The past, present and future of reproductive skew theory and experiments

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ABSTRACT

A major evolutionary question is how reproductive sharing arises in cooperatively breeding species despite the inherent reproductive conflicts in social groups. Reproductive skew theory offers one potential solution: each group member gains or is allotted inclusive fitness equal to or exceeding their expectation from reproducing on their own. Unfortunately, a multitude of skew models with conflicting predictions has led to confusion in both testing and evaluating skew theory. The confusion arises partly because one set of models (the 'transactional' type) answer the ultimate evolutionary question of what ranges of reproductive skew can yield fitness-enhancing solutions for all group members. The second set of models ('compromise') give an evolutionarily proximate, game-theoretic evolutionarily stable state (ESS) solution that determines reproductive shares based on relative competitive abilities. However, several predictions arising from compromise models require a linear payoff to increased competition and do not hold with non-linear payoffs. Given that for most species it may be very difficult or impossible to determine the true relationship between effort devoted to competition and reproductive share gained, compromise models are much less predictive than previously appreciated. Almost all skew models make one quantitative prediction (e.g. realized skew must fall within ranges predicted by transactional models), and two qualitative predictions (e.g. variation in relatedness or competitive ability across groups affects skew). A thorough review of the data finds that these three predictions are relatively rarely supported. As a general rule, therefore, the evolution of cooperative breeding appears not to be dependent on the ability of group members to monitor relatedness or competitive ability in order to adjust their behaviour dynamically to gain reproductive share. Although reproductive skew theory fails to predict within-group dynamics consistently, it does better at predicting quantitative differences in skew across populations or species. This suggests that kin selection can play a significant role in the evolution of sociality. To advance our understanding of reproductive skew will require focusing on a broader array of factors, such as the frequency of mistaken identity, delayed fitness payoffs, and selection pressures arising from across-group competition. We furthermore suggest a novel approach to investigate the sharing of reproduction that focuses on the underlying genetics of skew. A quantitative genetics approach allows the partitioning of variance in reproductive share itself or that of traits closely associated with skew into genetic and non-genetic sources. Thus, we can determine the heritability of reproductive share and infer whether it actually is the focus of natural selection. We view the 'animal model' as the most promising empirical method where the genetics of reproductive share can be directly analyzed in wild populations. In the quest to assess whether skew theory can provide a framework for understanding the evolution of sociality, quantitative genetics will be a central tool in future research.

Key words: animal model, cooperative breeding, game theory, indirect genetic effects, kin selection, maternal effects, quantitative genetics, reproductive skew, sociality.

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I. INTRODUCTION

A ubiquitous feature of cooperatively breeding groups is unequal sharing of reproduction, or reproductive skew. Given the obviously close connection between reproduction and fitness, skew can be viewed as an evolutionarily selected feature of group life (Vehrencamp, 1983*a*, *b*; Keller & Vargo, 1993; Reeve & Ratnieks, 1993). Such an adaptive evolutionary approach leads to a number of fundamental questions. How is skew set within groups? Are there limits to how large or small the skew can be, before groups become unstable and break up? Are all individuals treated similarly or are reproductive shares allocated in relation to genetic relatedness, competitive ability, and opportunities to leave the group? To answer such questions rigorously, reproductive skew has been extensively modeled and the resulting predictions tested numerous times. Furthermore, the methodology used in predicting skew has been extended to a much wider array of social behaviours. Reproductive skew type models have been suggested or used for predicting aspects of: parent-offspring conflict (Cant, 2006; Cant & Johnstone, 2009); dominance hierarchy formation (Buston & Zink, 2009); physiological stress due to agonistic social interaction (Rubenstein & Shen, 2009); caste conflicts over male parentage in social insects (e.g. "worker policing", Reeve & Jeanne, 2003); sex ratio conflicts (Nonacs, 2002);

the initial stages of the evolution of cooperation (Nonacs, 2002; Nonacs, Reeve & Starks, 2004); and evolution and regulation of within-organism multicellularity (Reeve & Jeanne, 2003).

The numerous models with multiple, duelling predictions have also, unfortunately, produced a rather confusing body of literature. Experimental results that are initially seen as unsupportive of reproductive skew theory (e.g. Field *et al.*, 1998) are later reinterpreted as supportive (Reeve & Keller, 2001). Models question each other's assumptions and predictions (Johnstone, 2000; Reeve & Shen, 2006; Nonacs, 2007; Cant & Johnstone, 2009). This confusion has created a situation where it is difficult to determine how successful reproductive skew theory has been, and more importantly, where future work would be most profitable. Therefore, herein we set out four goals: (1) explain and synonymize the mathematical bases of the various models; (2) derive a set of testable predictions valid across all reproductive skew models; (3) evaluate existing data relative to predictions and consider alternative models; and (4) develop a roadmap for future work. Although the first explicit mathematical treatments of reproductive skew started with Vehrencamp's work (Vehrencamp, 1979, 1983*a*), the latest models have followed or modified the format set forth in Reeve & Ratnieks, (1993). It is relative to this basic model that we will describe all subsequent theoretical work.

II. REPRODUCTIVE SKEW MODELS AND TERMINOLOGY

(1) The basic model

Reproductive skew models began by extending Hamilton's rule to compare inclusive fitness of group living to being solitary for two interacting individuals (Reeve & Ratnieks, 1993, modified as in Nonacs, 2001). Mathematically, we represent one individual (the dominant, d) cooperating with another (the subordinate, s) as:

$$k[p + r(1 - p)] \geq rx_d + x_s, \tag{1}$$

where k is the group's realized reproduction, p is the subordinate's proportion of group reproduction, and r is the relatedness of subordinate to dominant. The right-hand side of this equation is the subordinate's fitness if both individuals exercise their non-cooperative options to live solitarily and gain x_d and x_s respective offspring. Rearrangement defines the minimum proportion of group reproduction needed to favour the subordinate's cooperation, p_{min}, such that:

$$p_{min} = [x_s - r(k - x_d)]/k(1 - r). \tag{2}$$

[Corrections on equation (2) were introduced to the paper on 3 August 2010 after its first publication online in Wiley InterScience on 9 June 2010.]

This is the basic formulation for the set of models known as "Transactional" (Table 1). A similar approach finds the maximum proportion of reproduction (p_{max}) that the dominant is willing to surrender to the subordinate:

$$p_{max} = (k - x_d - rx_s)/k(1 - r). \tag{3}$$

To determine the minimum total productivity required for a stable group, we solve for k_{min} by setting $p_{max} = p_{min}$. This gives:

$$k_{min} = x_d + x_s. \tag{4}$$

These equations show that if $p_{max} \geq p_{min}$, a stable, mutually beneficial relationship is possible irrespective of the pair's genetic relatedness, as long as reproduction is shared appropriately.

The original transactional model assumed that differences between the dominant and subordinate (i.e. values for x_d and x_s) are intrinsic. However, they could reflect the added value of an extrinsic resource such as a territory. Therefore, the non-cooperative options might reflect the outcome of a fight for that resource. If we assume the fitness value of the resource is S and the fitness after losing and leaving is L, then:

$$x_d = (1 - c)S + cL \tag{5}$$

and

$$x_s = cS + (1 - c)L, \tag{6}$$

where c is the subordinate's probability of winning a fight (Buston *et al.*, 2007).

(2) Glossary of terms

One problem in relating reproductive skew models to each other is that their variable designations and definitions often differ. This can exaggerate real conceptual differences and obscure similarities. In some cases identical models appear to be mathematically different, but close inspection reveals the difference exists only in how variables are labeled or in the arrangement of the equations. To synonymize the various models we consider how each would estimate the inclusive fitness (*IF*) of an individual deciding to join a group as a subordinate (Table 1). This decision has five components: (1) realized group productivity if the subordinate joins; (2) the subordinate's proportional direct fitness, which is composed of offspring that the dominant either conceded (without a fight) or offspring that are gained through a competitive contest; (3) the subordinate's proportional indirect fitness, which is either conceded offspring or parentage lost in contest, prorated by relatedness; and (4 & 5) the direct and indirect fitness components for the subordinate if it chooses not to join (or loses the fight to control the group resource) and reproduces solitarily. Thus, for all the models we are describing: *IF* = (1)[(2) + (3)] − [(4) + (5)], and this value should be greater than zero to favour cooperation.

In our analysis, we follow the general convention of designating one individual as the "dominant" and the other as the "subordinate". The dominant is assumed to be the stronger competitor or likely to have higher reproductive success when breeding solitarily. These advantages translate to an expectation that p_{min} will be less than 0.5. This convention has been criticized as being too restrictive and making arbitrary assumptions as to whether individuals can control their partner's reproduction (Buston *et al.*, 2007). Instead, it has been suggested that any individual that has control over its own reproductive behaviour be designated as an "allocator" (Buston *et al.*, 2007). Nevertheless, unless both individuals have identical capabilities and options, one allocator can always be predicted to take a larger (dominating) portion of reproduction.

For some variables, there is great unanimity. Relatedness is always "r", except in Nonacs (2002), which considers skew in populations with sex investment asymmetries and biases. In such cases, it is important to consider both relatedness and the reproductive value of females and males.

If the subordinate can expect to receive a reproductive concession, that proportion is usually given as "p", although a variety of modifying subscripts have been used. The exceptions are Reeve (2000) where "q" is the proportion of the total reproduction exclusively available to either the subordinate or dominant. The subordinate's share is the proportion, $1 - d$. Reeve & Shen (2006) use "P". Finally, in one variant of Buston & Zink's (2009) model, the subordinate's share may be $q_{b\infty}$, which is the amount offered by the dominant. In

Table 1. Summary of variables used in reproductive skew models. Stable groups are possible when the inclusive fitness (direct + indirect) of the cooperative (inside) option is greater than the non-cooperative (outside) option for a potential subordinate. Reproduction can be conceded to other group members or contested. Model types are either ultimate (transactional models) in terms of predicting a range of stable skew values, or proximate (compromise models) in predicting a single evolutionarily stable state (ESS) skew value determined by relative competitive abilities. Models also can be relative or absolute in calculating inclusive fitness. Absolute models use the expected reproductive success of all groups and all single individuals. Relative models usually set the expected reproductive success of non-cooperative dominants to unity (= 1) and define k and x as ratios greater or less than one

Option: Fitness:		Cooperative					Non-cooperative			
		Direct		Indirect			Direct	Indirect		
Reference	(Group productivity) x	[(Conceded share +	Contested share) +	(Conceded share) +	Contested share)] –	Related-ness x	[Subordinate alone +	r(Others alone)]	Model type	Comments
Reeve & Ratnieks (1993)	k	p		$1-p$		r_{ij}	x	r_{ij}	Ultimate, relative	Basic transactional skew model. The "ij" subscripts can be used for asymmetrical relatedness. Symmetry is usually modeled.
Reeve & Emlen (2000)	$g[N]$	p_s		$1-p_s$		r	$g[1]$	$rg[N-1]$	Ultimate, absolute	Non-linear group productivity with N group members.
Nonacs (2001); Nonacs et al. (2004)	k	p_{min}		$1-p_{min}$		r	x_β or x_s	rx_α or rx_d	Ultimate, absolute	To revert to basic relative fitness model, divide k, x_β, x_α, x_s and x_d by the expected success of a solitary dominant (e.g. $x = x_\beta/x_\alpha$).
Reeve & Keller (2001)	g	p		$1-p$		r	s	rd	Ultimate, absolute	To revert to basic relative fitness model, divide g, s, and d by d (e.g. $x = s/d$).
Nonacs, (2002)	k	$p_{min}\{[(gv/F) + [(1-f)gv]/M\}$		$1-p_{min}$		$[(gv/F) + [(1-f)gv]/M]$	$x\{[(gv/F) + [(1-f)gv]/M]\}$	$[(gv/F) + [(1-f)gv]/M]$	Ultimate, relative	Applies only in populations with biased sex ratios: proportions of female (f, F) and male (M) offspring in group and in the population; v = reproductive value; g = relatedness.
Nonacs et al. (2006)	k_n	p_{min}		$1-p_{min}$		r	x_s	$r[(n-1)x_s + x_d]$	Ultimate, absolute	Linear productivity; all subordinates get equal share in group; r between focal individual and n other groups members is constant.
Nonacs et al. (2006)	$b_n s_n$	p_{min}		$1-p_{min}$		r	$b_s s_s$	$r[(n-1)b_s s_s + b_n s_n]$	Ultimate, absolute	Reproductive success of groups and solitary individuals is the product of expected number of young (b) and expected survival of the nest to maturity (s).
Buston et al. (2007)	G	p_{bl}		$1-p_{bl}$		r	L	rS	Ultimate, absolute	Assumes groups break up peacefully.

