure tactic while B uses a forcible eviction tactic; (3) both A and B use a forcible eviction tactic; and (4) both A and B use a voluntary departure tactic.

We now go on to show that the first two of these models (1 and 2) are equivalent to the previously published concession and restraint models (Reeve & Ratnieks 1993; Johnstone & Cant 1999). But we resolve a discrepancy in the assumptions of models (1) and (2), and show that this eliminates most differences in their predictions. Then we develop the third model (3) in which both A and B use a forcible eviction tactic which, based on inequality (inequality (2) and observations of eviction in nature, we believe will be applicable to many societies.

THE ALLOCATION OF REPRODUCTION

Within the transactional framework there have been two views on how reproduction is allocated within groups (Table 1): in the concession model the dominant has complete control over the allocation of reproduction but it may yield a share of the reproduction to prevent the subordinate from dissolving the group (Reeve & Ratnieks 1993); in the restraint model the subordinate has complete control over the allocation of reproduction but it may not claim all of the reproduction to prevent the dominant from dissolving the group (Johnstone & Cant 1999). This semantic difference in assumptions caused the models to make qualitatively different predictions about the relationship among key parameters and the subordinate's share of reproduction (Johnstone 2000; Reeve & Keller 2001). The idea that one individual controls the allocation of reproduction, yielding a share and claiming the remainder, is one of the founding concepts of transactional models of reproductive skew (Vehrencamp 1979; Emlen 1982). Because this concept is so fundamental we functionally define the individuals with complete control over the allocation of reproduction as 'the allocator'. Here we show that when predictions concerning reproductive shares are consistently framed from the perspective of the allocator, the predictions of concession and restraint models are basically identical.

Model

We assume that one of the two individuals has complete control over the allocation of reproduction, and we functionally define this individual as 'the allocator'. We call A the allocator, and we call B its partner. We assume that both individuals can dissolve the group, either by forcible eviction or by voluntary departure. Control of reproduction and the act of eviction are assumed to come at negligible cost within the model.

We develop three models. In the first, the allocator is assigned control of reproduction and eviction (matching the assumptions of the concession models). In the second, the allocator is assigned control of reproduction but the partner is assigned control of eviction (matching the assumptions of the restraint model). Note that absolute control of eviction found in these concession and restraint type models represents a special case where the probability of winning a contest over eviction (c) is equal to 1 for the evictor, because the other individual uses a voluntary departure tactic. In the third model, the allocator is assigned control of reproduction but both individuals adopt a forcible eviction tactic. Note that this new model is the only one that is internally consistent, because both individuals act as if their reproductive output if they were to stay alone (S) were greater than their reproductive output if they were to leave (L) (inequality (2)). We present a summary of the assumptions of the concession, restraint, and new models in Table 1.

The partner will require a share of the group's reproductive output to prevent it from dissolving the group, either by voluntarily departing or by forcibly evicting. We call the partner's required share either the staying incentive (p_{b1}) when the partner's group dissolution tactic is to voluntarily depart (equivalent to the subordinate's share in the concession models), or the toleration incentive (p_{b2}) when the partner's group dissolution tactic is to forcibly evict the allocator (equivalent to the dominant's share in the restraint model). When both the partner and the allocator adopt a forcible eviction tactic, the partner's required share will be a new type of toleration incentive (p_{b3}).

What incentive will the partner require to prevent it from dissolving the group?

Model (1). The partner may require a share of the group's reproductive output to prevent it from voluntarily departing: a staying incentive. By applying inequality (1) and the above variables to the partner's decision to stay or depart, we find that the inclusive fitness of a partner that stays will be greater than the inclusive fitness of a partner that departs when

$$p_{b1}G - L + r[(1 - p_{b1})G - S] > 0$$

which yields the staying incentive

$$p_{b1} = \frac{(L - r(G - S))}{(G(1 - r))} \qquad (3)$$

Equation (3) is equivalent to the share of the group's reproduction required by the subordinate, to prevent it from voluntarily departing, in the concession model (Reeve & Ratnieks 1993).

Model (2). The partner may require a share of the group's reproductive output to prevent it from forcibly evicting the allocator: a toleration incentive. By applying inequality (1) and the above variables to the partner's decision to tolerate or evict, we find that the inclusive fitness of a partner that tolerates will be greater than the inclusive fitness of a partner that evicts when

$$p_{b2}G - S + r[(1 - p_{b2})G - L] > 0$$

which yields the toleration incentive

$$p_{b2} = \frac{(S - r(G - L))}{(G(1 - r))} \quad (4)$$

Equation (4) is equivalent to the share of the group's reproduction required by the dominant, to prevent it from forcibly evicting, in the restraint model (Johnstone & Cant 1999).

Model (3). Alternatively, when the payoff to staying (S) is greater than the payoff to leaving (L) for both individuals (inequality (2)), the partner may require a slightly different share of the group's reproductive output to prevent it from forcibly evicting the allocator, a type 3, toleration, incentive. By applying inequality (1) and the above variables to the partner's decision to tolerate or evict in this situation, we find that the inclusive fitness of a partner that tolerates will be greater than the inclusive fitness of a partner that evicts when

$$p_{b3}G - [(c)S + (1 - c)L] + r\{[(1 - p_{b3})G]$$
$$- [(1 - c)S + (c)L]\} > 0$$

which yields the type 3, toleration, incentive

$$p_{b3} = \frac{\{(c)S + (1 - c)L - r[G - (c)L - (1 - c)S]\}}{(G(1 - r))} \quad (5)$$

Equation (5) represents a completely new type of incentive required by the partner, to prevent it from forcibly evicting when the allocator also uses a forcible eviction tactic. This contrasts to the share of the group's reproduction required by the subordinate, to prevent it from entering into a fatal fight for dominance, in the concession model (peace incentive; Reeve & Ratnieks 1993), because when determining the peace incentive it is assumed that the loser of the fight dies whereas here it is assumed that the loser of the contest ends up outside the group.

