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Social conflict resolution, life history, and the reconstruction of skew

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Summary

Models of reproductive skew have provided useful conceptual frameworks for analyzing social conflict and cooperation in groups of reproductively-totipotent individuals, in that they specify explicitly how aspects of ecology and genetic relatedness can generate within-group variation in behavior and reproduction. The main outcome of many years of development and application of these models, however, is a growing consensus that transactional models apply to few if any real situations, and that the models cannot be critically evaluated because assembling sufficient quantitative information to allow critical tests of their assumptions and predictions is not feasible. The 'top-down' approach of skew modeling, which makes strong yet unsubstantiated assumptions to extract explanations from data, can be contrasted with a 'bottom-up' approach, which involves inference of convergences in sets of diverse social, demographic and life-history traits across highly-diverse taxa, and analyses of fine-scale divergences in small sets of traits between conspecific populations and closely-related species. The bottom-up approach explicitly recognizes that each population and taxon exhibits a constellation of more or less similar evolutionarily inter-related traits, especially those that affect (1) the ecological circumstances that underly benefits of dividing labor, (2) the opportunities, costs and benefits of using force (taking control of behavior away), coercion (cost imposition or repression), or persuasion (providing benefits) to modify the expression of conflicts of interest, and (3) the life-history tradeoffs and feedbacks that coevolve with social adaptations. I

illustrate this approach with examples of social convergences among insects, birds, mammals, and humans that yield insights into selective pressures, and present a model based on such convergences for the role of cooperative breeding in the origin and expansion of modern humans. Finally, I argue that analyses based on wide-scale convergence and fine-scale divergence will ultimately demonstrate the degree to which social animals and social systems fall into a relatively-small set of more or less discrete categories with regard to how ecology, relatedness, behavior and reproduction are inter-related - categories that can usefully be subjected to the development of robust, predictive, category-specific models that seek to explain variation in skew.

A professor must have a theory as a dog must have fleas.

H. L. Mencken

1. Introduction

Grand unified theories are a mainstay of hope for scientific progress. Such theories integrate, subsume or sometimes vitiate previous ideas, and provide explicit, elegant and powerful predictive frameworks, as relativity and quantum mechanics have demonstrated in physics. In biology, our theories are more circumscribed, contingent, and specific, with the only true universalities being natural selection itself, and maximization of inclusive fitness. But beyond these fundamental processes, we are drawn to develop and apply theory that is as simple, general and as predictive as possible within any given domain, from, for example, sex ratios, to mating systems, and ecological constraints.

More-general models are more useful in having wider taxonomic scope, and simpler models can be better in being more intuitive and explicable with regard to causes and effects; by contrast, more specific and realistic models are more directly useful for explaining and predicting in any given application, and more precise models are amenable to more-rigorous tests. However, there are strong tradeoffs between model characteristics that prevent any given model from optimizing across all criteria: for example, more-general models will tend to be less realistic and less precise (Levins 1966; Matthewson and Weisberg 2008).

Perhaps most importantly in biology, models that make stronger assumptions can allow us to simplify a problem and make stronger predictions, thus potentially extracting more information from data. For example, maximum parsimony methods assume that phylogenetic change is rare and they thus allow the inference of unique historical sequences – which are, or course, wrong to the extent that change is not rare. Statistical tests based on parsimony may also be relatively powerful compared, for instance, to likelihood-based tests, but they are also more likely to suffer type 1 error.

Reproductive skew theory is simple, general, and apparently powerful. Social interactions involving conflict and cooperation among totipotent individuals are stripped by theory to bare bones: relatedness, ecological benefits, dominance, and reproduction, and small sets of assumptions can yield wide ranges of predictions. Skew-model reasoning has been with us for about 30 years, and models more or less specific to given situations and taxa have proliferated for about 15 years. Where and how has this approach been useful, and what are the alternatives for addressing the same questions?

I will evaluate the usefulness of skew models not just in terms of fitting predictions to data, but more generally in the context of how we think about social cooperation and conflict, and how we then study it. In this chapter I first consider the complexity of our problem and the dimensionality of the questions that are being addressed, and how suites of social and life-history traits evolve. “Skew”, or variation in reproduction within groups, is only one trait, and only one way of

characterizing social systems (Crespi and Yanega 1995; Sherman et al. 1995; Crespi, 2005). How can we maximize the conceptual power of this term? How useful is a skew perspective and focus, compared to other viewpoints?

Second, I suggest that we divide and conquer the analytic complexities of social cooperation and conflict from the animals up. I thus contrast the top-down modeling framework of skew theory with bottom-up, comparative approaches that are designed to ultimately build robust foundations for integrative and predictive social theory. This book provides a wealth of examples that help to illustrate the convergences among taxa that yield strong insights into selective pressures and trajectories, and components for future models. I will focus in particular on the coevolution of human life-history and reproduction, as exemplified in components of the chapters by Jones (this volume) and Johnstone and Cant (this volume). I also attempt to draw some general inferences regarding what I see as a core question in social evolution: specification of what factors determine how different forms of conflict are resolved, or remain ongoing.