Table 1. *(Cont.)*

Option:	Cooperative						Non-cooperative			
Fitness:	Direct				Indirect		Direct	Indirect		
Reference	(Group productivity) x	[(Conceded share +	Contested share) +	Related-ness x	(Conceded share +	Contested share)] –	[Subordinate alone + cS	r(Others alone)]	Model type	Comments
Buston *et al.* (2007)	G	p_{b3}	$by/(x+by)$	r	$1-p_{b3}$		$[(1-c)L+cS]$	$r[(1-c)S+cL]$	Ultimate, absolute	Assumes groups break up through fight, c = subordinate's probability of winning.
Buston & Zink (2009)	G	p_a		r	$1-p_a$		$[(1-c)L+cS]$	$r[(1-c)S+cL]$	Ultimate, absolute	Compares fitness offered by dominant to fitness from fighting.
Buston & Zink (2009)	G	$q_{b\infty}$		r	$1-q_{b\infty}$		$[(1-c)L+cS]$	$r[(1-c)S+cL]$	Ultimate, absolute	
Reeve *et al.* (1998)	$1-x-y$		$by/(x+by)$	r	$x/(x+by)$	$x/(x+by)$			Proximate, relative	Basic compromise (tug-of-war) skew model; no comparison to non-cooperation.
Johnstone (2000)	$1-d-s$		$bs/(d+bs)$	r	$d/(d+bs)$	$d/(d+bs)$			Proximate, relative	
Johnstone (2000)	$1-d-s$	p_{min}	$\frac{(p_{max}-p_{min})bs}{(d+bs)}$	r	$1-p_{max}$	$\frac{(p_{max}-p_{min})d}{(d+bs)}$			Proximate, relative	Assumes each member concedes minimum fitness to partner.
Reeve (2000)	$k(1-x-y)$	$q(1-d)$	$\frac{(1-q)by}{(x+by)}$	r	qd	$\frac{(1-q)x}{(x+by)}$			Proximate, absolute	Assumes proportion of reproduction can be monopolized.
Reeve & Shen (2006)	$G(1-x-y)$	P	$\frac{(1-P-Q)by}{(x+by)}$	r	Q	$\frac{(1-P-Q)x}{(x+by)}$	S	rD	Proximate, absolute	All reproduction can be conceded or contested, non-cooperation = leaving.
Reeve & Shen (2006)	$G(1-x-y)$	P	$\frac{(1-P-Q)by}{(x+by)}$	r	Q	$\frac{(1-P-Q)x}{(x+by)}$	$ft+(1-f)s$	$r[(1-f)t+fs]$	Proximate, absolute	All reproduction can be conceded or contested, non-cooperation = fight: t = fitness for winning; s = fitness for losing; f = probability of subordinate winning.
Cant & Johnstone (2009)	$k(1-x-y)$		$by/(x+by)$	r	$x/(x+by)$	$x/(x+by)$	dX	r	Proximate, relative	Compromise model with no concessions; compares to non-cooperation; d = probability of successful dispersal.
Present study	$G(1-x-y)$	$f(y)/[f(x)+f(y)]$	$f(y)/[f(x)+f(y)]$	r	$f(x)/[f(x)+f(y)]$	$f(x)/[f(x)+f(y)]$	x_s	rx_d	Proximate, absolute	$f(x)$ and $f(y)$ are non-linear functions of the amounts (x or y) invested into reproductive competition.

models without conflict, the proportional share conceded to the dominant is simply $1 - p_{min}$. Where conflict does occur, the dominant's conceded share might be the minimum direct reproduction needed to keep from evicting the subordinate ($1 - p_{max}$; Johnstone, 2000), or variable amounts given as qd by Reeve (2000) or Q by Reeve & Shen (2006).

All models that have contested shares of reproduction (variously known as "compromise" or "tug-of-war" models), assume the contest is resolved by the ratio of the resources invested by the subordinate and dominant into the conflict (given as y and x, respectively, except in Johnstone (2000) which uses the labels s and d). The subordinate's expected lower competitive ability is reflected through a competitive efficiency variable (b, and usually <1). The various models differ in how much of the total reproduction is contested (see Table 1, comments).

The greatest terminological confusion exists in describing the inclusive fitness of the non-cooperative option. The basic model of Reeve & Ratnieks (1993) set the solitary payoff for the dominant as unity (equal to 1). Hence the fitness of the subordinate (x) is a proportion of the dominant's ($x \leq 1$). In Cant & Johnstone (2009) X is the same as this x. (It is important to note that this x describes a realized number of offspring, and is very different from x in the compromise models, which quantifies offspring lost to investing in competition.) Other models use absolute values. Nonacs (2001) and Nonacs *et al.* (2004) give the productivity of the dominant as either x_α or x_d and the subordinate as x_β or x_s, such that $x_\beta = x_s \leq x_\alpha = x_d$. Reeve & Shen (2006) replaced these values with D and S, respectively, and then expanded them in another variant of their model with a set of terms reflecting probabilities for winning an eviction fight (see Table 1, comments). Buston *et al.* (2007) and Buston & Zink, (2009) also assumed eviction fights and replaced the respective Nonacs values with S and L, prorated by the subordinate's chances for winning the fight (c). Thus "S" is associated with the dominant in one set of models, but with the subordinate in another. Finally, the original compromise models did not include any measure of inclusive fitness for non-cooperative options (Reeve, Emlen & Keller, 1998; Johnstone, 2000; Reeve, 2000).

The distinction as to whether fitness is measured relatively or absolutely also has important consequences for how group productivity is described. It was originally "k", and a measure of the productivity of a group relative to the productivity of the dominant alone (Reeve & Ratnieks, 1993). This convention was followed by several later models (Nonacs, 2002; Cant & Johnstone, 2009). Reeve & Emlen (2000) replaced k with a productivity function, $g[N]$, that decreases with increasing group size (N). Nonacs (2001) and Nonacs *et al.* (2004) redefined k as an absolute value (e.g. k/x_α = original k). Models by Buston *et al.* (2007) and Buston & Zink (2009) replace Nonacs' k with "G". However, Reeve (2000) and Reeve & Shen (2006) define k and G as the amount of group productivity that would be possible if there was no within-group conflict ($x = y = 0$). Thus, in these models $k(1 - x - y) = G(1 - x - y)$ = Nonacs' k = Buston's G. Finally, Reeve *et al.* (1998) and Johnstone (2000) set maximum potential group productivity equal to unity (since they did not include the non-cooperative options).

(3) Ultimate *versus* proximate models

The use of similar variables across various skew models has helped obscure a more significant difference between them. In an evolutionary sense, transactional models ask an ultimate-level question: i.e. when do individuals gain more fitness by being in a cooperatively breeding group than by living alone? By contrast, compromise models predict the within-group skew that results from a given proximate competitive mechanism for apportioning reproduction. This has led to several misconceptions in predictions and testing across reproductive skew models. To unravel these problems, we now examine more closely the two types of models.

(4) Transactional models

From the standpoint of either dominant or subordinate group members, the reproductive skew of the group must lie between p_{min} and p_{max} for the inclusive fitness gained from cooperation potentially to equal or exceed that gained from non-cooperation. The difference between these two values is the window for group stability (Buston & Zink, 2009). If $k > x_s + x_d$ (the group stability minimum: Nonacs, 2001), then a potential solution window exists for any pair of individuals, regardless of their relatedness. Furthermore, if $r > 0$ then complete skew (where one individual does all the reproduction) is possible whenever $k > x_s/r + x_d$ (Reeve & Ratnieks, 1993). Thus, for any k between the stability and complete skew conditions we would expect to find a zone of "incomplete control" (i.e. both the dominant and subordinate would reproduce: Reeve & Ratnieks, 1993).

It is possible to narrow this window of incomplete control somewhat by considering internal threats: the subordinate could threaten a fight for dominance, and the dominant could threaten eviction from the group. If the subordinate has $f > 0$ chance of overthrowing the dominant in a fight, it may pay the dominant to grant it a peace incentive [$p_p = \{fx_d + r[(1 - f)x_d - k]\}/k(1 - r)$, (Reeve & Ratnieks, 1993) modified for absolute values of reproductive success rather than relative values where $x_d = 1$]. A peace incentive gives subordinates more to lose in a fight, and therefore, more incentive not to fight. It pays all dominants to 'bribe' subordinates into joining groups and not to fight for dominance whenever $p_p \geq p_{min}$, which is true if $f > x_s/[x_d(1 - r)]$. However, peace incentives are only possible if x_d and x_s are intrinsic individual qualities that cannot be won in a fight. If they also include the chances of winning an initial fight for resource possession (see Buston *et al.*, 2007; Buston & Zink, 2009), then no peace incentive is possible (p_p cannot be greater than p_{min}).

Buston & Zink (2009) show that dominants and subordinates can also negotiate skew relative to their inside (cooperative) and outside (non-cooperative) options. In this case, the dominant can 'extort' the subordinate by threatening to evict it from the group. Dominants can increase

skew until subordinates would do better by either leaving the group or engaging in a fight for dominance. Up to this point, subordinates still gain higher fitness by giving in to the extortion. Beyond this point, threats and aggression by the dominant become counterproductive, and group tranquility should be common. Not surprisingly, having a zone of conflict predicts that competitively inferior subordinates should rarely, if ever, proportionally dominate reproductive output.

Extortion can narrow the range of evolutionarily stable skews only if there is a group resource that can be won that is separate from the group members. Threats by the dominant are credible only if $k > x_d$ holds after eviction of the subordinate. For a number of cooperative group types, this is likely to be true. The group may share a nest, territory or access to mates that only the victor of the fight will possess. However, in other types of groups $x_s < x_d < k$ may be intrinsic to the individuals themselves. For example, one individual may be more robust and hence more likely to maintain a better nest and less likely to lose territory or be usurped by intruders. Also, attractiveness to mates may be intrinsic or a function of being in a group. Thus, the dominant displaying male in a pair of cooperating turkeys might be able to evict its subordinate (Krakauer, 2005), but only at the cost of reducing the total expected reproductive success from k to x_d.

Thus in summary, transactional models lay out three regions of skew. First, there are levels of skew that cannot be reconciled with all group members having higher *IF* than by being solitary. If such levels of skew are observed in a cooperative group, cooperation must evolve for reasons other than within-group sharing of reproduction. Second, there are levels of skew that are potentially possible from *IF* calculations, but are unlikely because fighting to monopolize resources has the higher payoff. Finally, there is a region where the levels of skew should be acceptable to all group members, and relatively peaceful coexistence is the rule because escalated conflict does not benefit any group member. No existing transactional model predicts where an ESS solution would lie within this zone of shared reproduction. Such predictions are the province of compromise models.

(5) Compromise models

All compromise models assume that individuals can potentially increase their reproductive share within groups by competing or acting in some selfish way. This competition is resolved such that the dominant's proportion of the offspring is: $f(x) / [f(x) + f(y)]$, where competitive "effectivenesses" are determined by functions of x and y. All previous compromise-type models set $f(x) = x$ and examine situations where $f(y) = by$, with b being an effectiveness constant ($0 < b < 1$) independent of both x and y (Fig. 1: black lines). Competition is costly for the group. Reproductive output is decremented linearly by the proportion: $1 - x - y$, with the constraint that $x + y < 1$ (Table 1). Skew is predicted by solving for the evolutionarily stable state (ESS) values of x^* and y^*, where
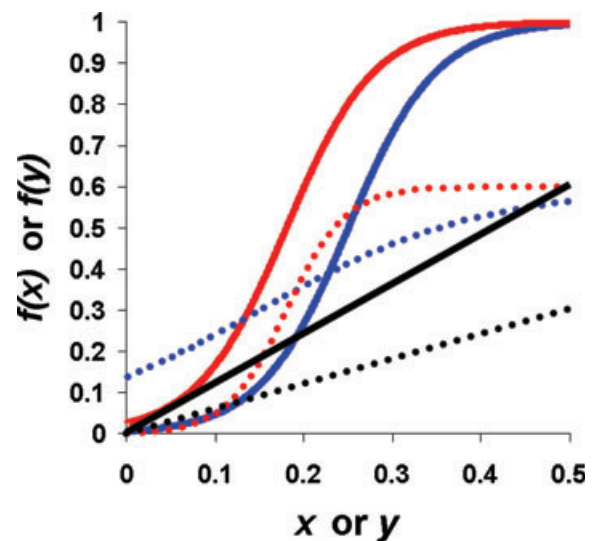

Fig. 1. Competitive effectiveness of dominants (solid lines) or subordinates (dotted lines) as a function of competitive investment (x or y). Competitive effectiveness is either linear with a constant value (black lines, where $f(x) = x$ and $f(y) = by$, and b is a constant), or determined by the non-linear function: $f(x)$ or $f(y) = b_i/(1 + e^{-a(i-m)})$, where b_i is a constant with $i = x$ or y and a and m are constants that define curve shape. Two non-linear cases are used. Case 1 (red lines) assumes both individuals use similar competitive mechanisms and is shown with equation constants of $a = 20$ for the dominant, $a = 30$ for the subordinate, and with $m = 0.18$ for both. Case 2 (blue lines) assumes individuals use differing competitive mechanisms and is shown with $a = 18$ and $m = 0.2$ for the dominant, and $a = 10$ and $m = 0.15$ for the subordinate. For the linear relationship and Cases 1 and 2, curves are drawn with $b_x = 1$ and $b_y = b = 0.6$.

no mutant dominant or subordinate strategy competing at a different level can invade the population (Reeve *et al.*, 1998). Compromise models are then used to predict the effects on skew and aggression of differing values of relatedness (*r*), competitive effectiveness (*b*), group productivity (*k* or *G*), and ecological constraints (various labels: Table 1).

