# Behavioral Ecology

# Reproductive skew and the evolution of conflict resolution: a synthesis of transactional and tug-of-war models

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The formation of animal societies is a major transition in evolution. It is challenging to understand why societies are stable, given the reproductive conflicts inherent within them. Reproductive skew theory provides a compelling explanation for how and why reproductive conflicts are resolved. Indeed, some have suggested that skew theory represents a general theory of social evolution. Lamentably, skew theory is composed of many independent models, with the generality of each model being restricted by its assumptions. Here, we tackle this problem, using Hamilton's rule to predict the conditions under which assumptions of major classes of skew models (transactional and tug-of-war) apply. First, building on transactional models, we define the amount of reproduction that individuals can negotiate based on the threat of group dissolution (the "outside option") and determine conditions under which groups will be stable (free of group dissolution). Second, building on tug-of-war models, we define the amount of reproduction that individuals can negotiate based on the threat of costly competition (the "inside option") and determine conditions under which groups will be tranquil (free of costly competition). Finally, synthesizing transactional and tug-of-war approaches, we determine the conditions under which individuals will negotiate based on outside rather than inside options. Simply, individuals will negotiate using their outside option when it is greater than their inside option and vice versa. We conduct a post hoc test of all predictions in one simple animal society - the clown anemonefish, *Amphiprion percula*. The product is a more general and demonstrably testable model of reproductive skew, which should help to refocus the debate surrounding the utility of reproductive skew theory as a general theory of social evolution. *Key words:* bargaining theory, conflict, cooperation, cooperative breeding, eusociality, game theory. *[Behav Ecol 20:672–684 (2009)]*

Animal societies are one of the most remarkable products of evolution (Maynard Smith and Szathmary 1995), and they have been a focus for tests of evolutionary theory ever since Darwin pointed out the difficulties that some features of societies (e.g., nonbreeding and helping strategies) posed for the theory of natural selection (Darwin 1859). Perhaps, the most remarkable aspect of animal societies is that they exist at all. Their existence requires that genetically selfish individuals come together and reproduce as part of a group. In these groups, whenever resources are limited, there will be potential conflict between individuals over the allocation of reproduction. This potential reproductive conflict must somehow be resolved, to the satisfaction of all individuals, for these groups to remain stable over time (Ratnieks and Reeve 1992; Frank 1995, 2003; Buston 2003a; Ratnieks et al. 2006; Wong et al. 2007).

Animal societies are also remarkable for the tremendous variation that they exhibit in their features. At the most basic level, the strategies that individuals adopt within societies can vary. For example, some individuals leave, whereas others stay (Clutton-Brock et al. 1998; Field et al. 1999; Serrano et al. 2001; Buston 2003b; Heg et al. 2004; Greisser et al. 2008); some individuals breed, whereas others forego or delay their reproduction (Bourke et al. 1997; East and Hofer 2001; Haydock and Koenig 2002; Sumner et al. 2002; Buston 2004a; Heg et al. 2006); and some individuals help, whereas

others do not (Emlen and Wrege 1991; Clutton-Brock et al. 2000; Cant 2003; Buston 2004b; Stiver et al. 2005; Field et al. 2006). On top of this variation in individual strategies, the relationships among individuals within societies can vary. For example, societies can be despotic, when one individual dominates all the resources, or they can be egalitarian, when individuals share the resources evenly (Emlen and Wrege 1992; De Luca and Ginsberg 2001; Packer et al. 2001; Haydock and Koenig 2002; Buston 2004b; Bradley et al. 2005). Finally, societies can vary in the total number of individuals, from just a few to tens, hundreds, thousands, and even millions (Clutton-Brock et al. 1999; Field et al. 1999; Balshine et al. 2001; Serrano et al. 2001; Safran 2004; Buston and Cant 2006).

Evolutionary biologists tend to investigate each of these features of animal societies in isolation, in the same way that they tend to study the phenotypic traits of individuals one at a time. This approach makes a particular problem tractable, but it is widely appreciated that the evolution of one characteristic influences another (Roff 2002; Pigliucci and Preston 2004; Futuyma 2005). Thus, one of the greatest challenges for students of social evolution is to develop an internally consistent theory that explains all the major features of all animal societies. Wilson (1975) was perhaps the first to suggest that there might, one day, be such a general theory of social evolution:

> "... *when the same parameters and quantitative theory are used to analyze termite colonies and rhesus macaques, we will have a unified science of sociobiology*"

It has been suggested that reproductive skew theory is a candidate for a general theory of social evolution (Keller and

Reeve 1994; Sherman et al. 1995; Emlen 1997; Johnstone 2000). Skew theory was originally conceived to predict the distribution of reproduction among individuals within societies (Vehrencamp 1979, 1983a, 1983b; Emlen 1982; Stacey 1982; Reeve and Ratnieks 1993): In high skew (despotic) societies, a small proportion of individuals obtain the vast majority of the reproduction; in low skew (egalitarian) societies, the reproduction is distributed more evenly among individuals. The theory is founded on 3 fundamental principles of evolutionary biology. First, natural selection favors individuals that maximize their genetic contribution to future generations (Fisher 1930). Second, individuals can contribute genes to future generations either directly, through their own reproduction, or indirectly, by enhancing the reproduction of kin (Hamilton 1964). Third, in social contexts, selection favors evolutionarily stable strategies, which permit individuals to produce best responses to other individual's best responses (Maynard Smith 1982).

Reproductive skew theory is appealing because it is relatively simple, incorporating just 3 parameters that describe the payoffs associated with alternative social contexts (grouping, staying, and leaving; Table 1) and 2 parameters that modulate these payoffs (competitive ability and genetic relatedness; Table 1; Keller and Reeve 1994). Basic skew models address the question of why societies exist at all, predicting the partitioning of reproduction within groups

**Table 1**

**The standard variables of reproductive skew models**

| Variable | Description |
|---|---|
| $G$ | The group's expected reproductive output if the individuals remain together. $G$ might depend on the quality of the territory occupied and the level of efficiency and coordination of action between individuals. |
| $S$ | Each individual's expected reproductive output if it stays. $S$ might depend on the quality of the territory occupied the likelihood of acquiring another partner. |
| $L$ | Each individual's expected reproductive output if it leaves. $L$ might depend on ecological constraints such as the mortality risk associated with dispersal and the likelihood of acquiring another territory or partner. |
| $c$ | The probability of individual $A$ winning a competitive interaction with individual $B$ (e.g., a contest over eviction or a unit of reproduction). $c$ might depend on relative body size, winner–loser effects, and motivational state. |
| $r$ | The probability that the individuals share a copy of a particular gene identical by descent (i.e., the coefficient of relatedness). $r$ depends on genetic similarity relative to the population mean. |

Three variables describe the payoffs associated with alternative contexts (grouping, staying, and leaving) and 2 variables modulate these payoffs (competitive ability and genetic relatedness). Payoffs are framed in terms of reproductive value (Fisher 1930) rather than just current reproductive success. This enables us to consider models that focused on current expectations (e.g., Reeve and Ratnieks 1993; Johnstone and Cant 1999) and future expectations (e.g., Kokko and Johnstone 1999; Ragsdale 1999) in the same framework. When the group dissolves, both individuals can stay or leave and both individuals may or may not acquire another partner. This enables us to consider models that made different assumptions regarding group dynamics (e.g., Reeve and Ratnieks 1993; Johnstone and Cant 1999) and population ecology (e.g., Reeve and Ratnieks 1993; Reeve 1998) in the same framework. Each of the variables subsumes multiple social and ecological factors, as an essential step to simplify reality. The multiple factors that influence each of the model variables must be understood to conduct rigorous tests.

and the conditions under which groups will be stable (Vehrencamp 1979, 1983a, 1983b; Emlen 1982; Stacey 1982; Reeve and Ratnieks 1993; Reeve et al. 1998; Johnstone and Cant 1999; Johnstone 2000). Extensions of the basic skew models address the issue of why societies vary in their features, predicting social queuing (Kokko and Johnstone 1999; Ragsdale 1999), parental care (Zink 2000, 2001), sex change (Buston 2002; Muñoz and Warner 2003), sterile castes (Jeon and Choe 2003), and group size (Hamilton 2000; Reeve and Emlen 2000). The predictions of basic and extended skew models have some empirical support (Reeve and Keller 2001) though the interpretation and extent of this support is a matter of debate (Nonacs 2006).