2. A complex problem

For every complex problem there is an answer that is clear, simple, and wrong.

H. L. Mencken

Models *per se* cannot be wrong, being ‘if-then’ statements set in the rigorous language of mathematics. But the ‘if’ components can be wrong in being

inapplicable or inaccurate for particular situations, and the ‘then’ components can be problematic to evaluate if the predictions are not sufficiently precise and specific to the model under evaluation, compared to alternatives that are more or less specified. Strong-inference tests (Taborsky, this volume) require risky falsifiability, which can seldom be achieved in evolution and ecology without comprehensive knowledge concerning a large number of variables, many of which are challenging to measure (McGrath and Heinsohn 2000).

One example of limitations on the specificity of predictions is provided by Koenig et al. (this volume), who demonstrate positive correlations of skew with relatedness, ecological constraints, and grouping benefits among species and populations of birds. Such patterns are generally consistent with detailed predictions of skew models involving concessions, but they are also generally consistent with simple predictions from inclusive fitness theory alone (such that individuals are unlikely to give up reproduction to non-relatives) and ecological constraints theory (see also Clutton-Brock 2006). As Koenig et al. (this volume) describe, a key component of the models is which behaviors, such as concessions, transactions, coercion, and direct aggression, actually modulate the reproductive success of group members. Does any dominant animal willingly give up reproduction to another one, in direct return for help? Or do relatedness, ecological benefits of group-living and cooperation, and variation among populations and species in opportunity or ability to coerce or force other individuals to cooperate ultimately drive the patterns that are observed? Whatever

the ultimate explanation, the results are encouraging because they show clear signals of convergence between diverse avian taxa (in sets of covarying traits), and divergence among populations, that are generally consistent with inclusive fitness theory and ecological constraints theory.

Skew theory developed from the trinity of perceived explanations for social cooperation that dominated this field in the 1970s and 1980s: mutualism (Lin and Michener 1972), parental manipulation (Alexander 1974), and genetic relatedness (Hamilton 1964). These have each come to be seen not as alternatives, but as key factors that must be integrated, in the context of social and sexual conflicts within cooperative systems or societies (Trivers 1972, 1974; Trivers and Hare 1976; Haig and Graham 1991), and in the context of specific mechanisms whereby cooperation evolves without being eroded by cheating and conflicts (Lehmann and Keller 2006; Bergmüller et al. 2007; West et al. 2007)

The degree to which conflicts are resolved or ongoing, and the preconditions and selective forces underlying resolution or overtness of conflict, have become central issues with regard to the development of models and the analysis of behavior (Ratnieks et al. 2006) – to such an extent that they may underly the categorization of social systems and their coevolved patterns of behavior and reproduction. But our understanding of the nature and functions of apparent conflict is rudimentary at best – for example, Hart and Ratnieks (2005) points out that aggression, a core behavior in social groups, may represent:

- (1) *physical domination*, that directly suppresses the reproduction of subordinates and pre-empts effective challenges,
- (2) a *response* by a dominant individual, to more or less obvious testing of the dominant by one or more subordinates,
- (3) a *signal of vigor* and vitality of the dominant, indicating that resistance is physically futile or, I might add,
- (4) a *signal of health and reproductive ability*, in the context of remaining an efficient egg-layer who provides sufficient inclusive fitness returns to subordinates that they are not selected to challenge.

Most generally, where the interests of individuals conflict, we expect selection for one party to win, with the outcome of such selection mediated by relative power and resource-holding potential (Parker 1974; Beekman et al. 2003), leverage (Lewis 2002) and other asymmetries, inclusive fitness benefits, costs of competition, pleiotropic effects (Foster et al. 2004), and other factors, most notably the alternative options of individuals who lose. Taken together, these factors should determine whether conflict is ongoing and overt or resolved. Under potential or ongoing conflict, one individual can influence another in three ways (Brown et al. 1997):

- (1) taking control of their behavior away ('force', such as killing, eviction, egg-eating, infanticide, or direct physical alterations),

(2) imposing costs to alter their behavior ('coercion', such as punishment, threats of punishment, or aggression via queen policing)(Clutton-Brock and Parker 1995; Crespi & Ragsdale 2001; Ratnieks and Wenseleers 2008), or

(3) providing benefits to alter their behavior ('persuasion', such as reproductive concessions, reciprocally-altruistic behavior, or other forms of mutualistic benefit) e. g., Bergmüller et al. 2007; West et al. 2007).