Results

Focusing on the classical staying (p_{b1}) and toleration (p_{b2}) incentives, inspection of equations (3) and (4) reveals that both of these incentives increase (1) as relatedness (r) decreases, (2) as the group's reproductive output (G) decreases, (3) as the reproductive output from leaving (L) increases, and (4) as the reproductive output from staying alone (S) increases (Table 2). There are, however, slight differences between the incentives (Table 2). The staying incentive is strongly dependent on the reproductive output from leaving (L) and weakly dependent on the reproductive output from staying (S), whereas the toleration incentive is strongly dependent on the reproductive output from staying (S) and weakly dependent on the reproductive output from leaving (L). For each incentive, the effect of the second variable is weak because it is discounted by relatedness (r).

Turning to the type 3, toleration, incentive (p_{b3}), at first glance equation (5) appears complex, but closer inspection reveals that it is made up of components from the classical staying (p_{b1}) and toleration (p_{b2}) incentives (see

Table 2. Summary of the predicted relationships between partner's required share of the reproduction and the variables of the model, for all three models presented here

Variable	Model (1): partner's staying incentive* (p_{b1})	Model (2): partner's toleration incentive† (p_{b2})	Model (3): partner's type 3 toleration incentive (p_{b3})
r	Negative	Negative	Negative
G	Negative	Negative	Negative
L	Positive (strong)‡	Positive (weak)‡	Positive (strong or weak)§
S	Positive (weak)‡	Positive (strong)‡	Positive (strong or weak)§
c**	None	None	Positive

Allocator's realized share of the reproduction shows opposite relationship, but allocator's required share shows same relationship.
*Staying incentive ≈ subordinate's required share of reproduction in concession models.
†Toleration incentive ≈ dominant's required share of reproduction in restraint model.
‡Effect is relatively weak because it is discounted by the degree of relatedness (r, see equations (3) and (4)).
§Effect is strong or weak depending on probability of partner winning a contest over eviction (c, see equation (5)).
**Model (1) assumes probability of partner winning a contest over eviction (c) = 0. Model (2) assumes (c) = 1. Model (3) allows (c) to vary.

equations (3) and (4))

$$p_{b3} = \frac{\{(c)S + (1 - c)L - r[G - (c)L - (1 - c)S]\}}{(G(1 - r))} \quad (5)$$

$$p_{b3} = (1 - c)p_{b1} + (c)p_{b2}$$

This indicates that this incentive, like the others, will increase (1) as relatedness (r) decreases, (2) as the group's reproductive output (G) decreases, (3) as the reproductive output from leaving (L) increases, and (4) as the reproductive output from staying alone (S) increases (Table 2). Whether the reproductive output from leaving (L) or the reproductive output from staying (S) has a strong or weak effect will depend on the probability of the partner winning a contest over eviction (c). The effect of c on the incentive will depend on the relative value of S and L; if $S > L$ then as c increases the incentive will increase, but if $L > S$ then as c increases the incentive will decrease. Here, because both individuals are using a forcible eviction tactic we know that $S > L$ (inequality (2)), thus we know that the incentive increases as c increases. The intuitive explanation for this incentive is that with probability c the partner will win the contest over eviction and stay inside the group, so it weights the toleration incentive (p_{b2}) with probability c, but with probability $1 - c$ the partner will lose the contest over eviction and ends up outside of the group, so it weights the staying incentive (p_{b1}) with probability $1 - c$.

Most importantly, although the quantitative relationships between the partner's required reproductive share and the key parameters may vary depending on the group dissolution tactic that each individual uses, the qualitative relationships between the partner's required reproductive

share and the key parameters are the same regardless of whether the share reflects a staying incentive, a toleration incentive, or the new type 3 incentive (Table 2). The simplest explanation for the magnitude of the incentives is that the partner must receive an amount equivalent to its payoff from voluntarily departing or forcibly evicting, otherwise it will be favoured to dissolve the group.

In summary, we highlighted that the role that the subordinate played in the restraint model was the same as the role the dominant played in the concession model: they both had complete control over the allocation of reproduction. To simplify things, we functionally defined the individual with complete control over the allocation of reproduction as the allocator. The allocator claims one reproductive share and yields the remainder, or, to put it another way, whenever the allocator yields a concession it also shows restraint. This simplification eliminates two apparent differences in the assumptions of the models (assumptions a and b). We show that, once these semantic differences are resolved, the qualitative predictions of the concession, the restraint, and the type 3 models are the same.

CONDITIONS FOR GROUP STABILITY

Previous transactional models explicitly assumed that the partner could dissolve the group, either by forcible eviction or by voluntary departure, and implicitly assumed that the allocator could dissolve the group by withdrawing the staying or toleration incentive (Table 1). The models we are developing here are logically more complete: both the allocator and the partner can dissolve the group by voluntary departure or by forcible eviction (Table 1, inequality (2)). This means that the allocator also will require a share of the group's reproductive output to prevent it from dissolving the group (p_{a1}, p_{a2}, or p_{a3}). This has the potential to change the model predictions regarding group stability. We show, however, that the condition for group stability is robust, regardless of the group dissolution tactics that individuals use.

