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Are reproductive skew models evolutionarily stable?

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Reproductive skew theory has become a popular way to phrase problems and test hypotheses of social evolution. The diversity of reproductive skew models probably stems from the ease of generating new variations. However, I show that the logical basis of skew models, that is, the way in which group formation is modelled, makes use of hidden assumptions that may be problematical as they are unlikely to be fulfilled in all social systems. I illustrate these problems by re-analysing the basic concessive skew model with staying incentives. First, the model assumes that dispersal is an all-or-nothing response: all subordinates disperse as soon as concessions drop below a certain value. This leads to a discontinuous 'cliff-edge' shape of dominant fitness, and it is not clear that selection will balance a population at such an edge. Second, it is assumed that subordinates have perfect knowledge of their benefits if they stay in the group. I examine the effects of relaxing these two assumptions. Relaxing the first one strengthens reproductive skew theory, but relaxing the latter makes evolutionary stability disappear. In cases where subordinates cannot accurately measure benefits provided by the individual dominant with which they live, so that their behaviour instead evolves as a response to population-wide average benefits, the logic of reproductive skew models does not apply. This warns against too indiscriminate an application of reproductive skew theory to problems in social evolution: for example, transactional models of extra-pair paternity assume perfect knowledge of paternity, which is unlikely to hold true in nature. It is recommended that models specify the mechanisms by which individuals can adjust their behaviour to that of others, and pay attention to changes that occur in evolutionary versus behavioural time.

Keywords: extra-pair paternity; evolutionary stability; reproductive skew; social groups

1. INTRODUCTION

In recent years, a group of so-called 'reproductive skew' models has become popular in explaining the evolution of social group formation (Reeve 1998; Johnstone 2000). To understand group living, it must be explained why it is beneficial for all members to stay in the group. Groups vary widely in how reproduction is shared among group members: in some species, skew is low so that most members obtain direct reproductive success (e.g. banded mongooses, *Mungo mungo* (de Luca & Ginsberg 2001); lions, *Panthera leo* (Packer *et al.* 2001)); in others, skew is said to be high and only one or a few dominant individuals breed (e.g. naked mole-rats, *Heterocephalus glaber* (Clarke & Faulkes 1998); Arabian babblers, *Turdoides squamiceps* (Lundy *et al.* 1998)). Skew models relate such variation to factors such as relatedness between group members, and the ease of finding breeding positions elsewhere ('ecological constraints').

Skew models by now exhibit an almost bewildering variety, although some effort has been made to understand them all under a comprehensive framework (e.g. Johnstone 2000). The most basic 'recipe' to build a skew model can be characterized in the following way. First, consider who can control reproduction: can the dominant decide this despotically, or is the matter more complicated? Next, specify what is the minimum fitness benefit that makes an association worthwhile for a specific individual (e.g. the subordinate). Then, calculate whether the individual who is in control (e.g. the dominant) benefits from yielding such a benefit to the other individual (e.g. the subordinate). For example, in a study where reproductive skew ideas were applied to extra-pair paternity in birds, it was assumed that females—who can decide on paternity—give just enough paternity to males to prevent them departing and not caring for the offspring (Shellman-Reeve & Reeve 2000). More complicated scenarios exist where there is not only one individual in the group who is in control (e.g. 'limited control' or 'tug-of-war' models (Reeve *et al.* 1998)).

(a) *Assumptions of who is in control are crucially important in reproductive skew theory*

Variation in this assumption can generate completely opposite relationships between, for example, relatedness and skew (Johnstone 2000; see also Clutton-Brock 1998; Clutton-Brock *et al.* 2001). Here, I will argue that the mechanisms of how individuals can influence others' decisions is even more important than previously recognized. I will show that reproductive skew models make implicit assumptions that may not always be met in nature. Consequently, some of the eagerness with which reproductive skew theory has been used to understand social behaviour may be problematical.

2. HIDDEN ASSUMPTIONS IN REPRODUCTIVE SKEW THEORY

To build my argument, I will develop an example that assumes dominant control as in the 'transactional' model

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of Reeve & Ratnieks (1993). According to this model, the dominant yields reproductive 'concessions' to subordinates. She will maximize her fitness if she yields the minimum concession p^* that is sufficient for the subordinate to benefit from staying more than from leaving. Consequently, groups in nature are expected to skew reproduction as predicted by p^*.