The degree to which force, coercion or persuasion mechanisms operate depends upon the phenotypes, life-histories, and other idiosyncracies of the species under consideration, but selection should, all else equal, favor force or threat of force, as it is most effective in generating control, and most efficient in mimimizing costs to self or benefits to others. Force or threat of force may be found most commonly in strongly-asymmetric interactions, such as between parents and offspring or between individuals who are otherwise old vs young, and its effectiveness should notably favor the evolution of self-suppression of reproduction, and helping, as in marmosets (Abbott et al. this volume) and workers in eusocial forms. Symmetric interactions may more commonly involve coercive interactions, with asymmetries in fighting ability ('resource-holding potential') and the relative value of winning vs losing being the prime determinants of outcome, as in classical models of animal contests (Parker 1974) but with inclusive fitness considerations across colony or group duration as key additional factors. Ratnieks and Wenseleer (2008) describe how some forms of collective force or coercion, such as worker policing, may also

be more powerful than kin selection in driving the evolution of altruistic self-sacrifice in social insects. Finally, the degree to which imposition or provision of costs vs benefits results in a more or less stable or cooperative group must be some function of the ecological costs and benefits of group-living, cooperation, and division of labor into reproductives vs helpers. For some taxa, such as bumblebees and vespine wasps, stability and mechanisms of control shift during a season, such that as the colony's end nears, workers depose the queen or engage in anarchic reproduction (e. g., Bourke 1994); these species may provide insights into the apparent evolutionary shift from physical domination by the queen in small-colony eusocial species, to apparent chemical-signalling of queen vigor in large-colony forms (Alexander et al. 1991; Keller and Nonacs 1993; Bourke 1994).

To the extent that opportunity and ability of dominants to repress the reproduction of other individuals, via aggression or any other means, varies idiosyncratically among social groups involving relatives (especially where options such as leaving are severely circumscribed), skew becomes more or less inaccurately predictable from any model that does not include accurate and specific assumptions. Relative fighting ability, which mediates skew in tug-of-war models (Nonacs 2007), is only one factor that modulate the degree of attempted and successful repression observed in any given case; Crespi and Ragsdale (2000) describe a skew-based model predicated on various forms of cost that dominants impose on subordinates, to manipulate the costs and benefits of the subordinate's options in their favor. Opportunities for such coercion, and its

inclusive fitness benefits, should vary widely between taxonomic groups that differ in their habitats, life histories, and phenotypic asymmetries among individuals, which may yield comparative associations that are broadly consistent with inclusive fitness theory and ecological constraints theory, but not consistent with an model that does not take account of the specific factors affecting how conflicts are pre-empted, resolved, or ongoing.

Patterns of conflict and resolution are also situated in the larger context of such key factors as life-history tradeoffs, inheritance, incest avoidance, lifespans, and effects of group size (Koenig and Dickinson 2004), any of which may critically affect trajectories of social evolution. Considering all of these issues together, we presumably need a family or hierarchy of models that make different assumptions regarding control of behavior and reproduction, conflicts, and other key variables for any given taxon or group. At one extreme, we have models that are so general that their predictions are nearly untestable because too much is assumed or neglected; several authors have recently put optimal skew models in this category (Magrath and Heinsohn 2000; Kokko 2003; Nonacs 2007; Hodge this volume). At the other extreme we have detailed models tailored to specific species or sets of very similar taxa (e. g., Stephens et al. 2005), which are more testable but yield few insights into the social world at large. Where, in between, is an optimum for progress in using models to understand social cooperation?

Models of optimal skew are based on two of the three possible mechanisms above: reproductive concessions, a form of persuasion, or on mutual attempted

coercion, via impositions of costs in tugs of war. To the extent that factors other than contest ability determine variation in reproduction, and where leaving the group or independent reproduction represent poor options due to extremely low success (e. g., Clouse 2001), skew is mediated by factors that are not currently encompassed in an optimal skew framework, but may, in theory, be predictable from knowing mechanisms of control, relatedness, and ecological costs and benefits, in the larger context of life-history

3. Taxonomic divide and conquer: ecology, phenotypes, life-histories, and tradeoffs

Models represent a ‘top-down’ approach, whereby pre-existing hypotheses are formalized. Such hypotheses, of course, are originally developed from comparative observations of nature that yield apparent convergences, whereby similarities across diverse, independent lineages yield evidence of adaptation. Convergences are ‘bottom-up’, from taxa to hypothesis, and models and novel data should undergo cycles of reciprocal, illuminating interaction, as clearly illustrated by progress in the study of cooperatively-breeding birds and mammals (Koenig and Dickinson 2004; Clutton-Brock 2006).

Skew models have motivated the collection of particular forms of data, designed to assess their predictions. Other forms of data, and other questions have, as a result, been neglected to some degree. In this section I discuss the use

of comparative and phylogenetic methods in developing and testing ideas salient to explaining variation among populations and species in social behavior, social system, and skew. My main goals are to discover which variables, currently missing from skew models and approaches, would be most useful to further incorporate, to assess how to infer more-accurate assumptions regarding control of behavior, and to develop novel perspectives on evaluating the roles of ecology, relatedness, and control in social evolution.