Model

When will the allocator gain by yielding the partner's incentive rather than having the group dissolve?

Model (1). First, by applying Hamilton's rule (inequality (1)) and the above variables to the allocator's decision of whether to yield the staying incentive or have the partner voluntarily depart, we find that the inclusive fitness of an allocator that yields the staying incentive will be greater than the inclusive fitness of an allocator that does not yield the incentive when

$$(1 - p_{b1})G - S + r(p_{b1}(G) - L) > 0$$

substituting the staying incentive (equation (3)) yields a condition under which the allocator will provide that incentive

$$G > L + S. \tag{6}$$

Inequality (6) is equivalent to the condition under which the dominant will yield the subordinate's required share in the concession model (Reeve & Ratnieks 1993). Importantly, the same inequality is derived when we consider whether the allocator will yield the staying incentive or forcibly evict its partner (Reeve & Keller 1995, 1997; Reeve 2000). The allocator is favoured to yield the partner's staying incentive up until the point that the allocator cannot meet its own required share, that is, up until the point that the two required shares sum up to one ($p_{a2} + p_{b1} = 1$).

Model (2). Next, by applying Hamilton's rule (inequality (1)) and the above variables to the allocator's decision of whether to yield the toleration incentive or to have the partner forcibly evict, we find that the inclusive fitness of an allocator that yields the toleration incentive will be greater than the inclusive fitness of an allocator that does not yield the incentive when

$$(1 - p_{b2})G - L + r(p_{b2}(G) - S) > 0$$

substituting the toleration incentive (inequality (4)) yields a condition under which the allocator will provide that incentive

$$G > L + S. \tag{7}$$

Inequality (7) is equivalent to the condition under which the subordinate will yield the dominant's required share in the restraint model (Johnstone & Cant 1999). Importantly, the same inequality is derived when we consider whether the allocator will yield the toleration incentive or voluntarily depart itself. The allocator is favoured to yield the partner's toleration incentive up until the point that the allocator cannot meet its own required share, that is, up until the point that the two required shares sum up to one ($p_{a1} + p_{b2} = 1$).

Model (3). Finally, by applying Hamilton's rule (inequality (1)) and the above variables to the allocator's decision of whether to yield the type 3, toleration, incentive or have the partner forcibly evict, we find that the inclusive fitness of an allocator that yields the type 3 incentive will be greater than the inclusive fitness of an allocator that does not yield the incentive when

$$[(1 - p_{b3})G] - [(c)L + (1 - c)S] + r\{[p_{b3}(G)] - [(1 - c)L + (c)S]\} > 0$$

substituting the type 3 incentive (equation (5)) yields a condition under which the allocator will provide that incentive

$$G > L + S. \tag{8}$$

Remarkably, this is the same condition under which the allocator will yield the classical staying and toleration incentives (inequalities (6) and (7)). Importantly, the same inequality is derived when we consider whether the allocator will yield the type 3, toleration, incentive or forcibly

evict its partner. The allocator is favoured to yield the partner's type 3, toleration, incentive up until the point that the allocator cannot meet its own required share, that is, up until the point that the two required shares sum up to one ($p_{a3} + p_{b3} = 1$).

Results

Focusing on the conditions for group stability, inspection of inequalities (6)–(8) reveals that the allocator will be less likely to let the partner dissolve the group (1) as the group's reproductive output (G) increases, (2) as the reproductive output from leaving (L) decreases, and (3) as the reproductive output from staying alone (S) decreases (Table 3). Furthermore, the allocator will be less likely to dissolve the group itself under these same conditions (Table 3). Remarkably, the conditions for group stability are the same regardless of the group dissolution tactics that the individuals use.

The simplest explanation for group stability is that the allocator will only be favoured to yield the partner's incentive if the allocator retains an amount greater than its payoff associated with group dissolution. Thus, the group is expected to be stable only as long as the required shares of both individuals can simultaneously be met, that is when $p_a + p_b < 1$. It is more likely that the required shares of both individuals can be met when those required shares are small, and this explains why group stability and the magnitude of the incentives are oppositely related to the parameters of the model.

Although the conditions for group stability are the same regardless of the group dissolution tactics that individuals use, it is likely that the process of group dissolution will look different in each case. In models (1) and (2) it is likely that group dissolution will be relatively rapid and involve relatively little conflict, because when it pays one individual to forcibly evict, it pays the other to voluntarily depart. In contrast, in model (3) it is likely that group dissolution will be a more drawn out process and involve relatively more conflict, because the individuals will be attempting to evict each other.

DISCUSSION

Justification for the Approach Presented Here

It has been suggested that skew theory might represent a unified theory of social evolution (sensu Wilson 1975; Keller & Reeve 1994; Sherman et al. 1995; Emlen 1997; Johnstone 2000). As expected for any theory that makes such claims, its models have come under intense scrutiny and constructive criticism (Clutton-Brock 1998; Johnstone 2000; Magrath & Heinsohn 2000; Kokko 2003). The most serious criticism is that the bewildering array of assumptions and predictions render the theory untestable (unfalsifiable). Here we have began to address this criticism, by clarifying the assumptions and predictions of basic transactional models of reproductive skew. We reduced the six different assumptions of concession and restraint models to two common assumptions and one prediction: (a) one individual, the allocator, controls the allocation of reproduction, and (b) it claims one share and yields the other to (c) prevent group dissolution by a tactic that can be predicted by Hamilton's rule and the standard variables of reproductive skew.