Some have attempted to synthesize transactional and compromise models by having some portions of reproduction that are conceded (transactional in nature) while other portions are contested (with a compromise solution) (Johnstone, 2000, Reeve & Shen, 2006). However, it is problematical as to whether any ESS solution is possible under the synthetic conditions. These issues are discussed extensively elsewhere (Reeve & Shen, 2006; Nonacs, 2007; Buston & Zink, 2009; Cant & Johnstone, 2009; Johnstone & Cant, 2009), and will not be revisited here. The most interesting results across all the compromise models are that four regions of interactions are possible. (1) At ESS, both dominant and subordinate have higher *IF* than compared to being alone. Cooperation is stable. (2) At ESS, both dominant and subordinate have lower *IF* than when being alone. Nonacs (2007) and Cant & Johnstone (2009) viewed cooperation as being unstable here. Reeve & Shen (2006)

argued that both dominant and subordinate would concede reproduction to maintain group stability (the mutual-pay model). (3 & 4) At ESS, only one group member has higher *IF* than when being alone. Nonacs (2007) viewed such groups as unlikely to be stable. Cant & Johnstone (2009) argued that whichever individual would lose *IF* due to group dissolution would be favoured to scale back competition to keep its partner cooperating. Hence like the Buston & Zink (2009) model, the threat of exercising an outside-the-group option results in negotiated stability. Reeve & Shen (2006) suggested that individuals with the higher *IF* would give minimum reproductive concessions (*P* or *Q*) to maintain stability (the dominant- and subordinate-pay models).

There is, however, an inherent problem shared by all compromise-type models in producing these four zones and their predictions about the effects of individual variables. They assume that competitive effort is translated linearly into both competitive effectiveness and reductions in group productivity. Reproductive skew is then determined by ratios of competitive effectiveness. One byproduct of this formulation is that any amount of selfish competition by the subordinate is rewarded in increased direct reproduction. Under most sets of conditions, this leads to very high predicted levels of conflict, particularly between unrelated individuals (Nonacs, 2007). Several other paradoxical predictions also follow (Reeve *et al.*, 1998; Nonacs, 2007). The subordinate is always expected to invest more in competition than the dominant ($y^* > x^*$), be it as a combination of competition, aggression, selfishness or laziness. The poorer the subordinate is at competing (decreasing b), the more effort it should invest (increasing y^*). Unrelated individuals should always use up exactly half the potential group productivity competing with each other ($0.5 = x^* + y^*$). It is interesting to note that these predictions have almost never been tested when matching compromise models to data. Indeed, they are just as mathematically valid and in many cases more testable than the ones mentioned above. The fact that these predictions are so obviously inconsistent with what is observed in cooperatively breeding groups may perhaps explain the paucity of empirical tests.

Let us now consider two exemplar cases where $f(x)$ and $f(y)$ are not linear with effort invested. In the first, $f(x)$ and $f(y)$ are similar S-shaped functions (Fig. 1: red lines). This would reflect a situation where minimal investment yields little return. Moderate investment yields an increasing payoff, but continued investment eventually asymptotes to maximum gain. Both dominant and subordinate employ the same competitive mechanism and thus the shapes of the curves are similar, but the dominant is the stronger competitor whenever $x = y$. The second case represents where the two use different mechanisms (e.g. the subordinate could be lazy, the dominant could use aggression). In this case, the subordinate has higher effectiveness with low levels of competitive investment, and the dominant is more effective at moderate to high levels (Fig. 1: blue lines). A linear effect ($1 - x - y$), on group productivity exists for both cases.

Using linear relationships for $f(x)$ and $f(y)$ produces "clean" results. As in Cant & Johnstone (2009), four zones of interactions result with combinations of G and the subordinate's relative maximum competitive ability (b in Fig. 2). As b increases from low to high, a dominant-concession zone is replaced with a subordinate-restraint zone. The subordinate is always more invested in competition than the dominant (Fig. 3). Decreasing relatedness predicts lower skew (the dominant takes a smaller proportion of reproduction: Fig. 4). None of these patterns, however, are always true with non-linear functions. The results are considerably less consistent (they are generated through numerical techniques as described in Nonacs, 2007). The subordinate-restraint zone can be greatly increased or vanish (Fig. 2). Dominants might concede with all levels of competitive ability (Fig. 2). Either group member might invest more in competition, or the subordinate may give up competing entirely (Fig. 3). Finally, the dominant's expected reproductive share may either increase or decrease as relatedness increases (Fig. 4). Interestingly, in Case 1 as the subordinate's competitive effectiveness approaches that of the dominant, the ESS solution predicts it will have the largest share of reproduction.

The results with non-linear functions can produce abrupt transitions in variable values because ranges of conditions have no ESS solutions. Instead, for every x value chosen by the dominant, the subordinate has a fitness-increasing y response, and *vice versa*. Thus, competitive interactions can cycle between two or three pairings of x and y depending on variable values (Fig. 3). The pattern is one of the subordinate escalating competition, followed by dominant escalation. However, as x increases, the subordinate's best strategy switches to not competing ($y \approx 0.001$). Thereafter, the dominant's best strategy is also to reduce competition and the escalation cycle begins again. Because we only consider two specific cases, the true variability in outcomes is likely to be much greater. Note also, that these results are without addressing the linear cost issue. Relaxing that assumption also may very well layer more variability on to the diversity of outcomes!

This variability in results emphasizes the proximate nature of compromise skew models. Relationships between variables depend explicitly on how conflicts are resolved within groups, the type of conflict, and the functional nature of how investment in competition pays off in direct reproduction gains. It has not been demonstrated that investment in competition has a linear payoff in competitive effectiveness. Indeed, intuitively it may be more likely to expect non-linear interactions. Regardless of which is expected, making specific, testable predictions becomes problematical. By simply choosing the appropriate functions, reproductive skew models could be made to fit all datasets. As a specific example, Rubenstein & Shen (2009) connect reproductive competition with overall social stress levels within cooperatively breeding groups. The connection is based on using the Reeve *et al.* (1998) compromise model. In this model, when $0 < b < 1$ then x^* is always less than y^*. This translates to predicting that subordinates are generally under greater levels of social
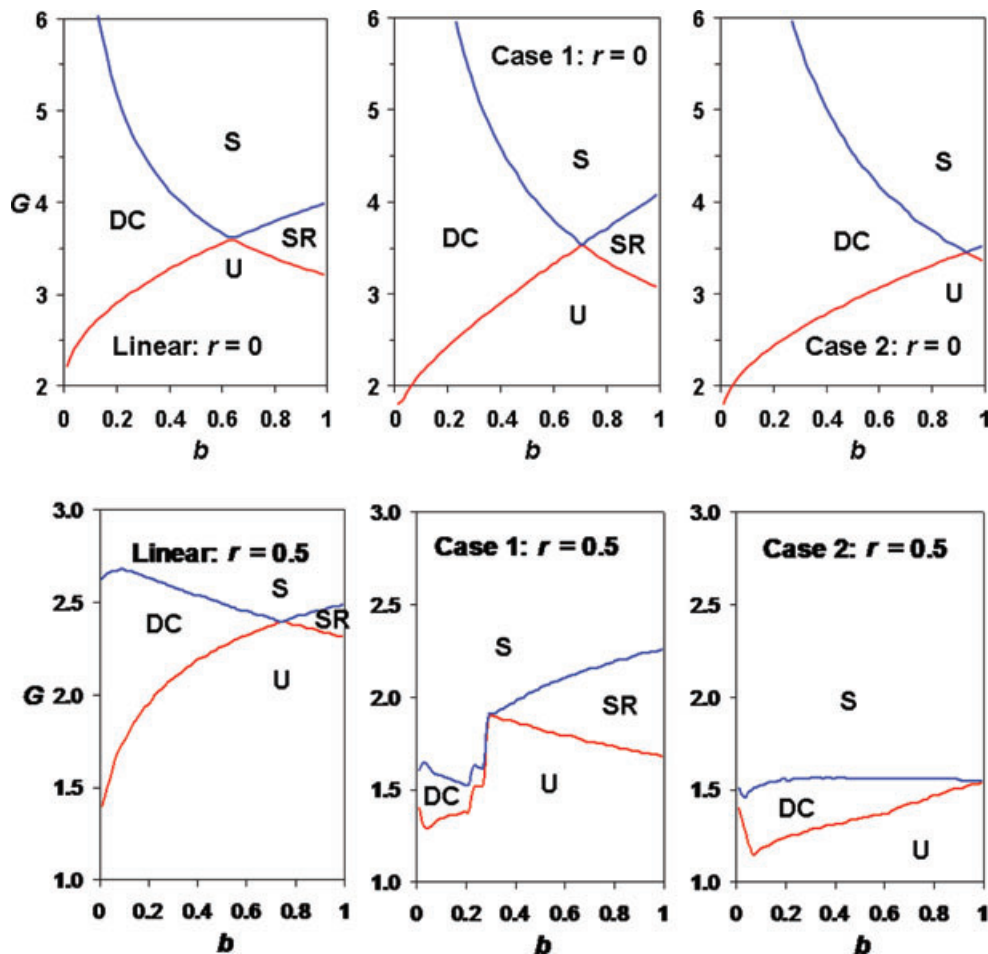
Fig. 2. Relationship of the relative maximum competitive ability of the subordinate (b) to group productivity (G) in predicting group stability. In all figures, groups below the red lines are unstable (U) because both the dominant and subordinate have better options outside the group. Above the blue lines both do better in a group and groups are stable (S). Following Cant & Johnstone (2009), the zones between the red and blue lines are where either dominants or subordinates must reduce their competitive levels to maintain group stability (DC = dominant concession; SR = subordinate restraint). The relationships of x and y to competitive effectiveness (linear, Case 1, Case 2) are as given in Fig. 1. Genetic relatedness $r = 0$ or 0.5.

stress. Every prediction made by Rubenstein and Shen's (2009) skew model is, however, potentially reversed if b, x and y interact non-linearly. This could be a serious limitation to the model's general applicability as a predictive connection between skew and stress could never be rejected.

III. PREDICTIONS FROM REPRODUCTIVE SKEW MODELS

Testing reproductive skew models can be greatly hampered by difficulties in measuring key variables. As noted above, for many species it may not be possible to measure competition-related variables such as "b", "x" and "y", their interactions, or their effect on skew. Thus testable predictions must be robust even when a number of quantitative relationships between variables are unknown. Across transactional and compromise models, we can derive four such predictions.