(a) Convergence and divergence

Analyses of convergence appear to be ingrained in the human pattern-recognizing, rationalizing psyche: we observe a wide variety of taxa, note that some appear quite similar for some traits even though they are taxonomically far removed, and devise hypotheses to explain why. Formal, statistical, comparative tests of social evolution have been surprisingly rare, but the ones that exist have been disproportionately important and influential (Faulkes et al. 1997; Arnold and Owens 1998) in that they serve to isolate a small number of specific selective factors that apply across entire large clades.

More usually, informal tests involve comparisons of taxa that are so far removed as to make the application of independent-contrasts impossible, such as between mole rats and ants (Hart and Ratnieks 2005), birds and wasps (Brockmann 1997), or aphids, thrips, termites and shrimp (Crespi 2007). Such

analyses are predicated on the wild improbability of sets of social variables covarying in exactly the same way in independently-evolved groups that differ profoundly in other aspects of their evolutionary histories; for example, red-cockaded woodpeckers, and *Austroplatypus* beetles, both uniquely burrow into living trees to create a costly, extremely-valuable breeding habitat, and both represent the apparent sole example of high-skew societies in their respective clades (Kent & Simpson 1992; Ligon and Burt 2004). Similarly, male parental care, and joint female nesting or oviposition, appear to have evolved convergently in joint-nesting birds and some arthropods (Tallamy 2001; Vehrencamp and Quinn 2004).

Data compiled by Koenig et al. (this volume, Table 3), in conjunction with recent work by Fanelli et al. (2008) allow such an analysis for skew theory models. Fanelli et al. (2008) noted that in three studies of primitively-eusocial wasps, aggression from subordinates is negatively correlated with reproductive skew, such that high levels of aggression are associated with low skew, and the reverse. For the species they studied, Fanelli et al. (2008) also showed that neither a tug of war nor a concession model could explain the observed patterns of association among sets of variables. Data from Koenig et al. (this volume, Table 3) similarly shows that lower skew is apparently associated with overt competition: among species of cooperatively-breeding birds: 4 (57%) of 7 species without obvious competition exhibit moderate or high skew, compared to only 1 (14%) of 7 species with obvious competition that did so ($p = 0.09$ by Fisher's exact test, two-tailed).

This comparison is only suggestive, but it does imply that coercion and aggression may unidirectionally influence levels of skew, across diverse taxa, in ways that are not encompassed by existing models (Fenelli et al. 2008). Indeed, to the extent that the nature of the mechanisms and selective pressures mediating control over reproduction determine levels of skew, current skew models are assuming what should instead be considered as a key outcome of any analyses, as also discussed by Hodge (this volume).

Comparative analyses based on statistical or broadly-inferential methods provide broad-scale results, usually for effects of one or two variables of interest. Such studies are therefore severely limited in that social traits are embedded in complex causal networks involving effects on sociality from competitors, predators, parasites and other ecological factors, all interacting with mating systems, life-history traits, and tradeoffs (Crespi 2007) – in such networks, the pull of selection on any single trait ramifies throughout the entire evolving system, with diverse effects. There are two main ways to deal analytically with such multidimensional variation within species.

First, among-population studies within species, as compiled for birds by Koenig et al. (this volume), allow inference of which sets of social and other traits covary between populations, and whether the inferred causes of among-population social differences are the same or similar between different species. Such studies benefit greatly from the fact that much variation is ‘held equal’ within species, or among very closely-related species (e. g., Doerr and Doerr 2006),

although the directionality of coincident changes can be difficult or impossible to infer. Directionality can, however, be inferred from a second method, whereby a considerable number of traits is mapped onto a species-level phylogeny, to analyze sequences of fine-scale divergent changes in social characters and their putative causes and consequences. This 'divergence' approach is illustrated by Chapman et al.'s (2008) analysis of social evolution in Australian gall thrips, where a species-level phylogeny, coupled with data on skew, demography, behavior, and ecology for social and related species, allowed inference of gall size and efficacy of defensive behavior as key determinants of the degree to which soldiers reproduce, in a system without overt dominance. More generally, fine-scale analyses of transitions between social systems allow inference of which transitions are actually observed, compared to which are theoretically possible, and inference of how specific traits, such as monogamy or particular values of relatedness, may potentiate transitions between systems, such as high relatedness at the inferred origin of soldiers in *Acacia* gall thrips (Chapman et al. 2000), or ecological shifts at the origins or losses of cooperative breeding in birds (Ligon and Burt 2004). Such changes provide information about which variables may be necessary vs sufficient for certain changes, such as high ecological constraints being necessary but not necessarily variable between related species with and without cooperative breeding (Doerr et al. 2007). Among arthropods, transitions can be inferred from taxonomic and phylogenetic data for shifts between maternal care and communal care, between maternal care and cooperative breeding (groups with totipotent

helpers and breeders), and, unidirectionally, from cooperative breeding to eusociality – with no transitions inferred at all between communal breeders (groups where all individuals help and attempt to breed) and cooperative breeding (Crespi 1996, 2007). To the extent that this pattern also appears to apply in groups of vertebrates, such as clades of birds with cooperative (singular) breeding vs plural breeding (Ligon & Burt 2004; Vehrencamp and Quinn 2004), societies with low skew may be fundamentally different from those with moderate or high skew, presumably due to differences in the selective pressures related to the establishment or costs and benefits of dominance. This idea can be evaluated further by the eventual expansion of Tables 3 and 4 of Koenig et al. (this volume), and via fine-scale phylogenetic studies of specific vertebrate groups.