Despite the appeal of reproductive skew theory, one of the aspects of the theory that has generated much criticism (Clutton-Brock 1998; Johnstone 2000; Magrath and Heinsohn 2000) and hampered significant progress toward a general theory is that each skew model makes different verbal assumptions. For example, most current skew models can be assigned to 1 of 2 major classes based on their assumptions (Johnstone 2000; Reeve and Keller 2001). Transactional models assume that one individual has control over the allocation of reproduction and that reproductive sharing is the product of a cost-free negotiation based on what the other individual can obtain by dissolving the group (Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007), that is, based on one individual's outside option (Muthoo 1999, 2000). Tug-of-war models assume that neither individual has control over the allocation of reproduction and that reproductive sharing is the outcome of a costly competition within stable groups (Reeve et al. 1998; Reeve and Shen 2006), that is, based on both individuals' inside options (Muthoo 1999, 2000).

These verbal assumptions of reproductive skew models create 3 distinct problems. First, the assumptions can be difficult to test empirically and, as a consequence, it can be difficult for empiricists to know which model's predictions apply (Magrath and Heinsohn 2000). Second, the assumptions impose artificial constraints on evolution: the assumption of reproductive control by one individual (transactional models) limits the evolution of better responses by the other; the assumption of costly competition by both individuals (tug-of-war models) impedes the evolution of more efficient forms of reproductive sharing. Finally, the verbal assumptions are restrictive, such that skew theory has become a patchwork of models each of which applies to an isolated region of parameter space (Reeve and Ratnieks 1993; Reeve et al. 1998; Johnstone and Cant 1999; Johnstone 2000; Reeve 2000; Reeve and Shen 2006). This, in turn, works against the goal of developing a general model for all regions of parameter space.

We believe that the solution to the problems associated with reproductive skew theory's restrictive assumptions is, simply, not to make those assumptions. This approach contrasts with the solution proposed by others (Johnstone 2000; Reeve 2000; Reeve and Shen 2006), which combined the assumptions of basic models to make synthetic models, though it builds on their insights. Instead of combining the assumptions of basic models, we explicitly model the conditions under which we expect the assumptions to apply, thereby converting the verbal assumptions of multiple models into mathematical predictions of a single model (Table 2). Elsewhere, we began this process by synthesizing 2 basic transactional models (concession and restraint; Buston et al. 2007). Here, we continue the process by synthesizing basic transactional and tug-of-war models (Table 2). This model makes 6 predictions and provides a fairly complete picture of how and why reproductive conflict can be resolved in simple societies. We conduct a post hoc test of all predictions in one simple animal society (see

**Table 2**

**The conversion of assumptions of skew models into predictions of skew models**

| Definition | Verbal assumption | Mathematical prediction |
|---|---|---|
| 1. Outside option$_{(1)}$ | Individuals will require a minimum amount of reproduction $pG$, equivalent to what they can obtain by group dissolution | $p_a = \frac{cS+(1-c)L-r[G-(1-c)S-cL]}{(1-r)G}$ <br> $p_b = \frac{(1-c)S+cL-r[G-cS-(1-c)L]}{(1-r)G}$ |
| 2. Group stability$_{(1)}$ | Individuals will not employ the threat of group dissolution, and groups will be stable, under certain conditions | $G > S+L$ <br> or <br> $p_a + p_b < 1$ |
| 3. Inside option$_{(2)}$ | Individuals will require a minimum amount of reproduction $qG$, equivalent to what they can obtain by costly competition | $q_{a0} = \frac{cS+cL-r[G-(1-c)S-(1-c)L]}{(1-r)G}$ <br> $q_{b0} = \frac{(1-c)S+(1-c)L-r[G-cS-cL]}{(1-r)G}$ |
| 4. Group tranquility$_{(2)}$ | Individuals will not employ the threat of costly competition, and groups will be tranquil, under certain conditions | $G > S+L$ <br> or <br> $q_{a0} + q_{b0} < 1$ |
| 5. Outside option$_{(1)}$ versus inside option$_{(2)}$ | Individual $A$ will negotiate based on outside options rather than inside options, under certain conditions | $p_a G > q_{a0} G$ <br> or <br> $c < \frac{1}{2}$ |
| 6. Group stability and tranquility | Individual $A$ will not employ threat of group dissolution and individual $B$ will not employ threat of costly competition, groups will be stable and tranquil, under certain conditions | $G > S + \frac{2L[1-c(1-r)]}{(1+r)}$ <br> or <br> $p_a + q_{b0} < 1$ |

Basic skew models tended to make verbal assumptions: 1) transactional models assumed that reproductive sharing was the product of a cost-free negotiation based on one individual's outside option (Reeve and Ratnieks 1993; Johnstone and Cant 1999); 2) tug-of-war models assumed that reproductive sharing was the product of a costly competition for both individuals' inside options (Reeve et al. 1998). The assumptions made the modeling more tractable, but they are difficult to test and they restrict the region of parameter space to which each model applies. Synthetic skew models provided insight into how basic skew models could be combined to make a more general model (Johnstone 2000; Reeve 2000; Reeve and Shen 2006; Buston et al. 2007), but these models still have limited applicability because they retain assumptions of basic models. Here, verbal assumptions of multiple models are converted into mathematical predictions of a single model, thereby revealing the region of parameter space to which previous models applied. Predictions 3–6 are based on most extreme threat, rather than least extreme threat, of costly competition.

Appendix). The result, we believe, is a more general and demonstrably testable model of reproductive skew.

## MATERIALS AND METHODS

### The model

We consider a simple group of 2 individuals, $A$ and $B$. We use 5 standard variables of reproductive skew theory (Table 1; Johnstone 2000; Reeve and Keller 2001; Zink and Reeve 2005; Buston et al. 2007). Three of these variables describe the payoffs associated with alternative contexts: the "group's" expected reproductive output if the individuals remain together is equal to $G$; each individual's expected reproductive output if it "stays" is equal to $S$; and each individual's expected reproductive output if it "leaves" is equal to $L$. The 2 remaining parameters modulate these payoffs: the probability of individual $A$ winning any "competitive" interaction (e.g., a contest over eviction or a unit of reproduction) is $c$; the probability that the 2 individuals share a copy of a particular gene identical by descent (i.e., the coefficient of "relatedness") is $r$.

We make the simplifying assumptions that $G$ is independent of which individual has the majority share of the reproduction, $L$ and $S$ are the same for both individuals, $c$ is the same regardless of what individuals are contesting for, and $r$ is symmetric. Also, we ignore the potential costs of the forcible eviction tactic as well as any diminishing returns from personal reproduction (Cant and Johnstone 1999; Johnstone and Cant 1999; Cant 2006; Loeb and Zink 2006). We consider these assumptions to be simplifying but not restrictive because, although they alter the quantitative predictions of the model, they do not restrict the region of parameter space to which the model applies. These simplifying assumptions can be easily relaxed though doing so makes the model more complex.

In contrast to previous skew models, we make no restrictive assumptions regarding 1) group dissolution tactics (forcible eviction or voluntary departure; Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007), 2) the mechanism of conflict resolution (cost-free negotiation or costly competition; Reeve and Ratnieks 1993; Johnstone and Cant 1999; Reeve et al. 1998), or 3) the basis for conflict resolution (inside options or outside options; Reeve and Ratnieks 1993; Johnstone and Cant 1999; Reeve et al. 1998). We also make no restrictive assumptions about 4) reproductive control (complete or incomplete; Reeve and Ratnieks 1993; Johnstone and Cant 1999; Reeve et al. 1998) or 5) reproductive status (dominant or subordinate; Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007). We consider that these assumptions (1–5) were restrictive because opting for one assumption or the other restricted the region of parameter space to which the model applied (Table 2; Johnstone 2000; Reeve and Keller 2001).

The behaviors favored by selection can be determined using the standard variables and Hamilton's rule (Hamilton 1964). Specifically, an action $i$ is favored over an action $j$ if

$$X_i + (r)Y_i > X_j + (r)Y_j,$$

where $X_i$ (or $X_j$) is the focal individual's reproductive output associated with the $i$th (or $j$th) action, $Y_i$ (or $Y_j$) is the other individual's reproductive output associated with the focal individual pursuing the $i$th (or $j$th) action, and $r$ is the coefficient of relatedness.