(1) Transactional models define the limits of acceptable skew between individuals of any given level of relatedness, and these limits apply to compromise models as well. Any group in which the skew lies outside of these bounds strongly rejects the whole of reproductive skew theory. A corollary to this prediction is that outside options matter. The relative ability of individuals, especially subordinates, to change groups or succeed on their own should affect within-group skew by changing the window of potential cooperation (Buston & Zink, 2009; Cant & Johnstone, 2009). There are two notes of caution, however. First, it is often predicted that increasing group productivity or decreasing solitary productivity increases cooperation and skew. This can be misleading as it is the relative, and not the absolute, productivity that matters (Nonacs, 2006b). For example if both are doubled or halved simultaneously, it will have no
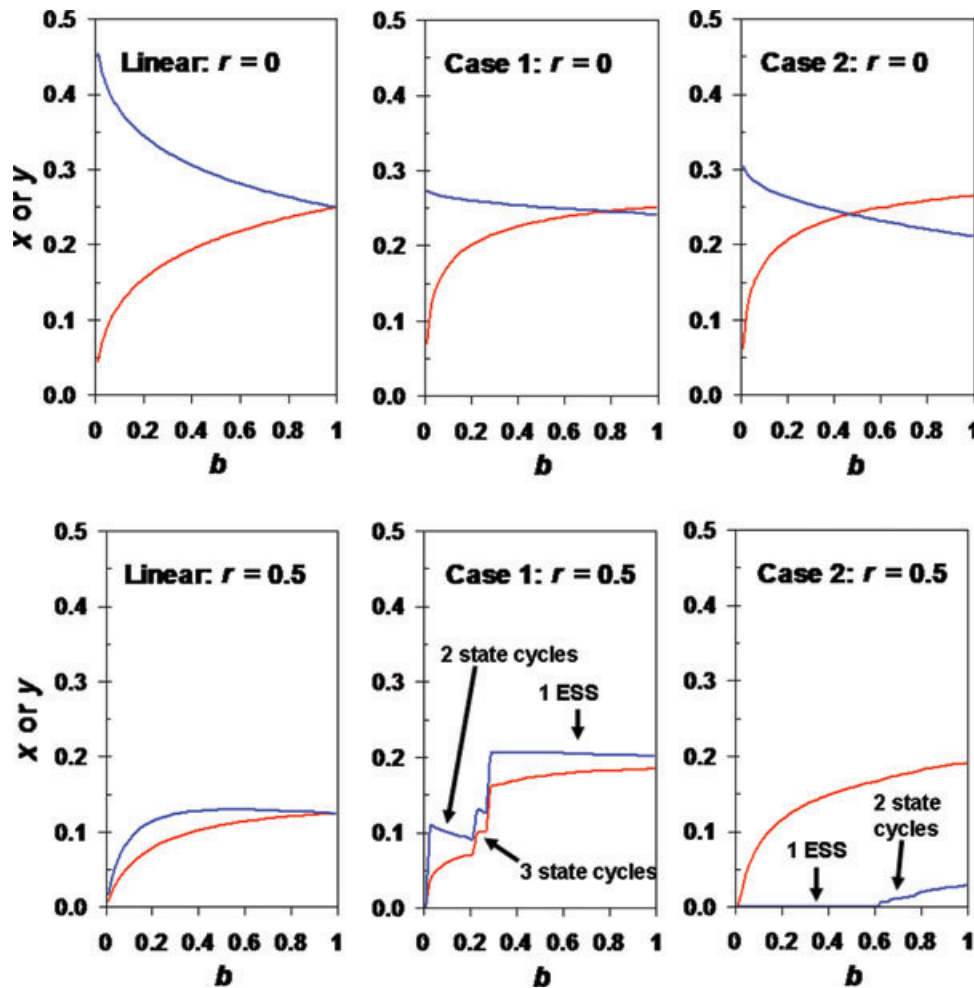
Fig. 3. Relationship of the relative maximum competitive effectiveness of the subordinate (b) to the ESS investment level in competition (x or y). In all figures, the red and blue lines are the dominant's and subordinate's evolutionarily stable states (ESS) for investment, respectively. The relationships of x and y to competitive effectiveness (linear, Case 1, Case 2) are as given in Fig. 1. Genetic relatedness $= 0$ or 0.5. With Cases 1 and 2, some ranges of b with $r = 0.5$ have no stable ESS and the groups cycle through 2 or 3 states of x and y (see text). For these non-ESS outcomes, the average x or y value is plotted. Neither in the linear nor non-linear cases did G (group productivity) have an effect on x or y.

effect on within-group dynamics. Only changes in the environment that differentially affect group success matter for reproductive skew models. Second, to define the window of acceptable skew requires individuals having realizable, non-cooperative outside options. In species where solitary living is absent or rare it may be impossible to test if skew is within acceptable bounds, and varying group productivity would have no predicted effect (see also Cant & Johnstone, 2009).

(2) Relatedness matters. Although it may be impossible to quantify how relatedness should affect skew or whether increased skew correlates with increased relatedness (Figs 2–4), it almost always has some effect. Thus, reproductive skew theory predicts that groups with differing relatedness structures should have consistent effects on skew, competition or group stability.

(3) Competitive ability matters whenever group members compete for reproductive shares. For the same reasons as for relatedness, quantitative predictions may be impossible. Furthermore, competitive effectiveness is a far more varied and nebulous concept than relatedness and could potentially be expressed in a myriad of ways. Yet similar to relatedness, across a wide range of functional relationships competitive ability affects skew (Figs 2–4) and group dynamics such as peace incentives (Reeve & Ratnieks, 1993). Thus, measurable variance in individuals' superiority or inferiority should correlate with skew across groups. [Note, relatedness and competitive ability will have no effect on skew only when both the dominant and subordinate have fitness equal to their expectation as solitary breeders (Reeve & Shen, 2006). This result has been challenged
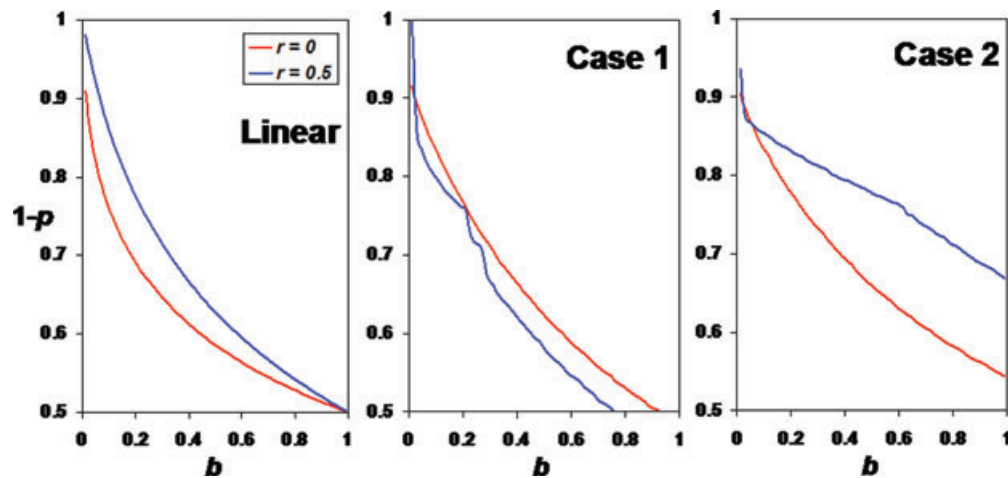
Fig. 4. Relationship of the relative maximum competitive ability of the subordinate (b) to the dominant's proportion of group reproduction ($1 - p$). The relationships of x and y to competitive effectiveness (linear, Case 1, Case 2) are as given in Fig. 1. Neither in the linear nor non-linear cases did G (group productivity) have an effect on p.

as unlikely to be common (Nonacs, 2007; Cant & Johnstone, 2009; Johnstone & Cant, 2009).]

(4) Stable groups may nevertheless exhibit unstable internal dynamics. The results from analysis with non-linear payoff functions suggest that levels of competition may be continually changing. Repeated patterns of competition steadily escalating and then suddenly subsiding would be consistent with conflict-resolution mechanisms with no stable equilibrium. Such cyclical dynamics may be more likely among groups composed of related individuals (Fig. 3).

IV. TESTS OF REPRODUCTIVE SKEW MODELS

Reproductive skew theory predicts that: (1) reproduction is routinely unequally divided within groups, sometimes to the point of complete monopolization by dominant individuals; (2) individuals may have varying degrees of control over the reproduction of other group members; and (3) some proximate mechanism of conflict resolution must exist by which individuals can adjust and react to changes in skew. However, the existence of skew is not in and of itself a validation of skew theory. Similarly, showing that a subordinate can control its own reproduction is consistent with some versions of skew theory, but does not test the basic premise of maximized *IF*. Finally, cooperative groups by their mere existence imply behavioural adjustments across their members and thus demonstrating the existence of conflict-resolution mechanisms does not validate either reproductive skew theory or any alternative model.

(1) Types of studies

We can align tests of reproductive skew theory according to their methodology and how likely the tests are to differentiate

between model variants, and more importantly, to reject optimal skew models, *in toto* (Table 2). Although transactional and compromise models do not describe processes at the same evolutionary level, we can distinguish them by assuming that if competition (and therefore all the correlates of competitive ability) is important, then a proximate compromise model would best match the observed results.

At the most basic level of testing skew theory, Category 1 (Table 2) broadly measures the effects of variables from skew models. The results of such tests may only suggest whether or not competition for reproduction is involved. For example, the reproductive skew among communally reproducing burying beetles (*Parastizopus armaticeps*), is random and size provides no apparent advantage (Heg *et al.*, 2006*b*). This result is consistent with a purely transactional skew model that requires no competition. However, if some correlate to potential competitive advantage had been found, a proximate compromise mechanism would have been supported. It is difficult, therefore, to imagine a result that would not be consistent with at least one type of model arising from reproductive skew theory. Thus it is not surprising that most studies in this category are consistent with reproductive skew theory, broadly considered (Table 2). Their main utility is to suggest future confirmatory tests in their particular study systems.

More informative as regards skew are Category 2 studies (Table 2) that measure correlations between model variables and skew or aggression. The latter is assumed to be an important competitive mechanism for resolving skew (Reeve & Nonacs, 1992, but see Nonacs *et al.*, 2004; Fanelli, Boomsma & Turillazzi, 2008). One problem with a correlational approach is that some variant of a skew model may match any given single prediction. This leads to many tests of skew theory tabling a range of predictions across models and then counting the matches from the observed data. The 'supported' model is the one with the most matches, or more often, the fewest mismatches. In a number of cases the best supported model also happens to be the one that makes the

Table 2. Summary of tests of reproductive skew models. Relationships between variables (r, relatedness; k, realized group productivity; x, realized productivity when solitary; b, competitive advantage or strength; N, number of group members; p, subordinate's proportion of group reproduction) that were found to be significant are denoted by "+" or "−", depending on their direction. No symbol means the relationship was non-significant. Under 'Model', "C" and "T" mean that the observed relationship is supportive of a compromise or transactional skew model, respectively. "None" means the result is not consistent with any skew model, and "?" means the result may be consistent with one or more skew models (depending on whether certain assumptions are met)

Organism	Methods	Relationships	Model	Results / conclusions	Reference
Category 1: tests for effects of skew model variables or for presence/absence of conflict resolution mechanisms					
Ant (*Linepithema humile*)	Established nests in lab with set number of workers and queens.	k & skew	C	Skew is low to absent across queens in terms of total offspring production. This is predicted when queens have no control over each other's reproduction. However, there is a negative correlation across sexes: if one queen produces females, the other produces males.	Fournier & Keller (2001)
Fish (*Neolamprologus pulcher*)	Created groups where helper varied in size relative to dominant breeders.	aggression & b (size)	T	Aggression very low overall, conflict resolution by submissive displays, avoidance, and reduced growth by helpers.	Hamilton *et al.* (2005)
Fish (*N. pulcher*)	Measured helping behaviour in naturally occurring and lab groups.	r & k (helping effort) +/−	T/C	Groups highly variable in relatedness and effect of r varies across sex in terms of whether unrelated individuals provide more or less help to breeders.	Stiver *et al.* (2005)
Beetle (*Parastizopus armaticeps*)	Induced communal breeding in lab.	b (size) & skew	T	Random sharing of reproduction, no competition observed between females.	Heg *et al.* (2006*b*)
Mammals (31 primate species)	Comparative analysis of male reproductive skew in species that vary in male number/group, tendency for philopatry and estrous in naturally occurring groups.	N (males) & skew − ; b (female synchrony) & skew	C None T	Assumes that control becomes harder as the number of competitors increases, thus reducing skew. Male philopatry is assumed to increase skew because outside options of leaving or switching groups are very poor. Female synchrony in estrous would allow males better control (higher b), but has no effect.	Kutsukake & Nunn (2006)
Fish (*N. pulcher*)	Varied separation between breeding substrata in aquaria.	b (proximity) & skew +	C	Reproductive skew correlates with physical proximity of dominant to subordinate (=ability competitively to control).	Heg & Hamilton (2008)
Mammal (*Callithrix jacchus*)	Analysis of reproductive success in marmosets in naturally occurring groups.	aggression & skew (not tested quantitatively)	C (T?)	Infanticide of subordinate females' offspring by dominant female, although there is little overt aggression prior to breeding.	Saltzman *et al.* (2009)
Bird (*Corvus brachyrhynchos*)	Genetic measure of parentage in naturally occurring breeding groups.	r & group membership	C	Only closely related male subordinates are tolerated within groups by dominant male. Although dominant disrupts all observed copulations, extra-pair paternity indicates incomplete control over parentage.	Townsend *et al.* (2009)

Table 2. *(Cont.)*

Organism	Methods	Relationships	Model	Results / conclusions	Reference
Category 2: tests for significant correlations to skew or aggression as predicted by transactional or compromise models					
Bird (*Sericornis frontalis*)	Measured shared paternity in groups, where males are unrelated to females in naturally occurring groups.	r & skew	None	Groups where males were related had higher skew than groups in which they were unrelated, but the effect was non-significant (see analysis in Koenig *et al.*, 2009).	Whittingham *et al.* (1997)
Wasp (*Polistes bellicosus*)	Measured relatedness and aggression on naturally occurring nests.	r & skew (whole nest) r & skew (pairwise) − b (size ratio) & skew + aggression & skew + N & skew +	None C T None None	No effect or a negative one of relatedness on skew. No effect of competitive advantage of larger size. Lower aggression by subordinates correlates with decreased skew. Skew is greater in larger groups. The latter two results are not predicted by any reproductive skew model.	Field *et al.* (1998)
Birds (*Turdoides squamiceps*)	Measured genetic parentage in cooperative Arabian babblers in naturally occurring groups.	r & skew + (males)	T	Unrelated male subordinates are more likely to sire offspring than related subordinates. However, skew is extremely high with the dominant male fathering 95% of the offspring.	Lundy *et al.* (1998)
Bees (*Ceratina* spp.)	Estimated skew model variable values from field and lab data.	r & skew − k & skew	None C	Individuals share reproduction within nests with little aggression (this combination is inconsistent with compromise models). Skew tends to increase as the relatedness of the subordinate to the brood decreases (this combination is inconsistent with transactional models).	Hogendoorn & Velthuis (1999)
Mammal (*Suricata suricatta*)	Genetic measure of skew in naturally occurring groups.	r & skew k & skew − b (weight) & skew − N & skew x & skew +	None None C ? None	Skew decreases with increased group productivity and subordinate body condition. However, skew increases for older subordinates even though their outside options are likely to be higher.	Clutton-Brock *et al.* (2001)
Wasp (*Po. carolina*)	Measured skew, aggression, body size and ovarian development on naturally occurring nests.	r & skew b (size) & skew k & skew aggression & skew	None T C T	A convention in terms of which wasp starts the nest or arrives first appears to be the strongest determinant of dominance.	Seppä *et al.* (2002)
Wasp (*Liostenogaster flavolineata*)	Measured skew and body size on naturally occurring nests.	r & skew b (size) & skew k & skew	None T C	One female almost always dominates the reproduction. Outside options may be very low and chances for nest inheritance are relatively high.	Sumner *et al.* (2002)

Table 2. (Cont.)