The four main methodological scales for the analysis of skew and social evolution are organized in Table 1. The complementarity of their strengths and weaknesses should help to motivate studies of the same taxa at multiple scales, for the same questions. As regards analyzing causes of skew, within-species studies will clearly be most effective at isolating the selective pressures and other factors underlying dominance and control of reproduction via persuasion, coercion, or force where interests conflict, but among-species studies will be required to evaluate the generality of predictions based on any given conception of who controls reproduction, how, and to what extent. This methodological exercise also underscores the tension between analyses of social systems based on the static, stable states predicted by models, and analyses of the dynamics of

change between systems such as cooperative breeding and eusociality, or large-colony forms and small-colony forms (Bourke 1999, 2007; Crespi 2004; Dickinson & Hatchwell 2004), which may involve self-reinforcing, positive feedbacks. Might such dynamics also mediate major transitions within social systems, such as between alternative-state high and low skew societies in cooperative breeders, where reproduction is controlled by different means? More generally, the evolution of new mechanisms for repression of competition between otherwise-cooperative entities, such as fair meiosis, queen or worker policing, or coercively-imposed monogamy in humans, represents a primary cause for the evolution of cooperation, on par with relatedness as a proximate cause of cooperation across all major groups of organisms (Frank 2003).

(b) Life-histories and tradeoffs

Analyses of divergence and convergence, designed to ultimately yield results that underpin the next generation of models, require as their most basic step the selection of variables to measure, beyond the most obvious ones such as relatedness, size, dominance, aggression, and individual reproductive success. One fundamental suite of variables, that has been considered in some models of social evolution but has yet to be comprehensively considered, is life-history traits, and most importantly the tradeoffs that they may entail. Social behavior, like all behavior, evolves embedded in the context of life history, with schedules of

reproduction, mortality, and, here, helping, driving variation in reproductive success subject to the tradeoffs that vary among taxonomic groups.

A central role for tradeoffs between helping and mortality, and consequent effects on opportunities for inheritance and long tenure as a reproductive, may, for example, help to explain some broad patterns in the social evolution of three main groups of animals, as illustrated in Figure 1. In each of these groups, life histories and social behavior evolve in the context of basic necessary resources – the nest, territory, hive, burrow, or gall that serves as a nursery and nexus for cooperative resource exploitation (Alexander et al. 1991). For factory fortress species, such as some thrips, aphids, termites, and shrimp, the basic necessary resource is quite special in providing combined, defensible food, shelter and nursery for a lifetime or more. Here, we observe high skew, and variation in skew among species with reproductive totipotency, but there is also a general lack of apparent dominance and aggression over reproduction, perhaps due in part to the high relatedness and common monogamy imposed by claustral habitats, coupled with extreme ecological benefits of cooperation in such a special habitat, and low or weak tradeoffs between helping and current or future reproduction. The distinction between cooperative breeders and eusocial forms may thus be mediated extrinsically, by life-history, especially by habitat duration in relation to individual lifespan. Cooperation in ‘factory fortress’ species is notable in that it appears to be highly predictable from a small set of necessary and sufficient ecological and phenotypic conditions (Crespi 1994; Queller and Strassmann

1998), perhaps because conflicts are reduced when relatedness and ecological benefits of cooperation are sufficiently high.

In Hymenoptera and other social animals that forage outside of a nest, skew evolves in the context of strong tradeoffs between helping and survival, which may drive transitions from cooperative breeding to eusociality if colonies are large and live sufficiently longer than do individuals (Alexander et al. 1991). By contrast, in small-colony forms with reproductive totipotency among some set of individuals, the evolution of competition among potential reproductives may be mediated by life-historical considerations such as chances for inheritance (Ragsdale 1999), which are some function of colony lifespan in relation to individual lifespan given options of helping or ‘waiting’ (e. g., Tsuji and Tsuji 2005), and the individual and colony-level costs of supercedure, which decline towards the end of the season as colonies of some bumblebee and vespine species descend into selfish and matricidal semi-chaos (Crespi 1992; Bourke 1994). Here, monopolization of reproduction, and prediction of skew, can apparently become strong functions of life-history coupled with relatedness.