The basic transactional framework now makes three sets of testable predictions. First, an individual will adopt a forcible eviction tactic if the individual's expected reproductive output if it stays (S) is greater than its expected reproductive output if it leaves (L), but it will adopt a voluntary departure tactic if L is greater than S (inequality (2)). Second, the allocator's share of the reproduction increases as the coefficient of relatedness between the two individuals (r) increases, as the group's expected reproductive output if the individuals remain together (G) increases, as L decreases, and as S decreases (equations (3)–(5)). Third, groups will be stable as long as G is greater than the sum of L and S (inequalities (6)–(8)). It is worth emphasizing, once more, that we showed that the predictions of concession and restraint type models are qualitatively the same, rather than opposite as originally supposed.

How do the results of our models compare or contrast with the synthetic model of Johnstone (2000)? Johnstone (2000) presented a window of group stability (range of reproductive sharing over which groups remain stable) that

Table 3. Summary of the predicted relationships between group stability, the variables of the model, and the process of group dissolution, for all the three models presented here

Variable	Model (1): group stability, when partner requires staying incentive*	Model (2): group stability, when partner requires toleration incentive†	Model (3): group stability, when partner requires type 3 incentive‡
r	None	None	None
G	Positive	Positive	Positive
L	Negative	Negative	Negative
S	Negative	Negative	Negative
c	None	None	None
Process of group dissolution	Allocator forcibly evicts or partner voluntarily departs	Allocator voluntarily departs or partner forcibly evicts	Both individuals attempt to forcibly evict

*Group stability when partner requires staying incentive and allocator can forcibly evict ≈ condition for stability in concession models.
†Group stability when partner requires toleration incentive and allocator can voluntarily depart ≈ condition for stability in restraint model.
‡Group stability when partner requires new type 3, toleration, incentive and allocator can also forcibly evict.

had a lower bound defined by the subordinate's required share of reproduction before it would voluntarily depart (equation (3)), and an upper bound defined by the dominant's required share of reproduction before it would forcibly evict (equation (4)). Using the allocator/partner terminology, rather than the dominant/subordinate terminology, Johnstone's upper and lower bounds on group stability become two lower bounds on group stability: a lower bound defined by the partner's required share of the reproduction before it will voluntarily depart (p_{b1}; equation (3)), and another lower bound defined by the partner's required share of the reproduction before it will forcibly evict (p_{b2}; equation (4)). We also reveal another lower bound on group stability defined by the partner's required share of the reproduction before it will forcibly evict when the allocator adopts a forcible eviction tactic (p_{b3}; equation (5)); which lower bound on group stability is relevant in any given group will depend on which group dissolution tactic that each individual adopts (inequality (2)). What has happened to the upper bounds on group stability? These are still present in our models as the allocator's required share (p_{a1}, p_{a2}, p_{a3}; conditions for group stability) but we clarify that, because the allocator has complete control over the allocation of reproduction, these shares are almost never met. Indeed the only time that the allocator obtains its minimum required share of the reproduction is at the point of group dissolution (inequalities (6)−(8) and associated text).

The refinements of the basic transactional framework presented here make for a more general and consistent transactional framework of reproductive skew. This, in turn, should make the framework more amenable to testing in the field. This brings us to our next topic, which is a consideration of how we think the assumptions and predictions of skew theory could be tested in the field. Our aim here is to start debate, because this is a topic that we believe needs to be discussed more widely and openly.

Testing the Assumptions Regarding Variables of the Model

Reproductive skew models assume that a small, well defined, set of variables influence the behaviour of individuals. Previous models have used the variables K, x, and l but we prefer to use the variables G, L, and S (see also Zink & Reeve 2005). There are several reasons for this switch. First, it is easier to grasp that G is the group's expected reproductive output, L is the leaver's expected reproductive output, and S is the stayer's reproductive output. Second, G, L, and S, can be measured simply, in terms of absolute numbers of offspring expected, rather than having to be standardized relative to a value of 1.0 (the dominant's standardized expected reproductive output if it stays alone). Most importantly, the standardization has been causing problems because it has led some to infer that the dominant's expected reproductive output could be set to the same value in all groups within a population. Yet, as suggested by Reeve & Ratnieks (1993) and emphasized by Kokko (2003), organisms are expected to respond in behavioural time to local variation in the parameters,

otherwise skew models are not evolutionarily stable. Note that an inability of the individuals to obtain accurate information on one of the variables does not necessarily make the entire model unstable, rather the individuals should just ignore this variable. For example, in model (1), if individuals were unable to accurately assess r (the coefficient of relatedness), then the group dissolution tactics and the conditions for group stability would remain unchanged (inequalities (2) and (6)), but the staying incentive would become a function of G, and L alone (equation (3)). By avoiding the standardization and emphasizing that we must understand and measure r, G, L, S, and c (probability of winning a contest) at the spatial and temporal scale that the organisms themselves measure the variables we hope to lay the foundation for more rigorous tests of skew.