Such a derivation of p^* may be problematical for two reasons. The first reason is what I call the 'cliff-edge assumption'. The model assumes that evolution will proceed to a point where subordinates are 'just about to leave': any further reduction in concessions would make departure beneficial for them. Throughout the parameter region where subordinates do *not* leave, dominants benefit from reducing the concession p, as they gain more through direct reproduction than through reproduction of subordinates. This generates selection pressure for dominants to reduce concessions. Can we expect that an evolutionary process will dictate that dominants stop reducing concessions just *before* they become too meagre for subordinates to stay? This maximizes fitness just before a 'cliff edge' is crossed, below which fitness—in the absence of stable group formation—is much lower.

The second cause for concern is the question of behavioural versus evolutionary responses of individuals. For reasons that will become clear in a moment, I call this the 'perfect knowledge assumption'. A proper evolutionary analysis will determine which alleles can invade a population, if it currently has a specific gene composition. Phrased in terms of evolutionary game theory, one has to consider a population in which a certain strategy (e.g. the level of concessions given, p) is in use, and ask if there are alternative strategies that can invade the population (Metz *et al.* 1992; Dieckmann 1997). Here, it is important to be explicit about the factors that determine the success of the alternative, mutant strategy. What exactly will happen if, say, in a population where concessions average p, a dominant starts giving no concessions at all? It turns out that the answer depends on whether changes in individual behaviour occur only as an evolutionary response to population-wide changes in p, or whether individuals can react to a change in the concession p that their own dominant gives them. In other words, if a dominant suddenly changes the concessions slightly, will the subordinate be able to perceive this and change her behaviour accordingly? Here, I will show that the stability of equilibria will crucially depend on this assumption.

3. A MODEL OF REPRODUCTIVE SKEW WITHOUT CLIFF EDGES OR PERFECT KNOWLEDGE

To examine how the 'cliff-edge assumption' influences reproductive skew theory, it is useful to replace it with an alternative. The cliff edge arises because every single subordinate is assumed to depart as soon as concessions drop below p^*, while concessions equalling or exceeding p^* lead to subordinates staying without exception. I will now examine a scenario where subordinate departures become much more common when concessions drop below p^*, but the relationship between concessions p and subordinate behaviour is nevertheless continuous and smooth.

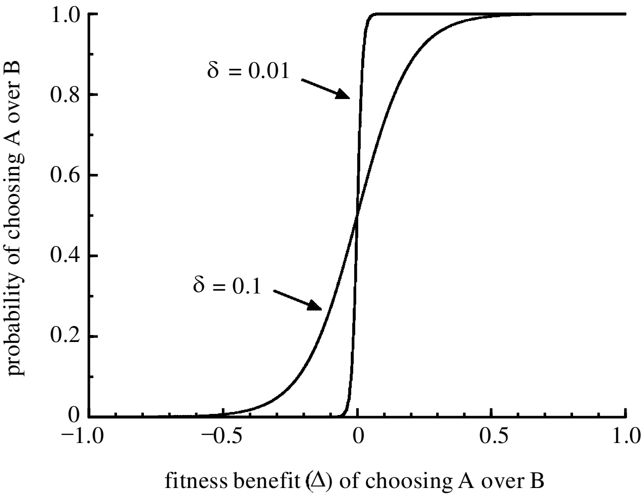

Figure 1. A simple way to model individual variability in behaviour (see McNamara *et al.* 1997 for details). When confronted with two alternative options A or B, individuals are assumed to usually choose A if it yields higher fitness ($\Delta > 0$). However, if the fitness difference is small, some individuals will choose B. The parameter δ indicates how many will do so: when δ is small, almost all individuals will make the correct decision.