To begin, we must determine the group dissolution tactics that individuals would employ, even though they might never use them, because these tactics influence individuals' outside option (Danchin and Wagner 1997; Buston 2003; Buston et al. 2007; Safran et al. 2007). It has been shown that individuals

**Table 3**

**The qualitative predictions of a more general reproductive skew model**

| Variable | Share of reproduction | | Size of window | | Likelihood Of negotiation | |
|---|---|---|---|---|---|---|
| | Outside option | Inside option | Stability | Tranquility | Outside option | Inside option |
| $G$ | − | − | + | + | n.a. | n.a. |
| $L$ | + | + | − | − | n.a. | n.a. |
| $S$ | + | + | − | − | n.a. | n.a. |
| $c$ | + | + | n.a. | n.a. | − | + |
| $r$ | − | − | + | + | n.a. | n.a. |

Abbreviation: n.a., not applicable. The predicted relationships between standard variables and 3 features of societies are summarized, revealing 3 important points. First, the qualitative relationships between variables and reproductive shares are the same regardless of whether the share is negotiated based on inside or outside options. Second, the qualitative relationships between variables and the size of the window are the same regardless of whether the window is that of stability or tranquility. Only 2 predictions discriminate former transactional and tug-of-war concepts: 1) an observational prediction, an individual is more likely to negotiate on its outside than its inside option when its $c$ is small; and 2) an experimental prediction, the reduction of an individual's reproductive share will result in group dissolution if the individual is negotiating on outside option but costly competition if the individual is negotiating on its inside option.

are more likely to use a forcible eviction tactic than a voluntary departure tactic when the payoff from staying $S$ is greater than the payoff from leaving $L$ (Buston et al. 2007). Here we pursue the case where $S > L$ and both individuals employ a forcible eviction tactic. In this case, when eviction is attempted, individual $A$ wins and stays with probability $c$ or loses and leaves with probability $1 − c$.

To proceed, we ask a sequence of 6 questions (Table 2): 1) What share of the group's expected reproduction will individuals be able to negotiate based on what they could obtain by group dissolution, i.e., based on their outside options? 2) When will individuals not employ the threat of group dissolution, i.e., when will groups be stable (free of group dissolution)? 3) What share of the group's expected reproduction will individuals be able to negotiate based on what they could obtain by costly competition, i.e., based on their inside options? 4) When will individuals not employ the threat of costly competition, i.e., when will groups be tranquil (free of costly competition)? 5) When will individuals negotiate based on outside options rather than inside options? and 6) When will groups be both stable and tranquil?

## RESULTS

### Reproductive shares based on outside options

Previous transactional models assumed that the amount of reproduction one individual obtained was the outcome of a cost-free negotiation based on the threat of group dissolution (Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007), that is, one individual obtained an amount equivalent to its outside option (Muthoo 1999, 2000). However, the assumption that only one individual's outside option is relevant in the negotiation process is unjustifiable. Instead, we consider that the amount of reproduction that each individual can negotiate based on the threat of eviction, that is, based on its outside option, is $pG$, where $p$ is the individual's share of the group's expected reproductive output $G$. We can determine the share $p$ for each individual, by applying Hamilton's rule to that individual's decision to negotiate or attempt to evict its partner. The inclusive fitness of individual $A$ that negotiates will be greater than that of individual $A$ that attempts to evict when

$$p_a G + r(1 − p_a)G > cS + (1 − c)L + r[(1 − c)S + cL].$$

Recall that, when eviction is attempted, individual $A$ wins and stays with probability $c$ or loses and leaves with probability $1 − c$. Converting the inequality into an equality and solving

for $p_a$ yield the share of reproduction that $A$ can negotiate based on the threat of eviction

$$p_a = \frac{cS + (1 − c)L − r[G − (1 − c)S − cL]}{(1 − r)G}. \quad (1a)$$

Inspection of this equality reveals that it depends on $A$'s probability of winning a competitive interaction ($c$), which means we must derive this condition for both individuals. Substituting $c$ for $1 − c$ and solving for $p_b$ yield the share of reproduction that $B$ can negotiate based on the threat of eviction

$$p_b = \frac{(1 − c)S + cL − r[G − cS − (1 − c)L]}{(1 − r)G}. \quad (1b)$$

Inspection of equalities 1a and 1b reveals that both $A$'s and $B$'s reproductive share negotiated based on the threat of eviction will increase 1) as the group's expected reproductive output $G$ decreases, 2) as each individual's expected reproductive output from staying $S$ increases, 3) as each individual's expected reproductive output from leaving $L$ increases, 4) because $S > L$ as the individual's probability of winning a contest over eviction $c$ or $1 − c$ increases, and 5) as the coefficient of relatedness $r$ decreases (Table 3). The intuitive explanation for the magnitude of these shares is that each individual must receive an amount equivalent to its payoff from attempting to evict its partner, that is, equivalent to its outside option, otherwise it will be favored to dissolve the group.

Equations 1a and 1b have been derived elsewhere (Buston et al. 2007). They are a composite of the staying and toleration incentives derived in concession and restraint models (Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007) distinct from the peace incentive (Reeve and Ratnieks 1993; Buston et al. 2007). However, here, for the first time, we have derived these equations without making any of the typical assumptions regarding reproductive status or reproductive control (Reeve and Ratnieks 1993; Johnstone and Cant 1999; Johnstone 2000; Buston et al. 2007). (The same applies to the conditions for group stability, inequalities 2a and 2b, derived below [see also Reeve and Ratnieks 1993; Reeve and Keller 1995; Reeve and Keller 1997; Johnstone and Cant 1999; Johnstone 2000; Reeve 2000; Buston et al. 2007.]) Deriving these equations without making these restrictive assumptions is an important step toward a more general model of reproductive skew because, down the road (Reproductive shares based on outside or inside options and Conditions for group

stability and tranquility), it will allow us to investigate the conditions under which the assumptions are likely to apply (Table 2).

## Conditions for group stability

The amount of reproduction that individuals $A$ and $B$ can negotiate based on the threat eviction, the outside option, is $p_aG$ and $p_bG$, respectively. We can determine the conditions under which the group will be stable (i.e., the individuals will not engage in group dissolution), by applying Hamilton's rule to an individual's decision of whether to negotiate or attempt to evict when its partner is demanding the outside option. The inclusive fitness of individual $A$ that negotiates will be greater than that of individual $A$ that attempts to evict when

$$(1 - p_b)G + r(p_b)G > cS + (1 - c)L + r[(1 - c)S + cL].$$

Substituting equality 1b for $p_b$ yields the condition under which the group will be stable

$$G > S + L. \tag{2a}$$

Inspection of inequality 2a reveals that the group is more likely to be stable 1) as the group's expected reproductive output $G$ increases, 2) as each individual's expected reproductive output from staying $S$ decreases, and 3) as each individual's expected reproductive output from leaving $L$ decreases (Table 3). Further, this condition for group stability is independent of each individual's probability of winning a competitive interaction $c$ or $1 - c$, which means the condition will be the same for both individuals. The intuitive explanation for this is that an individual is favored to agree to its partner's demands based on the threat of eviction up until the point that it cannot meet its own outside option, that is, up until the point where the 2 required shares sum to one ($p_a + p_b = 1$), as can be easily shown

$$p_a + p_b < 1. \tag{2b}$$

Substituting 1a for $p_a$ and 1b for $p_b$ yields the same condition under which the group will be stable

$$G > S + L.$$

Together, individuals' shares negotiated based on outside options $p_a$ and $p_b$ define a window of group stability (Figure 1; Johnstone 2000; Reeve 2000; Zink and Reeve 2005). Within this window, individuals can take any share of the reproduction without provoking group dissolution: $A$'s reproductive share can range from $p_a$ (minimum) to $1 - p_b$ (maximum); $B$'s reproductive share can range from $p_b$ (minimum) to $1 - p_a$ (maximum). The width of this window can be estimated as $1 - p_a - p_b$ (Table 3). At this point in the model, we can predict the bounds on reproductive sharing for groups to remain stable.