Organism	Methods	Relationships	Model	Results / conclusions	Reference
Bird (*Melanerpes formicivorus*)	Measured paternity in naturally occurring groups.	*r* & skew *N* & skew +	None None	Skew in reproduction by males unaffected by relatedness and increases with group size. Conflicting evidence whether increased ecological constraints correlate with increased skew.	Haydock & Koenig (2003)
Ant (*Formica fusca*)	Established nests in lab with set number of workers and queens.	*r* (queens) & skew − *r* (workers) & skew *b* (size) & skew *k* & skew	C None T C	Compromise model is best supported, but vital assumptions are not met (e.g. no overt queen-queen competition observed, and skew determined by workers).	Hannonen & Sundstrom (2003)
Ant (*Pheidole pallidula*)	Genetic measure of skew in naturally occurring nests.	*r* & skew *k* & skew *N* (breeders) & skew	None C ?	Skew in nests not consistent with transactional models and queen-queen competition is unlikely. Queens appear to tradeoff between producing sexual and worker-destined offspring.	Fournier *et al.* (2004)
Wasp (*Po. fuscatus*)	Experimentally removed brood from naturally occurring nests.	*r* & aggression *b* (size difference) & aggression *k* & aggression aggression & skew activity & aggression + aggression by other +	None None T None None C	Although wasps show numerous aggressive interactions, the frequency of acts does not correlate with variables predicted to be important by compromise models. Aggression is best explained by overall activity levels on the nest, which suggests it is not related to establishing reproductive skew.	Nonacs *et al.* (2004)
Mammal (*Macaca mulatta*)	Longitudinal data on reproductive success of male macaques in naturally occurring groups.	*r* & skew *b* (female synchrony) & skew	None T	Variable control of male reproduction that may be strongly affected by female choice.	Widdig *et al.* (2004)
Bird (*Cyanocorax morio*)	Genetic measure of skew in naturally occurring groups and observed aggression.	*r* & skew *r* & aggression −	None C	All offspring almost always produced by one female. Female choice may produce similarly high skew in males. Complete skew is difficult to reconcile with compromise model.	Williams (2004)
Wasp (*Parischnogaster mellyi*)	Measured skew and body size on naturally occurring nests.	*r* & skew *b* (size) & skew *k* & skew *N* & skew	None T C ?	Dominant produces most of the eggs, but skew does vary across nests. Egg-laying by subordinates is not done by the closest relative to the dominant.	Fanelli *et al.* (2005)
Ant (*Leptothorax acervorum*)	Genetic measure of skew in naturally occurring nests.	*r* & skew *k* (workers) & skew *r* & *k*	None C T	Low overall skew across nests, no observed queen-queen interactions. Individuals have no outside option.	Hammond *et al.* (2006)
Wasp (*Po. dominulus*)	Genetic measure of skew in naturally occurring nests.	*r* & skew *N* & skew	None ?	Rejects transactional skew models as groups can be composed of unrelated wasps, but still have complete skew.	Liebert & Starks (2006)

Table 2. *(Cont.)*

Organism	Methods	Relationships	Model	Results / conclusions	Reference
Mammal (*Meles meles*)	Genetic measure of skew in naturally occurring groups of badgers.	r & skew r & k k & skew r & N (females) −	None T C None	Skew models do not appear consistently to predict reproductive shares. Resource availability and access to breeding sites may be more important in determining skew.	Dugdale *et al.* (2008)
Wasp (*Pa. mellyi*)	Measured skew, aggression and body size on naturally occurring nests.	r & skew b (size difference) & skew k & skew N & skew aggression & skew − r & aggression b & aggression k & aggression + activity & aggression +	None T C ? C None None None None	Although aggression by subordinates appears to be effective in gaining reproduction (reducing skew), the magnitude of the effect is not consistent with compromise models. Dominants still control, on average, 95% of the reproduction. No skew model consistently matches the predictions.	Fanelli *et al.* (2008)
Mammal (*Eulemur fulvus rufus*)	Genetic measure of male skew in naturally occurring groups of lemurs.	r & skew N (# of males) & skew k (# of females) & skew −	None ? None	No evidence for reproductive control across males because number of competitors had no effect. Supports a priority-of-access model rather than the compromise skew models.	Kappeler & Port (2008)
Mammal (*Propithecus verreauxi*)	Genetic measure of male skew in naturally occurring groups of lemurs.	r & skew	None	Reproduction was almost always monopolized by one male, although little aggression or competition was observed. Suggests males are queuing for access.	Kappeler & Schäffler (2008)
Mammal (*Gorilla beringei*)	Observed skew in copulations of male gorillas in naturally occurring groups.	r & skew N & skew	None ?	No evidence that subordinate males' access to females is affected by their relatedness to dominant silverback. Subordinates not more likely to gain copulations when more males are present.	Stoinski *et al.* (2009)
Category 3: comparative analyses for significant differences across populations as predicted by transactional or compromise models					
Ants, bees & wasps (17 species)	Compared skew in groups composed of individuals from the same generation (semisocial) *versus* mother–daughter (matrifilial) associations.	matrifilial > semisocial	T	In 16 of 17 species skew in matrifilial groups was equal to or greater than in semisocial groups, within the same species.	Reeve & Keller (1995)
Birds & mammals (22 species)	Compared skew across species composed of individuals from the same generation (semisocial) *versus* mother–daughter (matrifilial) associations.	matrifilial > semisocial	T	13 species are known to reproduce only in matrifilial groups. All reproduction is done by one individual (complete skew). Two species are known to reproduce only in semisocial groups and reproduction is shared. Seven species reproduce in both types of groups. Of these; one always has complete skew, one always shares reproduction, and five have complete skew when matrifilial, but can have shared reproduction when semisocial.	Reeve & Keller (1995)

Table 2. (Cont.)

Organism	Methods	Relationships	Model	Results / conclusions	Reference
Bird (*Porphyrio porphyrio*)	Compared two populations with differing constraints on solitary nesting.	r & skew + x & skew − r & N + r & aggression +	T	The characteristics of the two populations vary in accordance with transactional skew models.	Jamieson (1997)
Bird (*Corcorax melanorhamphos*)	Compared social coalitions before and after a severe drought.	r & skew + x & skew +	T,C T,C T None	Coalitions have lower relatedness after a drought and skew decreases. This is consistent with predicted effect of relatedness, but increased constraints on breeding predict increased skew.	Heinsohn *et al.* (2000)
Ant (*Le. acervorum*)	Compared sociobiology and reproductive skew across populations.	r & skew +	T	Reproduction is more shared in populations with lower relatedness between queens. However, social structure and reproductive skew exhibit little variance within populations and do not respond to changes in environment. This suggests a fixed genetic polymorphism rather than flexible behavioural responses to relatedness or other factors.	Gill *et al.* (2009)
Birds	Meta-analysis across 15 populations of co-breeding females and 15 populations of co-breeding males.	r & skew +	T	Several patterns including coalition size, within-group skew, and ecological constraints were consistent with transactional skew models.	Koenig *et al.* (2009)
Category 4: manipulate variables predicted to be significant by transactional or compromise models					
Bee (*Exoneura nigrescens*)	Created groups of varying relatedness in naturalistic setting. Manipulated x and k.	r & skew − k & skew x & skew r & k +	C C None C	Best matches the compromise model. At the time of the experiment it was thought outside options should have no effect on compromise models (but see Cant & Johnstone, 2009).	Langer *et al.* (2004)
Wasp (*Po. dominulus*)	Experimentally removed brood from some nests.	aggression & skew	None	Subordinates increased laying and skew decreased on nests. No changes in aggression were triggered by this change in skew.	Liebig *et al.* (2005)
Fish (*N. pulcher*)	Set up lab groups with a breeding pair + one helper male and female. Created outside option by adding breeding pots.	b (size) & skew − x & skew	C None	A compromise model was assumed because conflict was observed between fish. The model, however, could not fully explain the results. At the time of the experiment it was thought outside options should have no effect on compromise models (but see Cant & Johnstone, 2009).	Heg *et al.* (2006a)
Bee (*Exoneura robusta*)	Skew measured in naturally occurring and semi-natural nests.	r & skew (reused nests) r & skew(new nests) − k & skew r & k	None C C T	No one model fully explains the data. Suggests that different reproductive skew models might apply at different life-history stages.	Langer *et al.* (2006)

Table 2. *(Cont.)*

Organism	Methods	Relationships	Model	Results / conclusions	Reference
Wasp (*Po. dominulus*)	Measured aggression on nests after removal of some wasps or addition of an adoptable nest.	N & aggression — x & aggression —	C C?	Aggression between wasps increases with fewer individuals on the nest. Aggression decreases when another nest is available. (It is unclear whether nest addition affects x or k. If the latter, the result does not support compromise.) Also, the manipulations increased wasp activity levels but this was not controlled for in the analyses (see Nonacs *et al.*, 2004).	Tibbetts & Reeve (2008)
Wasp (*Po. dominulus*)	Moved nests founded in the field into lab. Removed dominant or brood from some nests.	r & skew r & aggression	None None	When a subordinate replaced the removed dominant, there was no change in skew (the new dominant laid as many eggs as its predecessor). There was no conflict over succession. Many of the subordinates were unrelated, but this had no effect.	Monnin *et al.* (2009)
Category 5: estimate if inclusive fitness of group living exceeds outside option					
Bird (*Gallinula chloropus*)	Genotyped offspring from naturally occurring communal nests.	r & skew + p > outside option	C C	Skew higher in groups of more closely related birds (mothers and daughters mostly). Data consistent with subordinate fitness equaling or exceeding outside option.	McRae (1996)
Bee (*Xylocopa pubescens*)	Estimated skew model variable values from field data.	p < outside option r & skew	None None	Species has very high skew and high aggression (this combination is inconsistent with compromise models). Relatedness appears to have no significant effect within nests. Subordinates do not forage and may be waiting to inherit nest.	Hogendoorn & Velthuis (1999)
Bird (*M. formicivorus*)	Genetic measure of skew in naturally occurring nests.	p < outside option	None	Skews experienced by some females are such that they would seem to do better by leaving the group. Male skew is high but appears to be due to female choice.	Haydock & Koenig (2002)
Wasps (5 spp. with 11 populations)	Compared reproductive success of groups *versus* solitary individuals (under mostly naturally occurring situations).	p < outside option	None	Skew models correctly predict cooperation (or non-cooperation) in 10 of 11 populations. Cooperation between full sisters is predicted with any level of skew, but cousins and unrelated wasps would do better employing their outside options.	Nonacs *et al.* (2006)

fewest specific predictions (Nonacs, 2006*b*). Taborsky (2008, 2009) further points out that such an approach is also vulnerable to the pseudo-proof fallacy. A model's assumptions might be seriously violated, but results could nevertheless appear supportive for completely unrelated reasons. Thus the most insightful studies are those that examine multiple relationships (e.g. Field *et al.*, 1998; Nonacs *et al.*, 2004; Fanelli *et al.*, 2008). Consistently supported predictions across several comparisons are less likely to be pseudo-proofs. By contrast, mixed or consistently negative results strongly suggest cooperation has not evolved through the precepts of reproductive skew models. However, causation may not be obvious for significant correlations. For example, aggression may produce skew, but aggression could also be a response to an unfavourable skew.