McNamara *et al.* (1997) have argued that it is realistic to assume that some individual variation in behaviour always remains, especially when fitness differences between two behavioural options become very small. When two fitness options yield exactly the same fitness, the most natural assumption is to also assume neutrality in individual decisions (McNamara *et al.* 1997). Using the framework of McNamara *et al.* (1997), one may model the subordinate's departure probability as $d = 1/(1 + e^{-\Delta/\delta})$, where Δ indicates the fitness difference between departure and staying, and δ indicates the magnitude of 'error' in decision making (figure 1). When δ is small, subordinates almost invariably follow the strategy that yields them highest fitness. At larger values of δ, behaviour is variable so that 'incorrect' decisions occasionally occur.

Next, I will replace perfect knowledge with a less stringent assumption. Generally, selection pressure on any trait, such as concessions p given by dominants, depends on whether dominants with a lower (or higher) than average value of p have higher or lower fitness than average. According to the model of Reeve & Ratnieks (1993), a reduction in p is beneficial to the dominant, unless subordinates respond by leaving. But if subordinates (evolutionarily speaking) 'know' only the population-wide average p, they will not respond to individual variation in p, and subordinate departure decisions will not depend on the concessions that an individual dominant gives. This will give rise to selection pressure towards lower values of p. Over evolutionary time, this will increase the likelihood that subordinates depart. Nevertheless, even if subordinate departure is harmful for the dominant, an individual dominant is not penalized compared with the rest of the population if she gives smaller concessions than currently used in the population: the subordinates respond in evolutionary and not behavioural time. She can only be penalized if subordinates know the concessions given by the particular dominant that they associate with, and respond to lower than average concessions by departing more often than average.

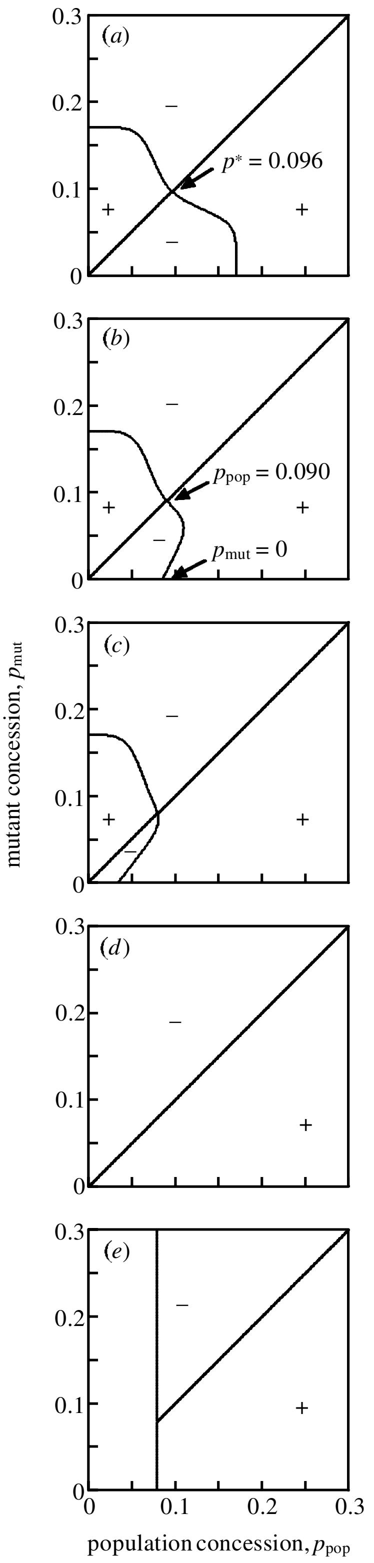

Figure 2. Model predictions for a case where classical reproductive skew theory predicts $p^* = 0.0789$. Parameters are $k = 1.2$, $x = 0.1$, $r = 0.05$, $\delta = 0.01$ and (*a*) $a = 1$, (*b*) $a = 0.5$, (*c*) $a = 0.2$, (*d*) $a = 0$. In (*e*), δ has been replaced by a dispersal probability that is a step function equalling 1 when Δ_{pop} is positive, and 0 otherwise. The model of (*e*) therefore makes the cliff-edge assumption (all subordinates behave identically) but does not assume that subordinates perceive changes in dominant behaviour (dispersal depends on Δ_{pop} rather than Δ_{mut}). Regions marked with '+' indicate a $\{p_{\mathrm{pop}}, p_{\mathrm{mut}}\}$ pair where the mutant strategy can invade the population strategy. Regions marked with '–' indicate that the population strategy cannot be invaded by this particular mutant strategy. Unmarked regions indicate that p_{mut} and p_{pop} are selectively neutral. Evolutionarily stable strategies occur if there is a point along the diagonal where the vertical deviations from the diagonal line $p_{\mathrm{pop}} = p_{\mathrm{mut}}$ indicating that all mutant strategies have lower fitness levels (there are only '–' regions above and below the point at the diagonal).