The big questions, then, for rigorous tests of skew, are whether the organisms are measuring and responding to changes in the parameters in behavioural time and whether we can understand and measure the parameters at the same temporal and spatial scale as the organisms themselves. Rather than conducting an entire literature review on this topic, we focus on insights that can be gleaned from a group that has been relatively understudied: fish (for consideration of other taxa see Reeve & Keller 2001 and Magrath et al. 2004). In social cichlids (*Neolamprologus pulcher*, Heg et al. 2004a), damselfish (*Dascyllus aruanus*, Coates 1980; Forrester 1990; *Amphiprion percula*, Buston 2003b, Buston & Cant 2006), and gobies (*Gobiodon histrio*, Munday et al. 2006; *Paragobiodon xanthosomus*, Wong et al. 2007) individuals are able to regulate their size in response to the size of other group members and, because size is related to reproductive output in fish, this suggests that they will be able to regulate their reproductive shares (p) too. In the bluegill sunfish, *Lepomis macrochirus*, males adjust their behaviour in response to variation in their share of reproduction (Neff & Gross 2001). In the cooperative cichlid, *N. pulcher*, individuals adjust their behaviour in response to variation in the relatedness of group members (r, Stiver et al. 2005). Also, in *N. pulcher*, although reproductive shares were not adjusted in response to one component of L, the leaver's expected reproductive output (availability of breeding substrate, Heg et al. 2006), dispersal behaviour was adjusted in response to two other components of L (availability of breeding vacancies, Balshine-Earn et al. 1998; level of predation risk, Heg et al. 2004b). Similarly, group living damselfish, *D. aruanus* and *Amphiprion clarkii*, adjust dispersal behaviour in response to availability of breeding vacancies on their reefs (Coates 1982; Ochi 1989; Hattori 1994). In fish, the relative probability of winning a contest (c) is related to relative body size (Rowland 1989; Wong et al. 2007), and in social cichlids, damselfish and gobies, individuals adjust their behaviour in response to variation in the relative body size of group members (Buston 2003b; Heg et al. 2004a; Buston & Cant 2006; Wong et al. 2007). What this brief survey shows is that organisms do respond to local variation in the parameters in behavioural time and that the variation is measurable by the investigator, which means that rigorous tests of skew models are possible.

Testing the Predictions Relating Model Variables and Group Dissolution Tactics

Previous transactional models have assumed that only one individual could dissolve the group, and that it could use only one tactic (voluntary departure or forcible eviction). We highlighted that both individuals can dissolve the group, and we have shown that the group dissolution tactic adopted by each individual can be predicted using Hamilton's rule and the standard variables of reproductive skew models. Specifically, the group dissolution tactic each individual adopts is predicted by the relative value of the payoff expected from leaving to breed elsewhere (L) and the payoff expected from staying alone (S). By converting the restrictive assumption, that individuals have a fixed group dissolution tactic (assumption c), into a prediction, based on Hamilton's rule and standard variables (inequality (2)), we increased the generality of the transactional framework.

How might this prediction, that individuals will adopt a forcible eviction tactic when S is greater than L but a voluntary departure tactic when L is greater than S, be tested? Focusing on our understudied taxa once again, consistent with the prediction, individual clown anemonefish, *A. percula*, which live in a context where level of predation outside territories is always high and L is always low, consistently use a forcible eviction tactic (Buston 2003a). Furthermore, both dominant and subordinate *A. percula* use a forcible eviction tactic even though the chances of a subordinate successfully winning a contest over eviction are close to zero. In the coral goby, *P. xanthosomus*, although individuals generally adopt a forcible eviction tactic (Wong et al. 2007) they might switch to a voluntary departure tactic when suitable breeding habitat is moved sufficiently close, thereby increasing L (M. Wong, P. Munday & G. Jones, unpublished data). Similarly, in the cooperative cichlid, *N. pulcher*, it has been suggested that individuals are more likely to voluntarily depart when breeding vacancies are created or the risk of predation is lowered, thereby increasing L (Balshine-Earn et al. 1998; Heg et al. 2004b). Although these observations and experiments were not designed to test this prediction concerning the group dissolution tactic that individuals will adopt, they show that the prediction is eminently testable.

Testing the Assumption Regarding the Existence and Identity of the Allocator

Previous transactional models have assumed either that the dominant has complete control over the allocation of reproduction but it yields a share of the reproduction to prevent the subordinate from dissolving the group, or that the subordinate has complete control over the allocation of reproduction but it may not claim all of the reproduction to prevent the dominant from dissolving the group. We revealed that the subordinate in the restraint model has the same function as the dominant in the concession model. We resolve this semantic difference by calling the individual with complete control over the allocation of reproduction the 'allocator', noting that this individual claims one share of the reproduction and yields the remainder. This means that we can remove the ambiguous assumptions (a) regarding whether the dominant or subordinate has control and (b) regarding whether that individual is claiming or yielding (i.e. showing restraint or providing a concession), from reproductive skew models, simplifying them greatly.

The key for testing transactional models will be determining whether there is an allocator and which individual is the allocator (Beekman et al. 2003). How might the existence and identity of the allocator be determined? We envisage three complementary ways to determine the identity of the allocator. First, there is a simple rule of thumb: in general, the allocator will obtain the greater share of the reproduction. This rule of thumb is, however, not foolproof. A better approach would be to conduct an appropriately controlled experimental manipulation of reproductive shares or parameters predicted to influence reproductive shares.

Second, following an experimental increase of the group's expected reproductive output, we predict that the absolute amount of reproduction by the allocator will increase but the absolute amount of reproduction by the partner will not increase (i.e. the allocator's share will increase). This is predicted because, the allocator only yields an amount of reproduction sufficient to prevent the partner from dissolving the group, and although the absolute amount that must be yielded is affected by variation in the payoff associated with leaving (L) and the payoff associated with staying (S), the absolute amount is unaffected by variation in group's expected reproductive output (G).

Third, following an experimental manipulation of actual (or perceived) reproductive shares and focusing on the response of the allocator, we predict that if the allocator's share has been raised, it will attempt to yield reproduction to its partner, but if the partner's share has been raised, then the allocator will attempt to claim reproduction from its partner. This is predicted because, prior to the manipulation the allocator is expected to be yielding precisely the amount needed to prevent the partner from dissolving the group, and after the manipulation the allocator is expected to readjust shares such that the partner once again has its minimum share required to prevent group dissolution.