## Reproductive shares based on inside options

Previous tug-of-war models assumed that the amount of reproduction that individuals obtained was the outcome of costly competition over reproduction within stable groups (Reeve et al. 1998; Johnstone 2000; Reeve 2000; Reeve and Shen 2006), that is, both individuals obtained their inside options (Muthoo 1999, 2000). However, the assumption that individuals must engage in costly competition is unjustifiable. Instead, we consider that the amount of reproduction that an individual can negotiate based on the threat of costly competition, that is, based on its inside option, is $q_iG$, where $q_i$ is the individual's share of the group's expected reproductive out-
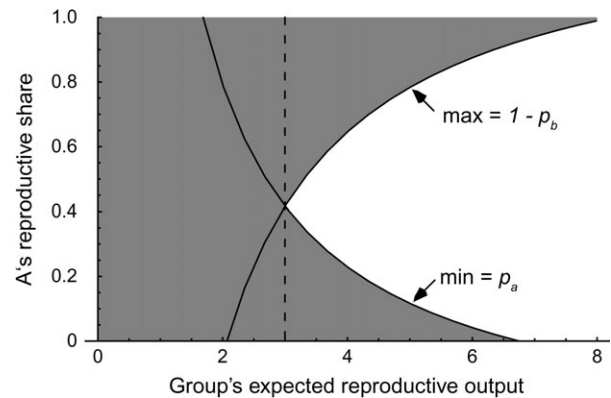


**Figure 1**
Outside options and the window of group stability. The $x$ axis is the group's expected reproductive output $G$, and $y$ axis is $A$'s potential share of the reproduction. Other variables are fixed: payoff associated with staying $S = 2$, payoff associated with leaving $L = 1$, probability of $A$ winning a competitive interaction $c = 0.25$, and coefficient of relatedness $r = 0.25$. Descending line is $A$'s minimum reproductive share $p_a$ based on what it can obtain by attempting to dissolve the group ($A$'s outside option). Ascending line is $A$'s maximum reproductive share $1 - p_b$ based on what $B$ can obtain by attempting to dissolve the group ($B$'s outside option). Vertical dashed line is $G = S + L$, which intersects other lines when $p_a + p_b = 1$, which is the point where the 2 minimum shares can no longer be met and group dissolution occurs. Dark gray area is the region in which group dissolution occurs because either one or both individuals' outside option is not met. White area is the window of stability, the region within which all levels of reproductive sharing are possible while avoiding group dissolution.

put $G$. Also, this amount of reproduction is $cG_i$, where $c$ is the individual's probability of winning a contest over each unit of reproduction and $G_i$ is the group's expected reproductive output when costly competition occurs ($G_i < G$).

Initially, the only credible threat of costly competition is the most extreme threat of costly competition $G_0$, which would reduce the group's expected reproductive output to the sum of the payoff associated with staying $S$ and the payoff associated with leaving $L$, because at this point $G_0 = S + L$ and any lower value of $G_i$ would make the group unstable (inequality 2; also Reeve and Shen 2006). (Other, less extreme, threats of costly competition become credible later [see section 7 below]). We can determine the share for each individual based on the most extreme threat $q_0$, by applying Hamilton's rule to an individual's decision to negotiate or engage in costly competition with its partner. The inclusive fitness of individual $A$ that negotiates will be greater than that of individual $A$ that engages in costly competition when

$$q_{a0}G + r(1 - q_{a0})G > cG_0 + r(1 - c)G_0.$$

Converting the inequality into an equality, substituting $S + L$ for $G_0$, and solving for $q_{a0}$ yield the share of reproduction that $A$ can negotiate based on the most extreme threat of costly competition

$$q_{a0} = \frac{cS + cL - r[G - (1 - c)S - (1 - c)L]}{(1 - r)G}. \tag{3a}$$

Inspection of this equality reveals that it depends on $A$'s probability of winning a contest $c$, which means that we must derive this condition for both individuals. Substituting $c$ for $1 - c$ and solving for $q_{b0}$ yield the share of reproduction that $B$ can negotiate based on the most extreme threat of costly competition

$$q_{b0} = \frac{(1-c)S + (1-c)L - r[G - cS - cL]}{(1-r)G}. \quad (3b)$$

Inspection of equalities 3a and 3b reveals that $A$'s and $B$'s reproductive shares negotiated based on the most extreme threat of costly competition exhibit the same qualitative relationships with the model variables as the shares negotiated based on the threat of group dissolution (equalities 1a and 1b; Table 3). The intuitive explanation for the magnitude of the shares $q_{a0}$ and $q_{b0}$ is that each individual must receive an amount equivalent to its payoff from the most extreme form of costly competition, that is, equivalent to its inside option, otherwise it will be favored to compete.

### Conditions for group tranquility

The amount of reproduction that $A$ and $B$ can negotiate based on the most extreme threat of costly competition, an inside option, is $q_{a0}G$ and $q_{b0}G$, respectively. We can determine the conditions under which groups will be tranquil (i.e., the individuals will not engage in such costly competition), by applying Hamilton's rule to an individual's decision of whether to negotiate or engage in costly competition when its partner is demanding this inside option. The inclusive fitness of individual $A$ that negotiates will be greater than that of individual $A$ that competes when

$$(1 - q_{b0})G + r(q_{b0})G > cG_0 + r(1-c)G_0.$$

Substituting equality 3b for $q_{b0}$ and $S + L$ for $G_0$ yields the condition under which groups will be tranquil

$$G > S + L. \quad (4a)$$

Inspection of this inequality reveals that the condition for group tranquility exhibits the same relationship with the model variables as the condition for group stability (inequality 2a; Table 3). The intuitive explanation for this result is that $A$ is favored to negotiate when $B$ is demanding this inside option because doing otherwise would reduce $A$'s personal fitness at no cost to $B$. Indeed, individual $A$ is favored to agree to $B$'s demands up until the point that $A$ cannot meet its own inside option, that is, up until the point where the 2 required shares sum to one ($q_{a0} + q_{b0} = 1$), as can be easily shown

$$q_{a0} + q_{b0} < 1. \quad (4b)$$

Substituting 3a for $q_{a0}$ and 3b for $q_{b0}$ yields the same condition under which the group will be tranquil

$$G > S + L.$$

Together, individuals' shares negotiated based on these inside options $q_{a0}$ and $q_{b0}$ define a window of group tranquility (Figure 2). Within this window, individuals can take any share of the reproduction without provoking the most extreme form of costly competition: $A$'s reproductive share can range from $q_{a0}$ (minimum) to $1 - q_{b0}$ (maximum); $B$'s reproductive share can range from $q_{b0}$ (minimum) to $1 - q_{a0}$ (maximum). The width of this window can be estimated as $1 - q_{a0} - q_{b0}$ (Table 3). At this point in the model, we can predict the bounds on reproductive sharing for groups to remain tranquil.

### Reproductive shares based on outside or inside options

Previous transactional models assumed that reproduction was divided based on outside options, whereas tug-of-war models
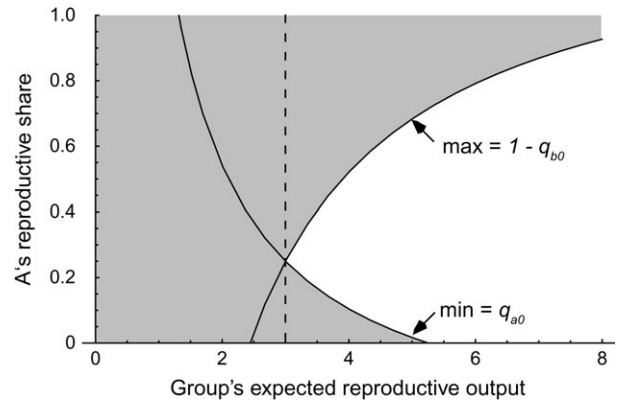