Category 3 studies (Table 2) analyze differences across species or populations where differences in ecology or social systems can generate robust predictions for how reproduction is apportioned. Such comparisons act as evolutionary manipulations of skew variables. The drawback is that multiple factors may vary simultaneously. For example, two populations of pukekos (*Porphyrio porphyrio*) vary in the ecological constraints on solitary nesting (i.e. *x*), but this could simultaneously affect group productivity (*k*) and potential group size (Jamieson, 1997). Thus, comparisons across multiple variables may not be independent.

Rather than over an evolutionary timescale, Category 4 (Table 2) includes studies that manipulate one or more variables predicted to be important in setting reproductive skew. Unlike Category 2, these tests can determine causal relationships, and unlike Category 3, variables can be manipulated independently (e.g. Langer, Hogendoorn, & Keller, 2004). However, even if results are consistent with one type of model, it may not test fully reproductive skew theory unless it can be shown that the inclusive fitness of group members is higher than their non-cooperative, outside options. Studies that do estimate the fitness of both inside and outside options are in Category 5 (Table 2).

(2) Summary of results

Inspection of Table 2 reveals several strong trends. First, Category 3 population or species-level differences in reproductive skew are reasonably well predicted, especially by transactional models. Because all reproductive skew models are based on Hamilton's rule, such a result argues that kin selection is an important factor shaping the dynamics of shared reproduction at the species level. However, the evidence is relatively weak that across-group, within-population differences in cooperation are driven by manipulation or conflict over reproductive skew. The strongest within-group tests (Categories 4 and 5) of reproductive skew theory rarely provide unequivocal support. Indeed, three of the four studies that measured the potential *IF* of the outside option found that the subordinate's share of reproduction (*p*) was often less than the required minimum for cooperation to have higher fitness (Table 2). Thus, reproductive skew theory is rejected in its entirety for these species.

Our previous analysis of reproductive skew models found that differences in relatedness across groups should affect skew (although the magnitude of these effects may not be quantitatively predictable). Furthermore, compromise models predict that competitive advantage (either as an expected physical correlate to *b*, or aggression itself), should also correlate with skew. The sum of studies of across-group variation within populations (Table 2, excluding Category 3), however, finds that 34 of 45 such measured correlations are non-significant (seven are significantly negative and four are positive). Recent studies on the effect of aggression on skew in wasps have suggested that the two may not be related (Nonacs *et al.*, 2004; Fanelli *et al.*, 2008). Instead, the behaviours generally labeled as "aggression" may be better viewed as activity regulation (Sumana & Starks, 2004). This highlights another problem with testing reproductive skew models—rarely is there independent validation that the proposed behavioural mechanism for resolving skew (e.g. aggression, selfishness, laziness) is actually involved in doing so. Therefore, it is possible that all the correlations that involve either "aggression" or characters assumed to be important for creating competitive effectiveness were measuring factors unrelated to setting skew. Nevertheless, if we restrict the analysis only to correlations between relatedness and skew, 21 of 27 are non-significant. This strongly suggests that reacting to the specific relatedness of other group members is not widely important for determining reproductive skew within groups.

Lack of correlation between certain variables can be predicted by reproductive skew models. For example, purely transactional models predict that reproductive shares are conceded and therefore competitive ability (*b*) should have no effect on skew or aggression. Thus, 13 of 18 such correlations being non-significant could be considered as support for that model type (Table 2). Conversely, only three of 18 correlations between skew and *x* or *k* was significant within populations. This pattern supports compromise-type models which predict that within-group competitive abilities primarily determine reproductive shares. Obviously it is difficult to reconcile these two contradictory patterns on the importance of competition into one reproductive skew model. On the other hand, the plethora of non-significant correlations involving *r*, *b*, *k*, and *x* seriously suggests that these factors are not being continually monitored by individuals for establishing or adjusting within-group reproductive skew. This constitutes a strong rejection of all forms of current reproductive skew models for predicting the dynamics of reproductive sharing within groups.

V. ALTERNATIVE MODELS

The majority of studies listed in Table 2 do not unequivocally support reproductive skew theory. In many such cases, failures have been attributed to factors not explicitly included within the models. Some of these include control of skew by non-breeders (Hannonen & Sundstrom, 2003), inbreeding avoidance (Clutton-Brock *et al.*, 2001), mate choice (Haydock

& Koenig, 2002; Williams, 2004), and limits to mating access to the opposite sex (Kappeler & Port, 2008). Although all of these factors may be important in setting skew, none of them address the fundamental mismatch between theoretical predictions and observed behaviour. Why do subordinates (mostly) remain in groups that do not maximize their inclusive fitness? To answer this question, it is important to consider alternative models to reproductive skew theory. Here, we discuss three such alternatives.

(1) Mistakes and rules of thumb

The simplest null alternative is that genetic kin recognition is difficult and potentially error-prone (Liebert & Starks, 2006). Also, there may be situations in which individuals would gain advantages if others were uncertain about their absolute level of genetic relatedness (Reeve, 1989). Thus, if a species has a life history such that close kin generally tend to aggregate, then simple rules-of-thumb may suffice usually to place individuals in fitness-maximizing situations. For example, full sisters in paper wasps appear to gain enough through increased group productivity that cooperation between them is favoured even with complete skew, as is commonly the case (Nonacs, Liebert & Starks, 2006). However, *IF* considerations predict that more distantly related individuals ought to demand more equal sharing of reproduction, and such individuals are often present in groups (Queller *et al.*, 2000; Liebert & Starks, 2006; Zanette & Field, 2008). Nonacs (2006*b*) therefore compared the predicted fitness outcomes for hypothetical wasps that behaved "transactionally" and set reproductive skew based on perceived genetic relatedness to those that behaved "conventionally" and cooperated with complete skew but only with individuals perceived to be full sisters. Therefore, transactional wasps would cooperate with perceived non-kin, but conventional wasps would not. Various levels of kin recognition mistakes were considered. The transactional strategy was always optimal and resulted in higher *IF*. However, the difference relative to acting conventionally was often trivial. Negligible gains in fitness could thus prevent the evolution from a conventional to a transactional system if costly kin recognition mechanisms must first be created. That the best solutions for problems might lie on relatively flat plateaus of fitness is a common problem for optimization approaches (Gladstein *et al.*, 1991). Hence the selective pressure to evolve such solutions may be too weak to overcome any costs or genetic correlations and drift. Future tests of reproductive skew theory, therefore, need to be cognizant of how likely the predicted behaviour is to increase fitness significantly relative to more simple rules for group structuring.

(2) Queuing, delayed and lifetime fitness

In a number of species the dominant reproductive individual can die or be superseded during the lifetime of a subordinate. In response, subordinates may form a queue waiting for an opportunity to become dominant (Hogendoorn & Velthuis, 1999; Kokko & Johnstone, 1999; Haydock & Koenig, 2002; Sumner *et al.*, 2002; Bridge & Field, 2007; Field & Cant, 2009). Thus measuring skew at one given moment in time may significantly underestimate a subordinate's expected *IF*, because while in a queue the subordinate may have no direct reproduction (e.g. Hager, 2009). Furthermore, if the subordinate never rises to the top, its lifetime direct reproduction may remain zero. Hence the expected *IF* for a queuing strategy would have to be estimated across the lifetimes of multiple subordinates. One such estimate for paper wasps found that queuing for dominance was unlikely to payoff at a high enough rate to predict that distantly or unrelated subordinates ought to join groups (Nonacs *et al.*, 2006).

Still queues seem to be a regular feature of wasp societies and replacement of dominant egg-layers appears to proceed smoothly when needed (Field *et al.*, 1998; Fanelli, Boomsma & Turillazzi, 2005; Bhadra & Gadagkar, 2008; Monnin *et al.*, 2009). In general, how queues and dominance hierarchies are created and maintained is one area where using a skew model framework may be particularly insightful (see Buston & Zink, 2009). Certainly if *IF* considerations are important this should create limits to the length of a queue and the willingness of unrelated or poorly competing individuals to enter into a group at the end of a long queue. Again in paper wasps, individuals that have different expectations about gaining reproductive status on a nest behave in predictably different patterns (Chandrashekara & Gadagkar, 1992; Bhadra & Gadagkar, 2008). In another example, unrelated wasps tend to be found near the top of dominance hierarchies rather than distributed randomly within hierarchies (Zanette & Field, 2009). Certainly the distribution of relatedness and activity patterns across individuals in different positions in a queue deserves considerably more study in order to reveal the dynamics of group stability.

(3) Group selection

Recently Wilson & Hölldobler (2005) reinstigated the group *versus* kin selection debate by arguing for the primacy of group-level benefits in the evolution of cooperative traits (and claiming that kin selection is mainly a "dissolutive" force). It is not our intent to review that ongoing debate here. However, considering a multilevel selection approach to the evolution of reproductive skew may be warranted because a number of within-group, nepotistic kin selection explanations for life-history traits have been found wanting. We can list several examples. (1) The haplodiploid genetic advantage in raising sisters rather than offspring is unlikely to be the causative factor for eusocial evolution in Hymenoptera (Queller, 1989; Gadagkar, 1990; Nonacs, 1991). (2) There is no evidence for nepotism in queen-rearing (i.e. favouring a full sister, $r = 0.75$, over a half-sister, $r = 0.25$) in social insect colonies composed of patrilines of half-sister workers (Tarpy, Gilley & Seeley, 2004). (3) Enforced worker sterility (worker policing) is consistent with kin-selective advantages, but an alternative hypothesis of colony-level efficiency has not been rejected or adequately tested (Pirk *et al.*, 2004; Nonacs, 2006*a*, but see Beekman & Oldroyd, 2005). Because the basic element

of reproductive skew theory is its emphasis on behavioural responses to differences in relatedness, its failure as a general explanation for within-group patterns of reproductive skew must be added to the above list of examples.

One important motivation for examining reproductive skew as a group-level phenomenon is to understand the role of genetic relatedness, *per se*. For example, four studies found that as relatedness increases, skew decreases (Field *et al.*, 1998; Hogendoorn & Velthuis, 1999; Hannonen & Sundstrom, 2003; Langer *et al.*, 2004). A genetic explanation can be that more related individuals have more similar fecundities and reproductive strategies. Thus genetic affinity rather than a transactional skew model could account for these results (Hannonen & Sundstrom, 2003).

Equally interesting is the idea that genetically dissimilar groups could be more productive due to positive, across-individual epistatic interactions (known as "social heterosis", Nonacs & Kapheim, 2007, 2008). Nonacs & Kapheim (2007) listed 32 examples from a wide range of taxa (viruses to humans) where genetically diverse groups gained functioning, survival or reproductive advantages. As genetic similarity may result in reduced skew, genetic dissimilarity could produce the opposite. Again, skew could be an evolutionary byproduct and not the driving factor for sociality. The evolution and maintenance of such interactive genetic diversity, however, is only possible in group-structured populations. Thus, a conceptual approach that includes multilevel selection is required to model the process.

Across-group selection would clearly favour more cooperative and peaceful groups over more selfish and antagonistic ones (Nonacs, 2007). Thus, increased within-group competition for reproductive share would diminish group productivity and lead to a disadvantage in competing with other groups. Indeed, Reeve & Hölldobler (2007) have shown that across-group competition will select for reduced within-group competition and aggression.

VI. FUTURE OF REPRODUCTIVE SKEW

Skew theory to date has primarily used a game theoretic approach to generate quantitative predictions about reproductive shares. An individual's behaviour or 'strategy' depends on the behaviour of other interacting group members (Reeve *et al.*, 1998; Johnstone, 2000; Reeve & Shen, 2006; Nonacs, 2007; Buston & Zink, 2009; Cant & Johnstone, 2009). In essence, models seek sets of strategies (which may determine the parentage of offspring by dominants and subordinates) that are evolutionarily stable states (ESS: Maynard Smith, 1982). At the ESS, no mutant strategy can invade the population and stability is defined by specific parameter values. Hence the game-theoretic approach to skew offers one set of explanations for why individuals are social rather than leading solitary lives. However the generally poor explanatory power of skew models (Table 2; Taborsky, 2009) leads to questions of whether they yield a

complete picture and truly capture the causes underlying the evolution of skew and sociality.

The failure of current reproductive skew theory to provide a robust explanation for the evolution and maintenance of cooperative breeding raises the question of how to proceed next. There are a number of available routes. Firstly, on a case-by-case basis we can examine reasons for why individual studies fail to support reproductive skew theory such as inadequacy of parameterization, difficulties in obtaining data that truly reflect model parameters, and implausibility of model assumptions. A number of these are discussed extensively elsewhere (Kokko, 2003; Taborsky, 2009). Secondly, as discussed above, is to develop a more comprehensive set of theoretical models that concentrate on conflict-resolution mechanisms. Such models would have to consider both internal group dynamics (e.g. how is cheating successfully deterred), and external factors such as options for solitary breeding and across-group competition for space and resources. A third route would be to examine closely the area in which skew theory has had some predictive success: the differences in patterns of reproductive sharing across species and populations (e.g. Reeve & Keller, 1995; Jamieson, 1997). Identifying and experimentally manipulating the potential causative factors would certainly help to illuminate the relative importance of reproductive skew in social evolution.