Now, considering the same experimental manipulation of reproductive shares but focusing on the response of the partner, we predict that if the allocator's share has been raised, the partner will dissolve the group or signal its intent to dissolve the group, but if the partner's share has been raised, then it will do nothing. The precise response of the partner, and the allocator, will depend on the magnitude of the experimental manipulation of reproductive shares relative to the sharpness of the group dissolution threshold and the width of the window of group stability (Kokko 2003; Buston & Cant 2006; Cant 2006; Wong et al. 2007).

Testing the Predictions Relating Model Variables and Reproductive Shares

The previous concession and restraint models made qualitatively different predictions about the relationship between key parameters of the model and the subordinate's share of the reproduction. This difference occurred because control of reproduction lay with the dominant in the concession models but with the subordinate in the restraint model. We show that when this semantic difference is resolved, by calling the individual with control over reproduction the allocator, then the predictions about the relationship between key parameters of the model and the partner's share of the reproduction are qualitatively the same regardless of whether the partner requires a staying incentive (concession type model) or a toleration incentive (restraint type model). In spite of this simplification, the predictions regarding the relationship between model variables and reproductive shares will be the most demanding to test because they are dependent on four or five parameters and involve subtle quantitative shifts in levels of reproduction rather than obvious qualitative shifts in behaviour. The key to testing these predictions lies in understanding the factors that influence the parameters themselves, and conducting appropriately controlled observational or experimental tests. To illustrate the challenges involved in effectively testing these predictions we focus on one recent study, which may have drawn somewhat premature conclusions.

Heg et al. (2006) used an experimental approach to investigate reproductive partitioning in the cooperative cichlid, *N. pulcher*. In the aquarium, they found no effect of manipulating the payoff associated with leaving to breed elsewhere (*L*), by providing additional breeding substrate, on the subordinate's reproductive share, and suggested that tug-of-war models may best describe reproductive skew in these societies. This may well turn out to be the case, but it's worth considering how the result was achieved. Heg et al. (2006) manipulated one component of *L*, the availability of breeding substrate, without knowing the extent to which *L* is influenced by that component. Indeed, it is likely that *L* is influenced primarily by the level of predation, which has been shown to influence subordinate dispersal (Heg et al. 2004b), and only secondarily by the availability of breeding substrate. If this was the case, then it might not be surprising that the subordinate's share was unrelated to the manipulation, because the level of predation was zero in both experimental and control treatments (Heg et al. 2006). A criticism of skew theory has been that the parameters in the models subsume too many social and ecological factors (see Kokko 2003). While this is not a fair criticism of the models, since the aim of a model is to simplify reality and make it understandable (Maynard Smith 1982), it does put an onus on empiricists to understand the factors that influence the parameters to conduct an effective test.

Testing the Predictions Relating Model Variables and Group Stability

Previous transactional models have predicted that group stability will depend on the relative value of the payoff associated with breeding as a group and the sum of the payoffs associated with leaving to breed elsewhere and staying alone. Here, we showed that this condition for group stability is robust, regardless of the group dissolution tactics that individuals use and in spite of the fact that both individuals are now able to dissolve the group. Indeed, we explain why this is the case: the group is expected to be stable only as long as the required shares of both individuals can simultaneously be met. Although the condition under which a group dissolves is generally robust, the process of group dissolution is expected to depend on the group dissolution tactics that each individual uses.

Can these predictions be tested? Observations and experiments similar to those used to identify group dissolution tactics could be used to determine the conditions under which groups dissolve and the process of group dissolution. In fish, consistent with the predictions, groups dissolve as the payoff associated with leaving to breed elsewhere (*L*) is increased in the anemonefish, *A. clarkii* (Ochi 1989; Hattori 1994), the cooperative cichlid, *N. pulcher* (Balshine-Earn et al. 1998; Heg et al. 2004b), the coral goby, *P. xanthosomus* (Wong et al., unpublished data), and the humbug damselfish *D. aruanus* (Coates 1982). The process of group dissolution in these cases seems to be relatively rapid and involves relatively little conflict, probably because one individual switches to a voluntary departure tactic when breeding vacancies become available. In contrast, the process of group dissolution in the clown anemonefish, *A. percula* (Buston 2003a) and the coral goby, *P. xanthosomus* (Wong et al. 2007), when breeding vacancies are not available locally, seems to be relatively long and drawn out, probably because both individuals are using a forcible eviction tactic since leaving the territory is generally dangerous. Although these observations are consistent with the predictions, rigorous tests will require experiments in which *G*, *L* and *S* are more precisely quantified and the process of group dissolution is more closely observed.

Future Extensions of the Theory

The clarification and extension of basic transactional models, presented here, lay the foundation for future clarifications and extensions of reproductive skew theory. The most pressing need is the clarification of the relationship between transactional and tug-of-war models, because these are commonly tested as alternatives (Clutton-Brock et al. 2001; Langer et al. 2004; Bradley et al. 2005; Heg et al. 2006). The problem with testing current transactional and tug-of-war models as alternatives is that there are too many differences in their assumptions for them to be usefully compared. Transactional models assume that (a) one individual has complete control over the allocation of reproduction, and (b) individuals engage in a cost-free negotiation over reproductive shares (c) to retain the benefits of a stable group (this study). Tug-of-war models assume that (a) no individual has complete control over the allocation of reproduction, and (b) individuals engage in a costly competition for reproductive shares (c) without regard for group stability (Reeve et al.