**Figure 2**
Inside options and the window of group tranquility. The $x$ axis is the group's expected reproductive output $G$, and $y$ axis is $A$'s potential share of the reproduction. Other variables are fixed: payoff associated with staying $S = 2$, payoff associated with leaving $L = 1$, probability of $A$ winning a competitive interaction $c = 0.25$, and coefficient of relatedness $r = 0.25$. Descending line is $A$'s minimum reproductive share $q_{a0}$ based on what it can obtain by engaging in extreme costly competition ($A$'s inside option). Ascending line is $A$'s maximum reproductive share $1 - q_{b0}$ based on what $B$ can obtain by engaging in extreme costly competition ($B$'s inside option). Vertical dashed line is $G = S + L$, which intersects other lines when $q_{a0} + q_{b0} = 1$, which is the point where the 2 minimum shares can no longer be met and costly competition ensues. Light gray area is the region in which costly competition occurs because either one or both individuals' inside option is not met. White area is the window of tranquility, the region within which all levels of reproductive sharing are possible while avoiding extreme costly competition.

assumed that reproduction was divided based on inside options. However, the assumption that individuals have only one option at their disposal is unjustifiable. Instead, we consider that the decision over which option to use can evolve. We can determine which option an individual will use as a basis for their negotiations, by applying Hamilton's rule to an individual's decision of whether to negotiate based on its inside or outside options. The inclusive fitness of individual $A$ that negotiates using its inside option will be greater than that of individual $A$ that negotiates using its outside option when

$$q_{a0}G + r(1 - q_{a0})G > p_aG + r(1 - p_a)G,$$

which yields the simple condition

$$q_{a0}G > p_aG. \quad (5a)$$

Substituting 1a for $p_a$ and 3a for $q_{a0}$ yields the condition under which $A$ will negotiate using its inside option

$$c > \frac{1}{2}. \quad (5a')$$

Inspection of this inequality reveals that it depends entirely on relative competitive ability $c$, which means that we must derive this condition for both individuals. Substituting $p_b$ for $p_a$ and $q_{b0}$ for $q_{a0}$ in inequality 5a, we find that the inclusive fitness of individual $B$ that negotiates using its inside option will be greater than that of individual $B$ that negotiates using its outside option when

$$q_{b0}G > p_bG. \quad (5b)$$

Substituting 1b for $p_b$ and 3b for $q_b$ yields condition under which $B$ will negotiate using its inside option

$$(1-c) > \frac{1}{2}. \qquad (5b')$$

Inspection of inequalities 5a' and 5b' reveals that individuals will be more likely to negotiate based on their inside rather than outside option when they are the better competitor (Table 3). The most general explanation for this result is revealed by inequalities 5a and 5b: an individual will be more likely to negotiate using its inside options when the amount of reproduction obtained by doing so is greater than that obtained by negotiating using its outside options. This conclusion has been reached independently by Cant and Johnstone (2009).

### Conditions for group stability and tranquility

When one individual negotiates its share based on its outside option $pG$, the other negotiates based on its inside option $q_0 G$ because 5a' and 5b' cannot be satisfied at the same time. This will create a new set of conditions under which groups will be both stable and tranquil. We can determine these conditions, by applying Hamilton's rule to an individual's decision of whether to negotiate or attempt to evict when its partner is demanding the inside option. Letting individual $A$ be the weaker competitor negotiating based on its outside options (inequality 5a), the inclusive fitness of individual $A$ that negotiates will be greater than that of $A$ that attempts to evict when

$$(1 - q_{b0})G + r(q_{b0})G > cS + (1-c)L + r[(1-c)S + cL].$$

Substituting equality 3b for $q_{b0}$ yields the condition under which groups will be both stable and tranquil

$$G > S + \frac{2L[1 - c(1-r)]}{(1+r)}. \qquad (6a)$$

Inspection of inequality 6a reveals that the group is more likely to be both stable and tranquil 1) as the group's expected reproductive output $G$ increases, 2) as each individual's expected reproductive output from staying $S$ decreases, 3) as each individual's expected reproductive output from leaving $L$ decreases, 4) as the individual's probability of winning a contest over a unit of reproduction $c$ increases, and 5) as the coefficient of relatedness $r$ increases (Table 3). The intuitive explanation for this result is that individual $A$ is favored to agree to $B$'s demands based on the threat of costly competition up until it cannot meet its own outside option, that is, up until the 2 required shares sum to one ($p_a + q_{b0} = 1$), as can be easily shown

$$p_a + q_{b0} < 1. \qquad (6b)$$

Substituting 1a for $p_a$ and 3b for $q_{b0}$ yields the same condition under which groups will be both stable and tranquil

$$G > S + \frac{2L[1 - c(1-r)]}{(1+r)}.$$

Together, individuals' required shares define a combined window of stability and tranquility, bounded by the threat of group dissolution and the threat of costly competition (Figure 3). Within this window, individuals can take any share of the reproduction without provoking group dissolution or extreme costly competition: $A$'s reproductive share can range from $p_a$ (minimum) to $1 - q_{b0}$ (maximum); $B$'s reproductive share can range from $q_{b0}$ (minimum) to $1 - p_a$ (maximum). The width of this window can be estimated as $1 - p_a - q_{b0}$ (Table 3). At this point in the model, we can predict the bounds on reproductive sharing for groups to remain both stable and tranquil.
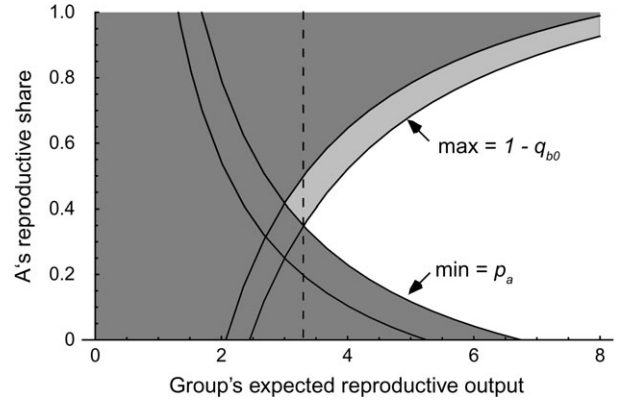


**Figure 3**
Outside options, inside options, and the window of stability and tranquility. The x axis is the group's expected reproductive output $G$, and y axis is $A$'s potential share of the reproduction. Other variables are fixed: payoff associated with staying $S = 2$, payoff associated with leaving $L = 1$, probability of A winning a competitive interaction $c = 0.25$, and coefficient of relatedness $r = 0.25$. Descending lines are $A$'s minimum reproductive shares based on $A$'s outside and inside options. Ascending lines are $A$'s maximum reproductive shares based on $B$'s outside and inside options. Vertical dashed line is $G = S + 2L[1 - c(1 - r)]/(1 + r)$, which intersects other lines when $p_a + q_{b0} = 1$, which is the point where the 2 minimum shares can no longer be met and extreme costly competition ensues or group dissolution occurs. Dark gray area is the region in which group dissolution occurs. Light gray area is the region in which costly competition occurs. White area is the window of stability and tranquility, the region within which all levels of reproductive sharing are possible while avoiding both costly competition and group dissolution.

### Reproductive shares based on inside options with varying levels of threat

Initially, the only credible threat of costly competition was the most extreme threat of costly competition, which would reduce the group's expected reproductive output to the condition for group stability ($G_0$, inequality 2; Figure 1). Now, however, we can consider a new credible, but less extreme, threat of costly competition, which would reduce the group's expected reproductive output to the combined condition for group stability and group tranquility ($G_1$, inequality 6; Figure 3). We can determine the share for each individual based on this less extreme threat ($q_1$), by once again applying Hamilton's rule to an individual's decision to negotiate or engage in costly competition with its partner. The inclusive fitness of individual $A$ that negotiates will be greater than that of individual $A$ that engages in costly competition when

$$q_{a1}G + r(1 - q_{a1})G > cG_1 + r(1-c)G_1.$$

Converting the inequality into an equality, substituting inequality 6a for $G_1$, and solving for $q_{a1}$ yield the share of reproduction that $A$ can negotiate based on this less extreme threat of costly competition

$$q_{a1} = \text{complex expression.} \qquad (7a)$$

This equality depends on $A$'s probability of winning a contest $c$, which means that we must derive this condition for both individuals. Substituting $c$ for $1 - c$ and solving for $q_{b1}$ yield the share of reproduction that $B$ can negotiate based on this less extreme threat of costly competition

$$q_{b1} = \text{complex expression.} \qquad (7b)$$

It can be shown that $q_{a1} > q_{a0}$ and $q_{b1} > q_{b0}$ because the new threat is based on the threat of a lesser reduction in the group's expected reproductive output (inequality 6, $G_1$) than the old threat (inequality 2, $G_0$). Consequently, selection will favor informed individuals that negotiate based on their less extreme threat rather than their most extreme threat because they stand to gain more by doing so. It follows that the better competitor (individual $B$ here) will continue to negotiate based on its inside options because $q_{bi} > q_{b0} > p_b$ (inequality 5b). Also, the worse competitor (individual $A$ here) will continue to negotiate based on its outside option until its inside option exceeds its outside option, that is, until $p_a \leq q_{ai}$ (inequality 5a).