Whether subordinates can measure an individual dominant's level of concessions depends on the system being studied: it is easier for a female mongoose to know if she is allowed to breed, than for a male woodpecker to know how much paternity he has in the brood. The accuracy of knowledge can be modelled by a parameter a ($0 \leqslant a \leqslant 1$), which gives the probability that subordinates respond to a change in an individual dominant's behaviour. When knowledge is incomplete and dominants may deviate from the population-wide concession average p_{pop} and instead give a 'mutant' concession level p_{mut}, the subordinate's departure probability is given by

$$d = a d_{\mathrm{mut}} + (1 - a) d_{\mathrm{pop}}, \tag{3.1}$$

where d_{pop} and d_{mut} are departure probabilities as calculated by the method of McNamara *et al.* (1997) as follows:

$$d_{\mathrm{pop}} = \frac{1}{1 + \exp(-\Delta_{\mathrm{pop}}/\delta)} \tag{3.2a}$$

$$d_{\mathrm{mut}} = \frac{1}{1 + \exp(-\Delta_{\mathrm{mut}}/\delta)}. \tag{3.2b}$$

According to Reeve & Ratnieks (1993), a subordinate's inclusive fitness equals $k((1 - p)r + p)$ if she stays in the group, while departure gives her fitness $x + r$ (k = relative productivity of group; x = subordinate's success if departing; r = relatedness between subordinate and dominant). Thus, we have $\Delta_{\mathrm{pop}} = x + r - k[(1 - p_{\mathrm{pop}})r + p_{\mathrm{pop}}]$ and $\Delta_{\mathrm{mut}} = x + r - k[(1 - p_{\mathrm{mut}})r + p_{\mathrm{mut}}]$.

With this information, one can ask if a specific value of p_{pop} is evolutionarily stable. In a population using p_{pop}, dominant inclusive fitness equals $W_{\mathrm{pop}} = d_{\mathrm{pop}}(1 + rx) + (1 - d_{\mathrm{pop}})\, k[(1 - p_{\mathrm{pop}}) + r p_{\mathrm{pop}}]$, with d_{pop} calculated from equation (3.2*a*). A dominant that deviates from this pattern obtains fitness $W_{\mathrm{mut}} = d(1 + rx) + (1 - d)\, k[(1 - p_{\mathrm{pop}}) + r p_{\mathrm{pop}}]$, where d is calculated from equation (3.1). If $W_{\mathrm{mut}} > W_{\mathrm{pop}}$ for any p_{mut}, p_{pop} is not evolutionarily stable. This model takes account of variation in subordinate behaviour as well as the possibly incomplete knowledge of changes in dominant behaviour.

4. RESULTS

Invasion plots are a practical way to summarize invasion prospects of various mutant strategies (Dieckmann 1997). In figure 2, invasion plots are derived for various values of a, the accuracy with which subordinates perceive changes in dominant behaviour. The parameters used are $k = 1.2$, $r = 0.05$ and $x = 0.1$, which predict a concession $p^* = 0.0789$ according to Reeve & Ratnieks (1993). The value of the error parameter is $\delta = 0.01$, indicating relatively low individual variation in subordinate behaviour (i.e. almost all subordinates are assumed to make adaptively correct decisions).