Birds and mammals differ from arthropods for a suite of phenotypic and ecological traits salient to the evolution of cooperative breeding, most notably long lifespans, large size relative to the scale of the habitat, high costs of reproduction for females, inability to greatly improve or expand nest sites to enhance the benefits of dividing labor, and the lack of structures such as the sting that can favor heroic, high-benefit nepotism (Alexander et al. 1991). Aside from these

differences, vertebrate cooperative breeders encompass a huge ecological and behavioral range, for which unitary explanations of skew and cooperation are unrealistic – like invertebrates, their causal linkages between ecological, behavioral and reproductive variation presumably fall into some set of selective clusters that are more or less discrete. At the largest comparative scale, however, vertebrates are apparently subject to relatively weak tradeoffs between helping and reproducing – indeed, in some species, and perhaps especially in males (Cockburn 1998) helping can increase personal reproduction over the long term. Inheritance of reproductive and dominance status is likely a much stronger selective force in vertebrates – as for the small-colony invertebrates that most resemble them (e. g., Sumner et al. 2002; Tsuji and Tsuji 2005), and mutualistic benefits of larger group size itself, in the contexts of territoriality defense and predation risk, are also of comparatively strong import in birds and mammals (Clutton-Brock 2002, 2006). All of these factors, and reduced benefits from the division of reproductive labor, should tend to work against strong tradeoffs between helping and reproduction, and favor retention of totipotency and lower skew than in invertebrates (Alexander et al. 1991). By contrast, in vertebrates, tradeoffs of maintenance with reproduction, and current with future reproduction, may remain strong in cooperatively-breeding forms, whereas in many invertebrates these tradeoffs are reduced in strength either by the special nature of the habitat, or the benefits of dividing labor. Transitions between social systems may commonly involve major shifts in the shapes of life-history trade-off

curves, such as stronger tradeoffs between work and survival or reproduction in incipient hymenopteran workers, weaker tradeoffs between reproduction and survival in incipient queens, and, at least potentially, lower costs of reproduction in female reproductives under avian or mammalian cooperative breeding.

Consideration of the three main modes of cooperatively-breeding animals, in the context of explaining skew from phenotypes, ecology and behavior, suggest that a key factor missing from most skew models in particular, most models of communal breeding, cooperative breeding and eusociality in general, and most comparative analyses of social evolution, is the structure of life-history tradeoffs. These structures may be especially-useful in that they integrate myriad ecological and demographic selective pressures, and coevolve closely with the costs and benefits that ensue from helping vs. reproducing. The presence, strengths and forms of such tradeoffs, in the context of colony and individual lifespans, have been considered before by some authors (e. g., Queller 1994a, 1996; Hardling and Kokko 2003; Tsuji and Tsuji 2005; Young et al. 2005; Field and Cant 2007), but families of models that comprehensively join life-history considerations with social-evolution theory are in their infancy (e. g., Bourke 2007).

4. Cooperative breeding in the origin and evolution of modern humans

Unusual taxa can provide unusual and powerful comparative insights, as seen, for example, by analyses of naked mole rats from the perspective of insect sociality

(Sherman et al. 1991). Hypotheses for the selective pressures that drove the evolution of perhaps the most unusual vertebrate of all, modern humans, have focussed predominantly on genes, brains, and tools and ratcheting cultural change (e. g., Kaplan and Robson 2002; Wolpert 2003; Bradley 2008). Such scenarios have largely neglected some key aspects of evolutionary ecology, notably breeding systems and life history, that affect the demographic bases of the large-scale population expansions that were more or less coincident with the evolution of modern human behavior (Mellars 2006; Templeton 2007).

Humans can be considered as cooperative breeders, albeit strange ones (Foster and Ratnieks 2005). We share a set of basic traits with some other primates (e. g., Sellen 2007), such as extensive parental care, as well as alloparental help from other individuals, mainly female kin, but we are also more or less unique for a small set of characteristics: (1) the presence of menopause, grandmothering, and a long lifespan, (2) high costs of infant production and feeding, due largely to the extreme fatness of human babies and their big brains, (3), despite such costs, the ‘stacking’ of children, such that a given reproductive female and her helpers care for multiple highly-dependent young via short inter-birth intervals compared to other apes, (4) a long duration of childhood, with alloparental care also provided by older, less-dependent, pre-reproductive offspring, mainly females (Kuzawa 1998; Kaplan 2000; Hawkes 2003; Gurven and Walker 2006; Sellen 2007; Quinlan and Quinlan 2008; Robson and Wood 2008). How might these traits be related, in the context of selective pressures mediating

the evolution of cooperative breeding? What insights might humans provide into cooperative breeding and reproductive skew more generally?