Now, we can derive a new set of conditions under which groups will be both stable and tranquil in the face of this lesser threat of costly competition ($p_a + q_{b1} < 1$) equivalent to inequality 6b. Repeating this entire process (Reproductive shares based on inside options with varying levels of threat so far), we can determine the share that each individual can negotiate based on subsequent steadily diminishing threats of costly competition ($q_1, q_2, q_3, \ldots q_n$). This is a sequence whose terms are related to each other by a series. We can use mathematical induction to prove the formula for the sum to $n$ terms for the series, thereby proving the formula for $q_{an}$ and $q_{bn}$

$$q_{an} = q_{a0} + \sum_{i=1}^{n} \frac{L(-1+2c)[c(-1+r)-r][1+c(-1+r)]^{i-1}}{G(1+r)^i}, \qquad (7a')$$

and

$$q_{bn} = q_{b0} + \sum_{i=1}^{n} \frac{L(1-2c)[1+c(-1+r)]^i}{G(1+r)^i}. \qquad (7b')$$

Equalities 7a′ and 7b′ can be recognized as geometric series in which the common ratio lies between one and zero, which means that we can find the sum to infinity of each series

$$q_{a\infty} = \frac{L[1+c(-1+r)] - G(r) + S[c(1-r)+r]}{G(1-r)}, \qquad (7a'')$$

and

$$q_{b\infty} = \frac{L[1+c(-1+r)]^2 - [c(-1+r)-r][-Gr+(1+c(-1+r))S]}{G[c(-1+r)-r](-1+r)}. \qquad (7b'')$$

Inspection of equalities 7a′ and 7b′ reveals that $A$'s and $B$'s reproductive shares negotiated based on the least extreme threat of costly competition exhibit the same relationships with the model variables as their shares negotiated based on the most extreme threat of costly competition (equalities 3a and 3b). Remarkably, inspection of equality 7a′ reveals that as $n$ tends to infinity the inside option of the weaker individual converges to be the same as its outside option (equality 1a). This indicates that the weaker individual will always negotiate based on its outside option, that is, $p_a \geq q_{an}$ (inequality 5a). The intuitive explanation for the magnitude of these shares is that each individual must receive an amount equivalent to its payoff from the least extreme threat of costly competition,

otherwise it will be favored to start engaging in such competition and may escalate the intensity of costly competition from that point as group output is eroded.

## Conditions for group stability and tranquility with varying levels of threat

When one individual negotiates its share based on its outside option $pG$ and the other negotiates based on its inside option with the least extreme threat of costly competition $q_\infty G$, a new set of conditions is created under which groups will be both stable and tranquil in the face of the least extreme threat of costly competition. We can determine these conditions, by applying Hamilton's rule to an individual's decision of whether to negotiate or attempt to evict when its partner is demanding this inside option. Letting individual $A$ be the weaker competitor that is necessarily negotiating based on its outside option (inequality 5a, inequality 7a′), the inclusive fitness of individual $A$ that negotiates will be greater than that of $A$ that attempts to evict when

$$(1 - q_{b\infty})G + r(q_{b\infty})G > cS + (1-c)L + r[(1-c)S + cL].$$

Substituting equality 7b″ for $q_{b\infty}$ yields the condition under which groups will be both stable and tranquil in the face of the least extreme threat

$$G > S + \frac{L[1 - c(1-r)]}{[c(1-r)+r]}. \qquad (8a)$$

Inspection of this inequality reveals that the condition for group stability and tranquility based on the least extreme threat exhibits the same relationship with the model variables as the condition for group stability and tranquility based on the most extreme threat (inequality 6a). The intuitive explanation for this result is that individual $A$ is favored to agree to $B$'s demands based on the least extreme threat of costly competition up until it cannot meet its own outside option, that is, up until the 2 required shares sum to one ($p_a + q_{b\infty} = 1$), as can be easily shown

$$p_a + q_{b\infty} < 1. \qquad (8b)$$

Substituting 1a for $p_a$ and 7b″ for $q_{b\infty}$ yields same condition under which groups will be stable and tranquil

$$G > S + \frac{L[1 - c(1-r)]}{[c(1-r)+r]}.$$

Together, both individuals' minimum required shares based on their outside options ($p_a$ and $p_b$), along with the stronger individual's shares based on its multiple inside options ($q_{b0}$ to $q_{b\infty}$), define 3 distinct regions of parameter space. First, there is the region in which groups are unstable because the outside option of one or both individuals is not met (Figure 4). Second, there is a region in which groups are stable but not tranquil, within which the stronger individual engages in costly competition and forces the weaker individual to accept its own outside option (Figure 4). Finally, there is a region in which groups are both stable and tranquil, within which individuals can take any share of the reproduction without provoking group dissolution or costly competition (Figure 4).

## DISCUSSION

Here, we have synthesized transactional and tug-of-war models of reproductive skew (Reeve and Ratnieks 1993; Reeve et al. 1998; Johnstone and Cant 1999; Johnstone 2000; Reeve 2000; Reeve and Shen 2006; Buston et al. 2007). We have done so by
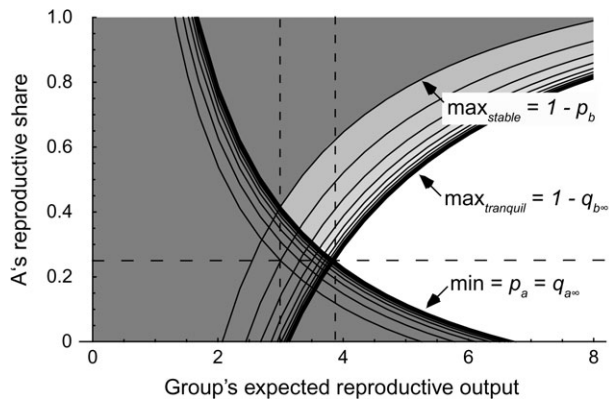
**Figure 4**

Windows of group stability and tranquility with varying levels of threat. The $x$ axis is the group's expected reproductive output $G$, and $y$ axis is $A$'s potential share of the reproduction. Other variables are fixed: payoff associated with staying $S = 2$, payoff associated with leaving $L = 1$, probability of $A$ winning a competitive interaction $c = 0.25$, and coefficient of relatedness $r = 0.25$. Descending lines are $A$'s minimum reproductive shares based on $A$'s outside and multiple inside options. Ascending line are $A$'s maximum reproductive shares based on $B$'s outside and multiple inside options. Left-hand vertical dashed line intersects other lines where $p_a + p_b = 1$, which is the point where these shares can no longer be met and group dissolution occurs. Right-hand vertical dashed line intersects other lines where $p_a + q_{b\infty} = 1$, which is the point where these 2 shares can no longer be met and costly competition based on the least extreme threat ensues or group dissolution occurs. Dark gray area is the region in which group dissolution occurs (groups are unstable). Light gray area is the region in which costly competition of various intensities occurs (groups are stable but not tranquil), in which the weaker individual will be forced to accept its outside option. White area is the combined window of stability and tranquility, the region within which all levels of reproductive sharing are possible and threats of group dissolution and costly competition are not credible.

using Hamilton's rule to predict the mathematical conditions under which the verbal assumptions of those models might apply. The result of this synthesis is a more general model of reproductive skew, which might help to refocus the debate regarding the potential of skew theory as a general theory of social evolution.