For the remainder of this review, however, we will concentrate on a fourth avenue: the new insights into the proximate and ultimate causes of skew that could be gained by adopting a quantitative genetics approach. We view this approach as complementary to the above as it expands the range of questions about reproductive skew that can be investigated. The utility of quantitative genetics is that it could answer a fundamental question about cooperative reproduction. Is reproductive skew, itself, the primary focus of natural selection? Secondarily, what are the individual traits that are responsible for reproductive skew and what is the nature of selection on them? An understanding of the genetics and selection pressures on reproductive skew would be useful to whatever avenues are traveled by future research.

(1) Skew and quantitative genetics: a new perspective

Beginning with Fisher's (1918) seminal paper, evolutionary change has been modeled using quantitative genetics. This emphasizes traits that vary by degree as opposed to traits that differ qualitatively such as eye colour. In predicting the consequences of selection, quantitative genetics makes two key assumptions. First, that individual gene effects, usually at many loci, are small compared to other sources of phenotypic variation. Second, that factors other than the direct effects of genotypes also influence the phenotypes of individuals in populations (which are loosely defined as a larger group of individuals, Falconer & Mackay, 1996). Among these factors are non-genetic sources of variation such as environmental effects, dominance and the interactions

between genes through epistasis. In essence, a quantitative genetic analysis allows the partitioning of phenotypic variation into genetic and non-genetic causes. This quantification permits predictions about evolutionary change for a given trait and the genetic composition of populations after selection.

In principle, there are two ways in which skew could be modeled as a quantitative trait. In the first approach, the focus is on reproductive share itself as the quantitative trait under selection. In the second approach, the focus is on the genetics of quantitative traits that affect skew. While the latter approach posits that reproductive skew is a consequence of selection on one or more specific behavioural or life-history traits the former approach allows a direct investigation of the genetics of an individual's reproductive share (see below for an example). Most experimental tests of skew models have implicitly adopted the second view through a reductionist approach of measuring individual behavioural variables (e.g. aggression as in Nonacs *et al.*, 2004).

The first approach's perspective is akin to Falconer's notion that 'the character that natural selection selects for is fitness' (Falconer & Mackay, 1996, p. 335) where other traits change because they correlate with fitness. This approach may seem counterintuitive at first since individuals differ in their share of reproduction because of individual differences in the expression of traits (e.g. the degree of dominance shown). Yet, adopting this view may yield a conceptually clearer approach both for theoretical and empirical work. The central advantage is that it captures any joint effects across the traits of interest and avoids the predicament of having to bridge the gap between how individual traits may evolve and how this will affect the partitioning of reproduction in the group as a consequence.

The second approach analyzes the genetics of traits expected to affect skew, such as aggressiveness or propensity to cooperate. This method investigates not only the genetic basis of the specific traits, but also important covariances that are crucial in understanding past evolution and constraints (Harris & Hager, 2009). However, looking at the genetics of individual traits does not answer the question of how the expression of these traits affects skew, which remains to be resolved for even those key traits identified by skew models. In the following section we give a brief outline of the genetical approach and how it may be applied to research on reproductive skew. We note that the discussed approaches are in principle applicable both to investigating the genetics of reproductive share itself and that of traits affecting individual reproductive share.

(2) The genetic basis of skew

(a) Variance components

In its most basic form, phenotypic variance (V_P) of a given trait in a population of individuals can be partitioned into genetic (V_G) and environmental components (V_E) (Falconer & Mackay, 1996):

$$V_P = V_G + V_E, \qquad (7)$$

where the genetic variance component can be further divided into additive (V_A), dominance (V_D), and that caused by gene-by-gene interactions (epistasis: V_I), such that:

$$V_P = V_A + V_D + V_I + V_E. \qquad (8)$$

Additive genetic variance is considered the most important component as it will respond to selection and thus determine the rate of trait evolution. Dominance occurs when a trait is affected by an interaction of alleles at the same locus while epistasis refers to allelic interactions across different loci. Historically, the latter two variance components are thought to have a generally smaller role in evolution than additive effects (Hill, Goddard & Visscher, 2008). This is summarized in Fisher's fundamental theorem, which states that the increase in fitness in a population is proportional to the additive genetic variance at that time in the population (Fisher, 1930). The response to selection (R), equivalent to the difference between generation means, is therefore predicted solely from the (narrow-sense) heritability of a trait, $h^2 = V_A/V_P$, such that $R = h^2 S$ where S is the strength of selection.

(b) Heritability

The heritability ($h^2 = V_A/V_P$) of a trait informs about the degree of environmental versus genetic influences and thus how a trait might respond to selection (see Visscher, Hill & Wray, 2008). High estimates signify that a large proportion of phenotypic variation is due to genetic variation in the focal population, while the reverse holds for low heritability. Traditionally, low heritability has been interpreted as an indication for strong directional selection of the trait in question and selection on traits closely correlated with fitness is expected to produce low heritability (e.g. Burt, 1995 but see Houle, 1992; Nonacs & Kapheim, 2007). However, several studies that measured fitness-related traits found substantial genetic variation for these (e.g. Mousseau & Roff, 1987; Houle, 1992). Two reasons for these findings have been suggested. First, fitness is a composite trait in the sense that many components contribute to variation and thus many combinations of values in the component traits may confer high fitness, not just one set ('the optimal world': Houle, 2000). Therefore, variation in the component traits can be maintained although little variation is found for fitness itself. The second hypothesis asserts that a lack of stabilizing selection and continual environmental perturbations prevent a population from attaining an optimal state in terms of fitness ('the cruel world': Houle, 2000). Note that low heritability does not imply the trait is not genetically determined, but instead, that the population exhibits little genetic variation in the trait.

We can apply this line of argument to reproductive skew. If reproductive share is strongly tied to fitness effects at one or a few loci, we would expect reproductive share as a

trait to exhibit low heritability. Conversely if reproductive share is largely due to overall physical robustness, we would predict high heritability due to many different loci affecting individual condition. Mutational input summed across loci would be high making it difficult for selection to act directly on reproductive share. As for future research, comparing the heritabilities of several key traits predictive of reproductive share ought to yield interesting insights into which traits appear to link closely to fitness (with low heritability) and which do not (high genetic variability and heritability; but keeping in mind the above qualification). With such information we can begin to unravel why and how cooperative breeding evolved.

(c) Covariance

The covariance of the focal trait with other fitness-relevant traits is particularly salient to making predictions about the potential for evolution. Covariance specifies how the expression of a trait X will affect expression of a correlated trait, Y. For example, if a negative covariance exists, an increase in X will cause a decrease in Y. This negative effect on Y can therefore constrain the evolution of X. Moreover, if we assume that reproductive share $\mathcal{Z}$ (or some other trait that affects skew) is likely to be correlated with fitness F, the response to natural selection will depend on the additive genetic covariance between the two and the response R is given by:

$$R = \text{cov}_A\left(\mathcal{Z}, F\right), \qquad (9)$$

which may be positive or negative. Assuming that multiple traits affect reproductive share, the change in share can be modeled as a function of covariances of the various traits:

$$\Delta\mathcal{Z} = G_{11}\beta_1 + G_{12}\beta_2 + G_{1j}\beta_j, \qquad (10)$$

where $\Delta\mathcal{Z}$ is the mean generational change for reproductive share $\mathcal{Z}$. G_{11} is the additive genetic variance of trait 1, with β_1 being the selection gradient on that trait. G_{12} is the genetic correlation between traits 1 and 2 and the selection gradient on 2, β_2. G_{1j} is the genetic correlation between traits 1 and any other trait, j, and its selection gradient β_j, which is given by the partial regression coefficient of selection acting directly on each trait (Lande, 1979; Lande & Arnold, 1983). Thus, the effect of selection depends on the strength of selection across all correlated traits on fitness. For example, antagonistic effects on fitness between correlated traits can explain why trait expression is lower than would be expected from focusing on isolated traits (e.g. Gratten et al., 2008).

How can the consideration of covariation among traits help answer questions about the ultimate causes of skew? While genetic covariances are more difficult to obtain empirically due to the large numbers of related individuals required, phenotypic covariances are often good estimates of genetic covariances [Cheverud's (1988) conjecture] and more easily obtainable. Correlations between traits most relevant to reproductive share such as aggression and cooperation could be quantified empirically and used to predict the direction of trait change. Consider a simple example where aggression determines both the propensity to cooperate and, thereafter, reproductive shares. Although there would be positive, directional selection favouring higher levels of aggression to gain reproductive shares, observed levels of aggression might be low or moderate. This would follow from a negative correlation to cooperation where highly aggressive groups either cannot form or break up before reproducing. In other words, evolution of aggression is balanced between the gain it provides within groups and the cost of increased destabilization of those same groups. Thus, to better understand causes of skew we need to know much more about possible correlations between traits that determine skew.

This would also be greatly informative for game-theoretic or optimality models in defining the parameter space in which stable solutions are possible where some areas of parameter space might be more likely to produce stability than others. The opportunity to evaluate the likelihood of parameter space seems particularly relevant to the recognition in the latest skew models that the behavioural mechanisms available for resolving reproductive conflicts may significantly affect the expected levels of skew (Nonacs, 2007; Buston & Zink, 2009; Cant & Johnstone, 2009).

(d) The social environment: indirect genetic and maternal effects

Skew occurs in groups of multiple breeders and can occur through social interactions between group members (Harris & Hager, 2009). If the behaviours displayed by other members in the group have a genetic basis, we can quantify the extent to which the phenotype (e.g. the reproductive share) of a focal individual is influenced by the genotypes of group members (see Box 2b. in Wolf et al., 1998). In other words, how does genetic variation of interacting individuals affect a focal phenotype? The notion of indirect genetic effects is conceptually important because an environment composed of other individuals would have a genetic basis and can thus be heritable and evolvable (Wolf et al., 1998; Wolf, 2003). Indirect genetic effects can be an important source of variation. For example, they explain up to 18% of variation in pupa length and mass in Drosophila melanogaster compared with 34% of direct additive effects (Wolf, 2003).

Perhaps the most influential effects in the social environment are those caused by maternal effects. This 'frequent, and often troublesome source of environmental resemblance, particularly with mammals' (Falconer & Mackay, 1996, p. 159) can both be genetic (maternal genes affecting maternal phenotype) and environmental (e.g. nutrition) in nature and may explain up to 50% of phenotypic variance in a trait (Cheverud & Moore, 1984). As with indirect genetic effects, maternal genetic effects are subject to selection and can thus evolve. In essence, the response to selection of a focal trait (given by $R = h^2 S$) is modified positively or negatively by the maternal effect's response to selection in the previous generation, thus generating a time-lag in evolutionary response (Roff, 2006). Especially if we are interested in the heritability and sources of variation in traits that affect

skew, maternal effects are important considerations since they influence trait heritability. Indirect genetic effects, on the other hand, may help to determine the extent to which variation in reproductive share is due to the genotypes of group members. This may be particularly useful in assessing the importance of social interactions in determining skew across taxa with very different physiologies and life histories.

(e) Non-genetic environmental effects

Ecological conditions are key predictors of skew since these will affect group productivity and solitary breeding success. Thus, environmental conditions are part of many game-theoretic skew models (e.g. Cant & Johnstone, 2000, 2009; Hager & Johnstone, 2004; Buston & Zink, 2009). For example, relatively harsher conditions for independent breeding could favour higher levels of reproductive skew (Buston & Zink, 2009; Cant & Johnstone, 2009). One simplification in these models, however, is that all group members are assumed to be affected similarly by a change in the environment. This can be misleading as different individuals (e.g. dominant *versus* subordinate) could be affected by the changes in a significantly different manner. For example, a given behaviour or trait may change in one individual as a consequence of environmental change but not in others.

In a quantitative genetic framework it is possible to determine how important environmental conditions are for trait expression. The environmental component becomes another source of phenotypic variation, albeit one without a genetic basis that cannot respond to selection (unlike indirect genetic effects). The environmental effect can either be direct and thus independent of genotype (main effect) or depend on genotype due to the presence of an interaction between genotype and environment. The genotype by environment interaction is given by:

$$z_i = G_i + E_i + G_i * E_i, \qquad (11)$$

where E_i is the direct (main) effect and $G_i * E_i$ is the interaction between genotype and environment that contributes to variation in trait i with value z. This allows assessing the importance of environmental effects relative to genetic variance components as well as the dependence of genetic effects underlying traits of interest on the environment. For example, Valdar *et al.* (2006) demonstrated in rodents that the proportion of variance accounted for by common environment ranges between 11 to 25% for body mass but was lower for behavioural traits. Importantly, the authors found that interaction effects were frequently greater than the main effects. A key question that can be resolved using the quantitative genetic approach is whether individuals and their reproductive shares differ in how they are affected by environmental conditions. Of course, appropriately quantified, environmental effects can be entered as main and interaction effects into any regression analysis of potential predictors of skew to estimate both significance and proportion of variance

in skew explained. This allows, for example, comparing levels of skew found in different populations and its dependence on ecological conditions (e.g. Hager, 2009).