1998). Simply, because three assumptions (a–c) differ between the two classes of models it is unclear which of these assumptions causes the difference in the predictions: it is as if we conducted an experiment and manipulated three things at once.

How can these differences between transactional and tug-of-war models be resolved so that they can be usefully compared and tested as alternatives? First, it will be useful to develop a transactional model in which no individual has complete control over the allocation of reproduction, eliminating the difference in assumption (a) (P. M. Buston & A. G. Zink, unpublished data). Second, it will be useful to develop a tug-of-war model in which individuals pay attention to group stability, eliminating the difference in assumption (c) (Johnstone 2000; Reeve & Shen 2006). Finally, comparison of these new transactional and tug-of-war models will shed light on the conditions under which individuals are predicted to engage in costly competition rather than cost free negotiation for reproductive shares, eliminating assumption (b) (P. M. Buston & A. G. Zink, unpublished data). This process of making the models more general, by eliminating some restrictive assumptions and converting other assumptions into predictions, in conjunction with rigorous field tests should move us further towards a unified theory of social evolution (Wilson 1975; Keller & Reeve 1994; Sherman et al. 1995; Emlen 1997; Johnstone 2000).

Acknowledgments

References

Balshine-Earn, S., Neat, F. C., Reid, H. & Taborsky, M. 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behavioral Ecology*, **9**, 432–438.

Beekman, M., Komdeur, J. & Ratnieks, F. L. W. 2003. Reproductive conflicts in social animals: who has power? *Trends in Ecology & Evolution*, **18**, 277–282.

Bradley, B. J., Robbins, M. M., Williamson, E. A., Steklis, H. D., Steklis, N. G., Eckhardt, N., Boesch, C. & Vigilant, L. 2005. Mountain gorilla tug-of-war: silverbacks have limited control over reproduction in multimale groups. *Proceedings of the National Academy of Sciences, U.S.A.* **102**, 9418–9423.

Buston, P. M. 2002. Group structure of the clown anemonefish *Amphiprion percula*. Ph.D. thesis, Cornell University.

Buston, P. M. 2003a. Forcible eviction and prevention of recruitment in the clownfish. *Behavioral Ecology*, **14**, 576–582.

Buston, P. M. 2003b. Size and growth modification in clownfish. *Nature*, **424**, 145–146.

Buston, P. M. & Cant, M. A. 2006. A new perspective on size hierarchies in nature: patterns causes and consequences. *Oecologia*, **149**, 362–372.

Cant, M. A. 2006. A tale of two theories: parent–offspring conflict and reproductive skew. *Animal Behaviour*, **71**, 255–263.

Clutton-Brock, T. H. 1998. Reproductive skew, concessions, and limited control. *Trends in Ecology & Evolution*, **7**, 288–292.

Clutton-Brock, T. H., Brotherton, P. N. M., Smith, R., McIlrath, G. M., Kansky, R., Gaynor, D., O'Riain, M. J. & Skinner, J. D. 1998. Infanticide and expulsion of females in a cooperative mammal. *Proceedings of the Royal Society of London, Series B*, **265**, 2291–2295.

Clutton-Brock, T. H., Brotherton, P. N. M., Russell, A. F., O'Riain, M. J., Gaynor, D., Kansky, R., Griffin, A., Manser, M., Sharpe, L., McIlrath, G. M., Small, T., Moss, A. & Monfort, S. 2001. Cooperation, control, and concession in meerkat groups. *Science*, **291**, 478–481.

Coates, D. 1980. Prey-size intake in humbug damselfish, *Dascyllus aruanus* (Pisces, Pomacentridae) living with social groups. *Journal of Animal Ecology*, **49**, 335–340.

Coates, D. 1982. Some observations on the sexuality of the humbug damselfish *Dascyllus aruanus* (Pisces, Pomacentridae) in the field. *Zeitschrift für Tierpsychologie*, **59**, 7–18.

Crespi, B. J. & Ragsdale, J. E. 2000. A skew model for the evolution of sociality via manipulation: why it is better to be feared than loved. *Proceedings of the Royal Society of London, Series B*, **267**, 821–828.

Danchin, E. & Wagner, R. H. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution*, **12**, 342–347.

Emlen, S. T. 1982. The evolution of helping. II. The role of behavioral conflict. *American Naturalist*, **119**, 40–53.

Emlen, S. T. 1997. Predicting family dynamics in social vertebrates. In: *Behavioural Ecology: an Evolutionary Approach*. 4th edn (Ed. by J. R. Krebs & N. B. Davies), pp. 228–253. Oxford: Blackwell Scientific.

Forrester, G. E. 1990. Factors influencing the juvenile demography of a coral reef fish. *Ecology*, **71**, 1666–1681.

Hamilton, W. D. 1964. The genetical evolution of social behavior I and II. *Journal of Theoretical Biology*, **7**, 1–52.

Hamilton, I. M. 2000. Recruiters and joiners: using optimal skew theory to predict group size and the division of resources within groups of social foragers. *American Naturalist*, **155**, 684–695.

Hattori, A. 1994. Inter-group movement and mate acquisition tactics of the protandrous anemonefish *Amphiprion clarkii* on a coral reef, Okinawa. *Japanese Journal of Ichthyology*, **41**, 159–165.

Haydock, J. & Koenig, W. D. 2003. Patterns of reproductive skew in the polygynandrous acorn woodpecker. *American Naturalist*, **162**, 277–289.