In figure 2*a*, subordinates always know if their dominant deviates from the population average (as indicated by $a = 1$). The invasion plot indicates that when dominants give small concessions, larger concessions are selected for (indicated by the '+' region for concessions $p_{\text{mut}} > p_{\text{pop}}$ when p_{pop} is small; figure 2*a*). If dominants give large concessions, smaller concessions are selected for ('+' region for concessions $p_{\text{mut}} < p_{\text{pop}}$ when p_{pop} is large; figure 2*a*). There is thus stabilizing selection that leads to an evolutionarily stable equilibrium p^*. The solution does not exactly coincide with the prediction of Reeve & Ratnieks (1993) of $p^* = 0.0789$, but is closer to $p^* = 0.096$ (figure 2*a*: the point at which deviating from the line $p_{\text{mut}} = p_{\text{pop}}$ upwards or downwards leads to regions marked with '–' only; marked with an arrow). This difference arises because figure 2*a* does not make the cliff-edge assumption, but assumes that some subordinates depart already when p^* somewhat exceeds the value derived by Reeve & Ratnieks (1993). Qualitatively, however, figure 2*a* is not in conflict with conventional reproductive skew theory. Also, any variations in k, x or r change the position of the equilibrium in a similar manner as in classical reproductive skew theory (not shown in the figure). Therefore, replacing the 'cliff-edge' assumption with a more realistic scenario that allows for individual variation in behaviour does not drastically alter the predictions of reproductive skew theory.

The matter is different, however, when one relaxes the assumption of perfect knowledge, $a = 1$. In figure 2*b*, the subordinates' accuracy to detect changes in dominant behaviour is $a = 0.5$. There is an evolutionarily stable strategy (ESS) candidate with $p_{\text{pop}} = 0.090$: at this value, small changes in the dominant behaviour are selected against. However, this value is not stable, because $p_{\text{mu}} = 0$ in this case lies in the '+' region. In other words, dominants who give no concessions at all have higher fitness levels than dominants giving $p_{\text{pop}} = 0.090$. There is no value of p_{pop} that could not be invaded by alternative concessions. In figure 2*c*, the accuracy is $a = 0.2$, showing a similar but aggravated problem: many other concession values can invade the ones currently used. Finally, figure 2*d* assumes that subordinates completely lack the ability to perceive changes in dominant behaviour ($a = 0$, indicating that they only evolve to respond to average levels of p_{pop}). Reducing concessions is now always favoured ('+' for any value of $p_{\text{mut}} < p_{\text{pop}}$), and even though dominant fitness would be higher if subordinates stayed, the only stable equilibrium is $p^* = 0$, with no group formation.

It therefore appears that if subordinates cannot gain accurate knowledge of dominants' behaviour in behavioural (rather than evolutionary) time, the evolutionary equilibrium predicted by skew models ceases to be stable. Figure 2*e* confirms that this problem is due to lack of knowledge (parameter a) rather than the introduction of individual variation in subordinate behaviour (parameter δ): in figure 2*e*, subordinates are always assumed to make identical decisions. There is no stable equilibrium in this case either. Instead, large values of p are selected against, and p is neutral when the population-wide average of p is too small for any subordinates to remain in groups.

5. DISCUSSION

Skew models have become a popular way to frame empirical tests of social evolution (e.g. Reeve & Keller 1995; Jamieson 1997; Whittingham *et al.* 1997; Magrath & Heinsohn 2000; Clutton-Brock *et al.* 2001; Gerlach & Bartmann 2002; Nonacs 2002; Seppä *et al.* 2002), and deriving new versions of such models appears even more popular (Cant 1998; Reeve *et al.* 1998; Johnstone *et al.* 1999; Johnstone & Cant 1999*a*,*b*; Kokko & Johnstone 1999; Ragsdale 1999; Cant & Johnstone 2000; Crespi & Ragsdale 2000; Reeve & Emlen 2000; Shellman-Reeve & Reeve 2000; Nonacs 2002). Skew models have undoubtedly contributed positively to the field: simple models can help focus attention to similarities of apparently widely divergent social systems (the 'eusociality continuum' (Sherman *et al.* 1995)), and define the most important variables to study. The main enticement of skew models is, indeed, their simplicity: deriving minimum or maximum acceptable values and examining their dependence on three or four parameters is mathematically straightforward. Likewise, empirical predictions are usually clearcut, although here the variety of predictions made by different versions of skew models can be a problem (Magrath & Heinsohn 2000).