Summers (2005) comprehensively applied reproductive skew theory and its components to the evolution of despotism vs egalitarianism in the mating systems of human males, over three main historical periods: (1) largely egalitarian hunter-gathering, (2) the rise of resource-concentrating agriculture, despotic dominance hierarchies, and higher skew, to (3) modern societies where reproductive options are partially curtailed by the socially-imposed repression of law. His analysis shows that historically, high male skew is broadly associated with coercion via punishment in conjunction with the ability of some males, with their kin and subordinate allies, to control the most basic of necessary resources, food supplies, labor, and coercive physical power, and thus gain cultural and social dominance. By contrast, in modern societies with socially-imposed, albeit serial, monogamy, male skew may be determined more by persuasion of females with the benefits of material reproductive resources, as control of behavior has generally shifted towards female interests.

The evolution of skew and life history in human females appears to be an older story than for males, and a more important one for major transitions in human evolution (Figure 2). The simplest concatenation of the four traits listed above has selection for large brains at the fulcrum, and selection for life-history and behavioral mechanisms that concentrate female reproduction into an almost insectan queenlike specialized period of about 20 years between a long childhood

and grand-maternal nepotism (Pavard et al. 2007), with clear physical signals of endocrine-mediated reproductive potential for individual females (Jasienka et al. 2004). Cant & Johnstone (2008) and Johnstone and Cant (this volume) provide evidence from theory, primatology, and anthropology that the evolution of menopausal ‘self-suppression’ of reproduction was mediated by a combination of life-history tradeoffs increasing in strength with age (Hawkes 2003; Shanley et al. 2007) in combination with conflicts of interest between young immigrant females and older-generation resident females that are resolved in the young female’s interests, due to her insensitivity to the costs imposed on the older female by her breeding, and her relatively-high reproductive value.

An additional key conflict of interest, not considered in the Cant and Johnstone (2008) model, arises between a mother and her son upon the death of a mother’s mate (Figure 3), which is likely to occur when a female nears the critical age for a decision to either allocate alloparental care to a son’s children, or have additional children of her own. The son would benefit greatly, in terms of family resources such as food and labor, expectations for inheritance, and higher relatedness to beneficiaries, by alloparental care from the mother, but the mother may commonly benefit from reproduction with a new mate. Emlen (1995) describes the common presence of severe conflict in this situation among non-human vertebrates, and in humans, the strength and resolution of conflicts is likely to depend upon a variety of cultural and demographic factors, including the strength of life-history tradeoffs involving help, survival, and current vs. future

reproduction. When the original father is still alive, such intra-family discord would be expected to be even more complex though perhaps less dramatic, including a range of predictable conflicts between the father, mother, son and his wife over reproduction by the parental vs. filial generations, and over the relative extents of alloparental and parental care engaged in by all parties.

Under a model considering effects of alloparental care in the evolution of modern humans, long childhoods may be beneficial both to offspring themselves, in terms of cognitive preparation for the social complexities of adulthood (e. g., Flinn and Ward 2005; Flinn et al. 2007) and physiological preparation for the rigors of breeding in females (Ellison 2003), and to mothers, via help that they receive from older children. Mothers are expected to be in a strong position to coerce help via manipulation of daughters (Alexander 1974), with mother-daughter conflict in this context increasing as the daughter matures.

Regardless of the details of the mechanisms underlying human life-history shifts, the outcome of reproductive stacking of costly offspring by mothers, potentiated by combined help from husbands, daughters, and grandmothers (Sear and Maceb 2008) was apparently a demographic breakthrough, raising the human intrinsic rate of increase far beyond that of even much smaller-brained large primates. The rest, as they say, may have been history – due in large part to the evolution of confluences of interest among different parties in the successful reproduction of the 20-40 year-old queenlike females in their family group, and a generally-egalitarian solution to the social conflicts underlying skew. Low skew in

human females, despite the clear potential benefits of helping, was likely also driven by the high energetic costs of human reproduction (such that females benefit relatively more from the reproduction of relatives)(Cant and Johnstone 1999), group augmentation effects (Kokko et al. 2001)(whereby extended family groups benefit from larger size, at least to some degree; Quinlan and Flinn, 2005), and the separation of the timing of periods for helping and breeding, across the life history. As in birds (Cockburn 1998), female humans may, under this view, help more for inclusive fitness benefits of producing young, while males help more in the context of maximizing personal reproduction, under more or less strong tradeoffs between parental effort and mating effort (Strassmann 1981); this hypothesis is also consistent with evidence for a lack of benefits to grand-children due to the local presence of grandfathers (Lahdenpera et al. 2007).