Heg, D., Bender, N. & Hamilton, I. 2004a. Strategic growth decisions in helper cichlids. *Proceedings of the Royal Society of London, Series B*, **Supplement**, **271**, S505–S508.

Heg, D., Bachar, Z., Brouwer, L. & Taborsky, M. 2004b. Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proceedings of the Royal Society of London, Series B*, **271**, 2367–2374.

Heg, D., Bergmuller, R., Bonfils, D., Otti, O., Bachar, Z., Burri, R., Heckel, G. & Taborsky, M. 2006. Cichlids do not adjust reproductive skew to the availability of independent breeding options. *Behavioral Ecology*, **17**, 419–429.

Jeon, J. & Choe, J. C. 2003. Reproductive skew and the origin of sterile castes. *American Naturalist*, **161**, 206–224.

Johnstone, R. A. 2000. Models of reproductive skew: a review and synthesis. *Ethology*, **106**, 5–26.

Johnstone, R. A. & Cant, M. A. 1999. Reproductive skew and the threat of eviction: a new perspective. *Proceedings of the Royal Society of London, Series B*, **266**, 275–279.

Keller, L. & Reeve, H. K. 1994. Partitioning of reproduction in animal societies. *Trends in Ecology & Evolution*, **12**, 99–103.

Kokko, H. 2003. Are reproductive skew models evolutionarily stable? *Proceedings of the Royal Society London, Series B*, **270**, 265–270.

Kokko, H. & Johnstone, R. A. 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proceedings of the Royal Society of London, Series B*, **266**, 571–578.

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., Johnstone, R. A. & Heinsohn, R. G. 2004. Reproductive skew. In: *Ecology and Evolution of Cooperative Breeding in Birds* (Ed. by W. D. Koenig & J. L. Dickinson), pp. 157–176. Cambridge: Cambridge University Press.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Maynard Smith, J. & Szathmary, E. 1995. *The Major Transitions in Evolution*. Oxford: W.H. Freeman.

Munday, P. L., Cardoni, A. M. & Syms, C. 2006. Cooperative growth regulation in coral-dwelling fishes. *Biology Letters*, **2**, 355–358.

Muñoz, R. C. & Warner, R. R. 2003. A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. *American Naturalist*, **161**, 749–761.

Neff, B. D. & Gross, M. R. 2001. Dynamic adjustment of parental care in response to perceived paternity. *Proceedings of the Royal Society of London, Series B*, **268**, 1559–1565.

Ochi, H. 1989. Acquisition of breeding space by non-breeders in the anemonefish *Amphiprion clarkii* in temperate waters of southern Japan. *Ethology*, **83**, 279–294.

Ragsdale, J. E. 1999. Reproductive skew theory extended: the effect of resource inheritance on social organization. *Evolutionary Ecology Research*, **1**, 859–874.

Reeve, H. K. 2000. A transactional theory of within-group conflict. *American Naturalist*, **155**, 365–382.

Reeve, H. K. & Emlen, S. T. 2000. Reproductive skew and group size: an *N*-person staying incentive model. *Behavioral Ecology*, **11**, 640–647.

Reeve, H. K. & Keller, L. 1995. Partitioning of reproduction in mother–daughter versus sibling associations: a test of optimal skew theory. *American Naturalist*, **145**, 119–132.

Reeve, H. K. & Keller, L. 1997. Reproductive bribing and policing as evolutionary mechanisms for the suppression of within group selfishness. *American Naturalist*, **150**, S42–S58.

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. by L. Keller), pp. 45–85. Oxford: Oxford University Press.

Reeve, H. K. & Shen, S. 2006. A missing model in reproductive skew theory: the bordered tug-of-war. *Proceedings of the National Academy of Sciences, U.S.A.*, **103**, 8430–8434.

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.

Rowland, W. J. 1989. The effects of body size, aggression, and nuptial coloration on competition for territories in male threespine sticklebacks, *Gasterosteus aculeatus*. *Animal Behavior*, **37**, 282–289.

Sherman, P. W., Lacey, E. A., Reeve, H. K. & Keller, L. 1995. The eusociality continuum. *Behavioral Ecology*, **6**, 102–108.

Stacey, P. B. 1982. Female promiscuity and male reproductive success in social birds and mammals. *American Naturalist*, **120**, 51–64.

Stiver, K. A., Dierkes, P., Taborsky, M., Gibbs, H. L. & Balshine, S. 2005. Relatedness and helping in fish: examining the theoretical predictions. *Proceedings of the Royal Society of London, Series B*, **272**, 1593–1599.

Vehrencamp, S. L. 1979. The roles of individual, kin and group selection in the evolution of sociality. In: *Handbook of Behavioral Neurobiology. Vol. 3*, Social Behavior and Communication (Ed. by P. Marler & J. G. Vandenbergh), pp. 351–394. New York: Plenum Press.

Vehrencamp, S. L. 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behavior*, **31**, 667–682.

Widemo, F. & Owens, I. P. F. 1995. Lek size, male mating skew, and the evolution of lekking. *Nature*, **373**, 148–151.

Wilson, E. O. 1975. *Sociobiology: the New Synthesis*. Cambridge: Belknap Press of Harvard University Press.

Wong, M., Buston, P., Munday, P. & Jones, G. 2007. The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. *Proceedings of the Royal Society of London, Series B*, **274**, 1093–1099.

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, U.S.A.*, **103**, 12005–12010.

Zink, A. G. & Reeve, H. K. 2005. Predicting the temporal dynamics of reproductive skew and group membership in communal breeders. *Behavioral Ecology*, **16**, 880–888.