Simplicity, however, appears to have been achieved with assumptions that one may call into question. For example, it has been argued that summarizing 'constraints' with a single parameter, x, is oversimplistic. Constraints arise from intraspecific competition and therefore they depend on life-history characteristics of the species (Arnold & Owens 1998; Pen & Weissing 2000; Hatchwell & Komdeur 2000; Kokko & Lundberg 2001; Kokko & Ekman 2002). These, in turn, influence dispersal decisions, so that variation in life-history traits sometimes generates opposite relationships between constraints and philopatry than those predicted by skew models (e.g. Kokko & Lundberg 2001). Social groups may show important biological features not captured by skew models: for example, lack of breeding in subordinates can sometimes be explained by incest avoidance rather than dominant control (Cooney & Bennett 2000). Haydock & Koenig (2002) and Cockburn (2003) have similarly commented on the importance of mating systems as factors shaping social behaviour in birds—a factor that skew theory has ignored. Finally, the way in which reproductive skew models automatically link the decision to stay with the decision to provide help can be criticized (Kokko *et al.* 2002).

Here, I have examined the effect of relaxing two assumptions of skew models that have previously not been explicitly stated. The first assumption specifies that no subordinate ever disperses if concessions make staying beneficial, and it always disperses as soon as this is not the case. This sudden switch in behaviour generates a discontinuity ('cliff edge') in the relationship between concessions and dominant fitness. Relaxing this assumption appears to strengthen reproductive skew theory: the discontinuity disappears and is replaced with a smooth selection pressure, where subordinates become more likely to depart as dominants become more selfish.

The second implicit assumption is that subordinates respond to concessions in behavioural rather than evolutionary time: a dominant who gives too small concessions will be individually penalized through subordinate departure. This assumption cannot hold if subordinates lack the means to measure concessions, or the dispersal decision has to be made before concessions can be measured. When measurement is impossible or not accurate enough, stable groups cannot form in the transactional way. In such a case, subordinates base their behaviour on average concessions that prevail in the population. Nothing thus prevents a dominant from cheating and offering lower concessions than average. Evolving selfishness of the dominant will then prevent group formation.

Does this concern extend to other versions of skew theory? 'Limited control' models ('tug-of-war' (Reeve *et al.* 1998)) do not consider group stability at all, whereas a synthetic approach (Johnstone 2000) combines group stability considerations with conflict resolution. However, such an approach again assumes that dominants and subordinates receive at least the minimum that makes staying worthwhile, without justifying this assumption. The results of the current model indicate that models of social evolution should be explicit about the mechanisms by which individuals can adjust their behaviour to that of others, and pay attention to changes that occur in evolutionary versus behavioural time.

Johnstone (2000) and Magrath & Heinsohn (2000) have pointed out that empirical work on reproductive skew theory should set out to test assumptions, and not only predictions, of skew models. The current results add to this requirement the testing of the assumption that individual dominants have the means to convince their subordinates that their pay-offs will be sufficiently high (or, more generally, that individuals cannot cheat and reap benefits of group living while subjecting the other individual to an invisible reduction in benefits). If mechanisms that allow accurate assessment of benefits do not exist, the logic of reproductive skew theory simply does not apply. The apparent ease with which skew models can be modified to fit a variety of evolutionary problems should, therefore, be followed with caution.

For example, Shellman-Reeve & Reeve (2000) generated a set of interspecific predictions for extra-pair paternity in birds using reproductive skew theory, yet it is likely that a male bird lacks the means to assess paternity (the 'concession' given by his mate) accurately. Kokko (1999) had earlier analysed the same scenario without using the reproductive skew framework. These results showed that groups (in this case social pairs of birds) can cease to be evolutionarily stable and disband, if paternity assessment is too inaccurate. In this case, assessment can be possible using proximate cues of paternity. Such assessment does not have to be completely accurate for biparental care to remain stable (Kokko 1999). Interestingly, the interspecific predictions generated by the two modelling approaches (Kokko 1999; Shellman-Reeve & Reeve 2000) are very similar, and several appear to hold in nature (Møller 2000; Møller & Cuervo 2000). Whether this means that reproductive skew theory is robust enough to produce accurate predictions even when some of its assumptions are violated, or that good fit with data does not mean that the model is correctly derived, is an interesting question to debate.

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