(3) Empirical work

(a) Identifying predictor variables

Several quantitative genetic approaches can be used in empirical work on the genetics of skew to partition variance components and estimate genetic and non-genetic effects. Although obvious perhaps, a first step is to identify key predictors of skew using appropriate statistical tools. While many parameters identified in skew models such as competitiveness, ecological constraints and, indeed, the level of skew itself might be rather difficult to quantify (see Kokko *et al.*, 1999; Tsuji & Kasuya, 2001; Nonacs, 2003), it is not an insurmountable task if one considers proxy parameters that are more easily measured. For example, individual competitiveness can be measured by the degree to which individuals win agonistic interactions (Ellis, 1995) and ecological constraints may be measured by rainfall (assumed to correlate with resource abundance: Emlen, 1982; Clutton-Brock *et al.*, 2001; Hager, 2009; Rubenstein & Shen, 2009). In a similar manner one can identify and measure parameters thought to influence skew empirically and then ask which of these significantly predict skew and calculate the relative importance of specific predictor variables using the corresponding mean square error and total model error (bearing in mind pitfalls about causality). This can be achieved with general linear models (GLMs) or mixed models that allow the inclusion of both random and fixed effects. At the same time, a statistical analysis of skew can help inform future theoretical work by identifying parameters affecting skew. This approach may also be useful when comparing skew across different groups of the same species that live under different environmental conditions (e.g. Jamieson, 1997).

(b) Experimental design

The goal of using quantitative genetics tools is to obtain estimates of the variance components such as additive effects, and thus heritability, or the interaction of genotype with environmental factors. The most common approaches are breeding designs and intercrosses between inbred strains, so-called F2 designs. On the one hand, breeding designs take advantage of known relatedness between individuals (either parents and their offspring or among siblings) and then use phenotypic correlations to estimate genetic variance components. On the other hand, in an F2 design, two inbred strains are intercrossed and the F2 generation is geno- and phenotyped to conduct a marker-based quantitative trait locus (QTL) analysis. This searches for locations in the genome that harbour genes underlying the variation in the phenotypic traits of interest. While potentially appropriate to study the genetics of skew-relevant traits, at present these two approaches appear to have limited utility for

research on group-living, cooperative species with multiple group members. A challenge for future work is establish how such methods can be used to study the genetics of reproductive share directly due to the constraints imposed by the required experimental design in taxa in which skew can be meaningfully investigated. For details on breeding designs and QTL mapping see Falconer & Mackay (1996), Lynch & Walsh (1998), and Mackay, Stone & Ayroles (2009).

(c) Recombinant inbred lines

With the development of large panels of so-called recombinant inbred (RI) strains in mice it is now possible to investigate the genetic basis of a given trait, such as propensity to cooperate, without the need for genotyping. Many mouse species are cooperative breeders where more than one female breeds at a time. Prior work has investigated reproductive skew in several species (Solomon & Getz,1997; Gerlach & Bartman, 2002; Rusu & Krackow, 2004). Recombinant inbred mice capture a large part of the naturally occurring genetic variation in mice and seem a good system to study the genetics of cooperative behaviour for example. Briefly, RI strains consist of many lines, each of which is defined by a fixed recombination pattern of exactly two possible alleles (e.g. Silver, 1995). RI lines are homozygous at all loci but there is no complete homogenisation of the genome (as in inbred strains) and can be maintained indefinitely. From the parental intercross of two inbred mouse strains, families are derived and then continuously inbred within a family, thus 'freezing' the unique recombination pattern of the resulting line (Silver, 1995), and no costly genotyping is required. We can therefore directly investigate the genetic basis of phenotypes we are interested in because the genotypes are known at a vast number of loci. Using marker-based statistical models we can determine the additive genetic variance and search for QTL across the genome for candidate genes that affect the trait in question. Any data obtained in subsequent experiments can be used additively in further mapping studies because the genotypic variance does not depend on individual experiments. Thus, if additional experiments are required, these can be performed at later stages using the same genotypes.

The use of RI lines seems particularly suitable to investigate the genetic basis of traits thought to determine skew as one 'only' has to phenotype several individuals from a sufficiently large number of RI lines. The phenotypic data become response variables in a statistical QTL model, and the genotypic scores (derived from the genotypes) are the predictors (see e.g. Hager et al., 2008). The QTL model then yields information (logarithm of odds, LOD, scores) on where in the genome possible candidate genes are located that modify the measured phenotypes and what their effect sizes and heritabilities are (see e.g. Hager et al., 2009a, b for details of calculations). Heritabilities can be obtained from the estimates of the additive effects and phenotypic variance (Falconer & Mackay, 1996, p. 126).

To give an example, in a laboratory setting the genetics of reproductive share could be established in an experiment using RI lines. The most suitable set of RI lines is the largest mammalian genetic reference panel, the BXD mouse set (e.g. Chesler et al., 2005). In a hypothetical experiment using females from 30–40 different BXD lines, cooperative behaviour among communally breeding females could be measured in groups with a standard genotype female, such as from the inbred mouse strain C57Bl/6J. We assume that variation in cooperative behaviour among females from the 30–40 lines is due to genetic differences between these RI lines. Once quantified, our measure of cooperative behaviour can be analyzed using web-tools (www.genenetwork.org) or using appropriate QTL models (see above). The result of such analyses obtains the probabilities of QTL that may harbour candidate genes for cooperative behaviour across the entire genome. Thus, we can assess whether variation among individuals in the propensity to cooperate has a genetic basis or not. Furthermore, we can calculate the heritability of cooperative behaviour and make inferences about past selection on this trait but also covariances with other traits. Of course, having established the genetic basis of cooperative behaviour does not answer the question of how reproductive skew in a group is affected by the degree of within-group cooperation. This question can be addressed using linear models (see Section VI. 3a).

(d) Animal model: variance components

More promising than breeding or F2 designs is the animal model approach, which can estimate genetic and environmental variance components in systems with complex pedigrees (Lynch & Walsh, 1998). With its origins in animal and plant breeding research, this statistical model has been used to study the genetic basis of life-history traits in a number of wild populations (see e.g. Milner et al., 1999; Kruuk et al., 2000). Using mixed linear models that allow both fixed and random effects, the animal model requires pedigree information in addition to phenotypic data. In its most simple form, the animal model is:

$$y_i = \mu + a_i + e_i, \tag{12}$$

where y_i is the trait value of individual i, μ is the population mean, a_i is the additive genetic effect, and e_i is the residual error or associated environmental effect. The model assumes that traits are affected by a large number of loci with small effects, with random sampling from a large, panmictic population. Thus, the additive genetic effects enter as random effects into the model. The model can be expanded to matrix form that specifies the genetic covariance between individuals, which takes into account the relatedness among individuals using the probability that a random allele in one individual is identical by descent to a randomly chosen allele in another individual (coefficient of coancestry; in the case of parents and offspring this value is 0.25):

$$y = X\beta + Zu + e, \tag{13}$$

where $\boldsymbol{y}$ is the vector of phenotypes from all individuals, $\boldsymbol{X}$ is the design matrix that relates each observation to fixed effects given in the vector $\boldsymbol{\beta}$, $\boldsymbol{Z}$ is the design matrix that relates each observation to the corresponding random effect represented by vector $\boldsymbol{u}$, which represents the variance—covariance matrix derived from the expected covariance between relatives (Pelletier *et al.*, 2007). The univariate animal model can be further expanded to accommodate multiple phenotypic traits in a multivariate set-up that allows estimating correlations between traits and thus the joint response to selection and evolution of a suite of traits. A multivariate approach seems particularly suitable to investigate the genetic basis of key traits influencing reproductive share as well as their covariances. Both life history (e.g. body size) and behavioural phenotypes (e.g. aggression) could be entered as response variables. Kruuk (2004) gives a comprehensive introduction into the model characteristics and its application to the study of phenotype data in wild populations.

(e) Animal model: QTL

In addition to determining genetic and non-genetic variance components, a few studies have searched for QTL underlying the variation observed in a trait of interest using an expanded animal model (polygenic model: Slate *et al.*, 2002; Slate, 2005; Beraldi *et al.*, 2007). To give an example, in a study on the genetics of birth mass in a wild population of red deer (*Cervus elaphus*), Slate *et al.* (2002) established a pedigree of over 350 individuals based on paternity analysis and behavioural observations. The pedigree was genotyped for 90 variable microsatellite markers and a linkage map was constructed to allow QTL mapping. The animal model was then parameterized as described above and the linear regression analysis revealed that birth mass (the response variable in their model) had moderate heritability and was affected by three distinct QTL located on three chromosomes. These results suggested that variation in birth mass does have a genetic basis explained by a few major genes with low to moderate heritability and may be under directional selection, contrary to predictions from Fisher's fundamental theorem.

(f) Genetics of reproductive share

Using the animal model, individual reproductive share could be measured in a wild population with a known pedigree and represent the response variable y in the above model. Using maximum-likelihood-based statistical models in appropriate programs (e.g. *Genstat*), the additive genetic variance and heritability can be estimated. Further, with suitable markers a QTL analysis could be conducted to find relevant genomic regions in which candidate genes are located that impact individual reproductive share. Undoubtedly, we expect many genes to be involved in this 'composite' trait because a multitude of different mechanisms, from developmental to behavioural, will affect individual reproductive share. While no study has yet looked at the genetics of reproductive share, Kruuk *et al.*'s (2000) work on a wild population of red deer provides a classic example for the use of the

animal models in studying the heritability of fitness. In line with predictions from Fisher's fundamental theorem, fitness (as measured by lifetime reproductive success) had a very low heritability. Importantly however, this was most likely caused by increased environmental variance for traits closely linked to fitness such as longevity as other traits not associated with longevity did show significantly higher heritabilities. The study further highlights that using the coefficient of additive genetic variance (which is scaled to the trait mean as opposed to the total phenotypic variance used to calculate heritability) yields a more accurate picture of underlying genetic variance of fitness-related traits. For any such analysis a good population pedigree with precise measures of paternity is required and the effects of sampling sub-populations or dispersal would have to be considered carefully when studying the heritability of reproductive share.

VII. CONCLUSIONS

(1) Reproductive skew theory has had a profound influence on the study of cooperative breeding and the division of reproductive shares. Since Reeve & Ratnieks' (1993) seminal work, the dominant theoretical paradigm has employed the dual ideas of maximizing Hamiltonian inclusive fitness and game-theoretic solutions to conflict. Across a large body of field and experimental work, however, the main tenets of reproductive skew theory have not been borne out. There is little evidence that individual group members routinely evaluate patterns of relatedness or competitive ability in order to set reproductive skew. The result is that differences in skew across groups in the same population have been poorly predicted by skew theory. Also counter to skew theory, some individuals appear to behave suboptimally and lose fitness by either joining disadvantageous groups or not leaving them.

(2) Reproductive skew theory has not been a failed pursuit. Negative results are often very illuminating and useful in guiding future research. We believe it is now important to re-examine the first principles of cooperative breeding. One would be to measure the advantages of group living, *per se*. To what degree is cooperation favoured by across-group advantages? Are particular patterns of skew or behavioural characteristics consistently associated with the most successful groups? How important is manipulation by parents or perhaps dominant group members in creating suboptimal behaviour in subordinates? None of these questions reject the fundamental importance of kin selection or conflict resolution as a game. They do, however, expand our consideration of group life to include group- and population-level context and across-generational indirect genetic effects.

(3) It is critical to answer the very basic question of whether reproductive skew, itself, is under strong selection. High heritability is certainly suggested in species where

reproductive skew appears unresponsive to internal group characteristics such as relatedness (e.g. Gill *et al.*, 2009). Quantitative genetics applied to studying skew could yield critical information on whether evolution acts on skew or particular characters that produce it. Given that a number of studies found little correlation of key behavioural or life-history traits to the level of skew we suggest that looking at the genetics of individual reproductive share itself seems more likely to advance our understanding of skew than focusing on particular traits associated with skew. However, investigating the degree to which covariance across traits facilitates or constrains the evolution of sociality may shed light on the discrepancies between the predicted and observed role of specific traits on the partitioning of reproduction in groups. For future empirical research, the animal model methodology may be particularly useful in this pursuit. Results of genetic studies on skew would be important guides for future development of both theoretical models and other directed experimental studies.

VIII. ACKNOWLEDGEMENTS

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