## A synthesis of transactional and tug-of-war models

This more general model makes 6 clear predictions regarding the characteristics of any simple society (Table 2). Individuals can negotiate an amount of reproduction based on the threat of group dissolution—the outside option (equality 1, a transactional concept); and, in a logically equivalent manner, individuals can negotiate an amount of reproduction based on the threat of costly competition—the inside option (equality 3, a tug-of-war concept). Further, when individuals are negotiating using outside options, there is a window of group stability, within which reproductive conflict is unresolved and all levels of reproductive sharing are possible (inequality 2; Figure 1); analogously, when individuals are negotiating using inside options, there is a window of group tranquility, within which reproductive conflict is unresolved and all levels of reproductive sharing are possible (inequality 4; Figure 2). Finally, the weaker individual will negotiate based on its outside option, whereas the stronger individual will negotiate based on its inside options (inequality 5), resulting in a combined window within which groups are both stable and tranquil (inequality 6; Figure 3). In addition, it can be shown that individuals will negotiate

based on less extreme threats of costly competition rather than more extreme threats of costly competition (inequality 7), revealing a window within which groups are stable but not tranquil (inequality 8; Figure 4).

This more general model reveals the regions of parameter space in which the concepts and predictions of previous reproductive skew models might apply (Table 2, Figure 4). First, there is a region in which groups are unstable (low $G$, high $S$ and $L$; Table 2, Figure 4), consistent with the predictions of all transactional models (Reeve and Ratnieks 1993; Johnstone and Cant 1999; Johnstone 2000; Buston et al. 2007). Second, there is a region in which groups are stable but not tranquil (intermediate $G$, intermediate $S$ and $L$; Table 2, Figure 4). In this region, the weaker individual negotiates based on its outside option, consistent with the predictions of transactional models (Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007). Ironically, however, it is the stronger individual's willingness to engage in costly competition, a tug-of-war concept (Reeve et al. 1998), which forces the weaker individual to negotiate based on its outside options. Third, there is a region in which groups are both stable and tranquil (high $G$, low $S$ and $L$; Table 2, Figure 4). In this region, the outside and inside options, transactional and tug-of-war concepts, respectively, set the bounds on acceptable levels of reproductive sharing but do not define the level of reproductive sharing (Figure 4). In this region, all levels of reproductive sharing are possible, and reproductive conflict is left unresolved.

To clarify exactly what we have done, in the original tug-of-war models, the threat of and execution of costly competition were not distinguished (Reeve et al. 1998; Reeve and Shen 2006). In these models, individuals had no choice but to engage in costly competition for reproductive shares. In contrast, in our model, there is a difference between the threat of and the execution of costly competition (in the same way that there is a difference between the threat of and the execution of group dissolution [Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007]). The threat of costly competition enables individuals to negotiate what could be obtained by costly competition without actually engaging in costly competition (in the same way that the threat of group dissolution enables individuals to negotiate what could be obtained by group dissolution without actually dissolving the group [Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007]). The threats of costly competition and group dissolution should never be carried out, given that $p + q_i < 1$ and assuming that individuals have complete information regarding all variables (Buston, Fedele, Zink, unpublished results) and conditions are stable (see Appendix).

This more general model reveals ways in which we may, and may not, determine whether inside options (a tug-of-war concept) or outside options (a transactional concept) are more relevant in nature (Table 3, Figure 3). First, we emphasize that it is essential to understand both options (inside and outside) in order to understand the partitioning of reproduction because when one individual is negotiating based on its outside option and the other is negotiating based on its inside option (Figures 3 and 4). Second, the qualitative relationships between reproductive shares and the parameters of the model are the same regardless of whether shares are negotiated based on the inside options or the outside options (Table 3). Third, the qualitative relationships between the size of the window, which might be related to levels of conflict (Reeve 2000), and the parameters of the model are the same regardless of whether the window is that of stability or tranquility (Table 3). The similarity of the qualitative predictions that are derived from consideration of inside and outside options

means that correlational studies alone will not be able to determine whether inside or outside options are more important to individuals in nature.

How can we determine whether individuals' reproductive shares are more strongly influenced by their inside or outside options? There are 2 predictions that enable us to discriminate these transactional and tug-of-war concepts. First, a supporting/correlational prediction is that if an individual's relative competitive ability $c$ is small, then that individual will be more likely to negotiate based on its outside option than its inside option (inequalities 5 and 7a″; Table 3). Second, a critical/experimental prediction is that if the individual is negotiating based on its outside option, then experimentally reducing its reproductive share will cause group dissolution; whereas, if the individual is negotiating based on its inside option, then experimentally reducing its reproductive share will cause costly competition (and perhaps subsequent group dissolution). The problems associated with testing models of behavioral and life history evolution using correlational approaches are well recognized; the most powerful tests of reproductive skew models will likely be those that directly or indirectly manipulate reproductive shares (Lessells 1991). We present a case study with a post hoc test of this model's predictions in the Appendix.

## A step toward a more general theory of social evolution

Looking beyond the synthesis of transactional and tug-of-war models of reproductive skew, perhaps the most valuable advance that we have made is to strip skew theory of many of its restrictive verbal assumptions. Previous skew models always made some assumptions regarding 1) group dissolution tactics (forcible eviction or voluntary departure; Reeve and Ratnieks 1993; Johnstone and Cant 1999), 2) the mechanism of conflict resolution (cost-free negotiation or costly competition; Reeve and Ratnieks 1993; Reeve et al. 1998; Johnstone and Cant 1999), or 3) the basis for conflict resolution (inside or outside options; Reeve and Ratnieks 1993; Reeve et al. 1998; Johnstone and Cant 1999). Elsewhere, it has been shown that selection will tend to favor individuals that use a forcible eviction tactic rather than a voluntary departure tactic when the payoff associated with staying is greater than that associated with leaving (Buston et al. 2007). Here, we have shown that selection will favor individuals that resolve conflict using the mechanism of cost-free negotiation based on threats of group dissolution or costly competition rather than costly competition itself (inequalities 3 and 7). Further, we have shown that selection will favor individuals that resolve conflict based on outside rather than inside options when their payoff associated with group dissolution is greater than that associated with costly competition (inequality 5; see also Cant and Johnstone 2009).

Previous skew models have also made some assumption regarding 4) reproductive control (complete or incomplete; Reeve and Ratnieks 1993; Reeve et al. 1998; Johnstone and Cant 1999) and 5) reproductive status (dominant or subordinate; Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007). Considering reproductive control, we suggest that complete reproductive control referred to the region of parameter space in which one individual negotiates based on its outside options (Figure 4). For example, if individual $A$ is forced to negotiate based on its outside option, then it might be said that individual $B$ has complete control. In contrast, we suggest that incomplete reproductive control has no analog in our model because there is no region of parameter space in which both individuals will engage in costly competition. Regardless, we suggest that the term reproductive control was somewhat misleading because it is hard to see,

biologically, how one individual could ever have control over another's reproduction. It is more reasonable to assume that individuals have control over their own reproductive physiology and make the best reproductive decisions they can contingent on what other in their society are doing (Maynard Smith 1982).

Finally, turning to consider reproductive status, most models have called one individual dominant and the other subordinate and endowed each of these individuals with special attributes (e.g., control of reproduction or group membership; Reeve and Ratnieks 1993; Johnstone and Cant 1999). The trouble with this approach is that there is no clear dominant in many societies. In addition, inconsistencies in the usage of the term dominant may have impeded progress toward a general theory (Reeve and Ratnieks 1993; Johnstone and Cant 1999; Buston et al. 2007). We suggest that the dominant be defined simply as the individual with the greater reproductive share, that is, as a reproductive or evolutionary dominant, as is consistent with most people's intuition. Our model makes no strong predictions about which individual will be reproductively dominant because the window within which reproductive conflict is left unresolved is often large (Figure 4). However, the model reasonably predicts that the dominant is more likely to be the one with the better options. The ideas of emergent reproductive status and emergent reproductive control, espoused here, are appealing because they enable us to make testable hypotheses about why one individual will be dominant (have the larger reproductive share) and when there will be apparent complete control (negotiation based on outside options), rather than just taking these things as given.

To conclude, by stripping reproductive skew theory of its intangible and unnecessary assumptions, we reveal its fundamentals. Reproductive skew theory is just Hamilton's rule, combined with 4 socioecological factors ($G$, $L$, $S$, and $c$), rigorously applied to the decisions that individuals can take within a society. The corollary of this is that all the major features of societies can emerge as a product of individuals' decisions. The idea that features of animal societies such as group dissolution tactics, forms of conflict resolution, reproductive sharing and reproductive status emerge as predictions from Hamilton's rule is appealing because this enables us to make testable hypotheses about the causes of variation in these features. This clarification will, we hope, remove barriers to testing skew theory in animals and allow for a wider application of skew theory to other organisms (e.g., plants, fungi, microbes, and humans). If this results, then this study has the potential to change the way we think about the evolution of societies in all taxa, uniting them in a more general theoretical framework.

## APPENDIX

### Case study

We suggest that the real power of reproductive skew theory does not lie in the fact that it makes predictions about reproductive shares per se but rather that it makes an entire suite of predictions all of which can be tested simultaneously in a given animal society. We do not believe that it is appropriate for us to conduct a post hoc reanalysis of others' empirical results to see if they provide support for our model. Instead, we hope that this general model will provide the stimulus for a formal meta-analysis of all predictions (e.g., Griffin and West 2003). However, it is illustrative and potentially useful to assess the plausibility and testability of the model's predictions, post hoc, in one society that we understand well, the clown anemonefish *Amphiprion percula* (Buston 2002; Buston 2003a, 2003b, 2003c; Buston 2004a, 2004b; Buston and Cant 2006; Buston and García 2007; Buston et al. 2007), with some additional insights from the coral goby *Paragobiodon xanthosomus* which has a similar socioecology (Wong et al. 2007, 2008a, 2008b). It is worth highlighting at this point that neither of these

societies are societies that the original architects of skew theory were thinking about when they developed the theory.

## Study species

Groups of clownfish occupy giant sea anemones (*Heteractis magnifica*), which provide the fish with protection from predators (Mariscal 1970; Elliott et al. 1995; Buston 2003b). Each group is composed of a breeding pair and 0–4 nonbreeders (Fricke H and Fricke S 1977; Fricke 1979; Mitchell 2003; Buston 2004a). Within each group, there is a size hierarchy (Fricke H and Fricke S 1977; Buston 2003c; Buston and Cant 2006): the female is largest (rank 1), the male is second largest (rank 2), and nonbreeders get progressively smaller as the hierarchy is descended (ranks 3–6). These fish are protandrous hermaphrodites; if the female of the group dies, then the male changes sex and assumes the position vacated by the female, and the largest nonbreeder assumes the position vacated by the male (Fricke H and Fricke S 1977; Moyer and Nakazano 1978; Buston 2004a). The size hierarchy reflects a queue for breeding status; individuals join groups at the back of the queue and only advance as those ahead of them die (Fricke 1979; Buston 2004b; Mitchell 2005). Here, we investigate the extent to which the general model can help us to understand the interaction between the male (rank 2) and the largest nonbreeder (rank 3) within groups of *A. percula*. (The interaction between nonbreeders can be understood using similar logic, whereas the interaction between the breeders is considered elsewhere [Buston 2002]).

## Standard variables

First we must come up with quantitative parameter estimates for the rank 2–rank 3 pair's interaction (Table 1). Ideally, these would be determined by experiment, but we can use expert knowledge to come up with reasonable estimates of the parameters for the population of *A. percula*, in Madang Lagoon, Papua New Guinea (Buston 2002). We consider that the pair's expected reproductive output $G$ is, on average, 2.00 because the population size at this study site is stable over time (Fautin 1992; Buston 2003a). An individual's expected reproductive output if it stays $S$ is, approximately, 1.96 because lost partners are rapidly replaced (Buston 2004a). An individual's expected reproductive output if it leaves $L$ is, generously, 0.02 because leaving is dangerous and the habitat is saturated (Mariscal 1970; Buston 2003a). The probability of the rank 3 individual winning a competitive interaction $c$ is, approximately, 0.01 because of the well-defined size differences found between individuals adjacent in rank (Buston 2003c; Buston and Cant 2006; Wong et al. 2007). The coefficient of relatedness $r$ between the 2 individuals is, on average, 0 (Buston et al. 2007) because the pelagic larval phase breaks up kin associations.

## Model predictions

Given these parameter estimates, we can use the model to predict individuals' group dissolution tactic (Buston et al. 2007); individuals' outside option, inside option, and choice of option; and group stability and tranquility (Table 2). Both individuals are predicted to adopt a forcible eviction tactic, rather than a voluntary departure tactic (Buston et al. 2007). Rank 3 is predicted to negotiate about 2% of the pair's expected reproduction based on its outside options (equality 1, inequality 5; Figure 5). Rank 2 is predicted to negotiate about 98% of the pair's expected reproduction based on its inside options (equality 3, inequality 5, inequality 7; Figure 5). Note that individuals outside options and most extreme inside options are almost indistinguishable because the payoff associated with leaving $L$ is close to zero (equality 1, equality 3; Figure 5). The pair is predicted to be stable but prone to intense costly competition and group dissolution because the group's expected reproductive output $G$ is not much greater than the sum of the payoffs associated with staying $S$ and leaving $L$ (inequality 2, inequality 4, inequality 8; Figure 5).

## Tests of predictions

Post hoc, it seems that the entire suite of predictions has some support. Both individuals adopt a forcible eviction tactic, even though the likeli-
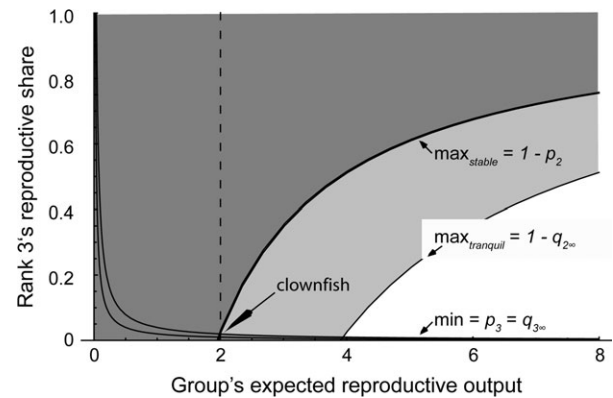


**Figure 5**
Case study: the clown anemonefish *Amphiprion percula*. The $x$ axis is group's expected reproductive output $G$, and $y$ axis is rank 3's potential share of reproduction. Other variables are fixed: payoff associated with staying $S \approx 1.96$, payoff associated with leaving $L \approx 0.02$, probability of rank 3 winning a competitive interaction $c \approx 0.01$, and coefficient of relatedness $r \approx 0.00$. Descending lines are rank 3's minimum shares based on its outside and inside options. Ascending lines are rank 3's maximum shares based on rank 2's outside and inside options. Locale where payoff associated with grouping $G \approx 2.00$ is, in combination with other variables, the socioecological context of clownfish, in Madang Lagoon, Papua New Guinea. The model predicts that rank 3 will negotiate a small share of the group's expected current and future reproduction rank 2 will negotiate a large share of the group's expected reproduction, and the group should be stable but not tranquil. Further, the model predicts that direct or indirect enhancement of rank 3's reproductive share will lead to costly competition (aggression) and group dissolution (eviction). All predictions seem to have some support (see text).

hood of rank 3 winning the contest is close to zero (Buston 2003a). Considering reproductive shares, rank 3 obtains none of the current reproduction, but it stands to gain more than 2% of the pair's expected (current and future) reproduction by outliving rank 2 (Buston 2002; Buston 2004b); rank 2 obtains 100% of the current reproduction and could do no better unless it were able to influence relative mortality rates through it actions. Finally, considering group stability and tranquility, group dissolution events are rare under natural conditions (Buston 2003a; Elliot and Mariscal 2001), and there is little to suggest that costly competition (indicated by aggression) occurs within stable groups (Buston and Cant 2006). Compellingly, however, an experimental manipulation in which the size of rank 3 is increased, which is an indirect way of increasing its reproductive share, means that rank 2's minimum reproductive shares based on its inside and outside options cannot be met and, as predicted, rank 2 is aggressive toward and attempts to evict rank 3 (Buston 2003c; Buston and Cant 2006; Wong et al. 2007, 2008a). While acknowledging concerns associated with such post hoc analyses, to our knowledge, there is no other model that could predict all these features of this society in an internally consistent manner.

insights on and discussion about assumptions; Jordi Bascompte, James Dale, Daniel Stouffer, and several anonymous reviewers for their comments on earlier versions of the manuscript.

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