Are humans uniquely unique (Alexander 1990) as regards the evolution of their cooperative breeding system? Apparently not, in at least two regards. First, by the ‘supersaturation’ model for population–level effects of the evolution of kin-based cooperative polygamy in birds (Dickinson & Hatchwell 2004), an increase in helping should lead to higher group productivity, increased carrying capacity, larger intrinsic rate of increase, larger benefits of inheritance and coalition-forming, and stronger within-group and between-group competition; in turn, such strong competition may lead to strong group-level selection processes (Wright 2007) and nested hierarchies of social organization, as found, for example, in bell miners (Dickinson and Hatchwell 2004) as well as humans. These considerations suggest

that cooperative breeding and stacking of offspring in humans represent a key innovation that, coevolving with large brains, high parental investment and strong between-group competition, generated a positive-feedback loop driving human population increases as well as cognitive capacities (Crespi 2004; Flinn et al. 2005). Once established, such a process involves a strong component of selection among groups, which in turn selects for within-group cooperation and against within-group competition (Lahti and Weinstein 2005). In humans, as in some carnivore and insectivore cooperative breeders (e. g., Courchamp et al. 1999), it is the social group itself, and not just the territory or habitat, that represents the most basic core resource mediating survival and reproduction. But most importantly, in these groups humans can cooperate to compete, such that population expansions encompass not just the colonization of initially human-vacant territory, but also forms of warfare at ever-increasing scales of organization (Alexander 1989, 1990).

Second, the only other primates with a clearcut alloparental breeding system, callitrichids (marmosets and tamarins), show a number of notable convergences with humans, such as relatively high costs of child-rearing (due here to obligate twinning), the relatively-common presence of infanticide by mothers of their own infants under conditions when little alloparental help is available (Hrdy 1999, p. 180), and ‘honest’ physiological self-suppression of females that help (Abbott et al. this volume). Marmosets are also known as rare primate examples of potentially fast-breeding ‘colonizer’ species – suggesting that,

as in humans, helping has evolved in the context of strong demographic benefits to the family and social group. Did humans colonize the globe due to a combination of ecological dominance with the demographic feedbacks that follow from enhanced cooperative breeding?

An important difference between marmosets and humans, of course, is that marmoset helpers tend to be young (older siblings of the helped offspring) yet potentially reproductive. By contrast, evidence of menopause in other animals is restricted to a few long-lived taxa, such as some whales with matrilineal kin groups (Foote 2008); here, the selective pressures involved have yet to be analyzed in enough detail for strong comparative inferences to be drawn, but benefits from accumulated knowledge and information – neural capital, in addition to more-direct reproductive benefits, may, as in humans (Kaplan 2000; Gurven et al. 2006), also underlie selection for post-reproductive life.

How can this scenario for the role of cooperative breeding in the evolution of modern humans be evaluated? Data from molecular phylogenetics and fossils dates the large-scale expansion of modern humans out of Africa to about 60,000–50,000 years ago (Mellars 2006; Fagundes et al. 2007), which is tens of thousands of years after the origin of anatomical modernity but generally coincident with paleontological evidence for a major shift about 50,000 years ago towards a higher proportion of older individuals among human fossils (Caspari and Lee 2004). Mellars (2006) associates the population expansion with roughly concomitant improvements in tool technology, and with evidence for symbolic

thought as exemplified by bodily adornments. Certainly a better, more-reliable food supply would have been a prerequisite for producing more babies faster, although more alloparental help in provisioning, and the evolution of a life history more like the highly-productive, super-organismal social insects, may also have provided economic benefits even in the absence of tools that allowed the hunting and gathering of substantially more food. More generally and directly, these ideas can be evaluated via comparative studies of traditional human societies, testing predictions of theory for the evolution of cooperative breeding that were developed for less unusual creatures.

5. Conclusions

The essence of science is that it is always willing to abandon a given idea, however fundamental it may seem to be, for a better one.

H L Mencken

Skew models were one of the most innovative and insightful developments in the study of cooperative breeding, in that they explicitly integrated all of the core determinants of Hamilton's inclusive fitness equation in the context of individuals forming social group under varying degrees of personal reproduction. I would argue however, as have others (Magrath and Heinsohn 2000; Kokko 2003; Nonacs 2006, 2007; Hodge this volume), that their simple assumptions of control

are unjustified and their predictions are too general, in most cases, to be of much practical use for the planning or interpretation of empirical studies. The study of social evolution is extremely difficult compared to other enterprises in behavior, ecology and evolution, in that quantitative understanding requires measuring effects of alternative behaviors on lifetime personal and inclusive fitness, in networks of multiple - normally more than two – kin and non-kin that differ in age, power, and other phenotypic traits. Students of social cooperation have spawned extremely detailed terminology systems to classify behavior (e. g., Bergmüller et al. 2007), and constellations of more and less general models (e. g., Nonacs 2007) but only for a few species, such as meerkats (e. g., Stephens et al. 2005), have long-term field studies accumulated enough information for robust interpretations and predictions of social-behavioral interactions in their life-historical contexts. These are too few to compare, and we are left with a vast mosaic of partial information on hundreds of diverse animal taxa to which we can apply classical and statistical comparative methods. The main problems then become what variables to measure, and what specific questions to address, in animals at what taxonomic scales for the most effective progress.

If the last 15 years of skew models have told us little else of general significance, they have made clear that the nature and extent of control over reproduction in cooperative social groups must be specified before the selective pressures underlying a social system can be well understood. Such analyses are set in the wider framework of how conflicts of varying forms evolve, be they parent

vs. offspring, maternal-gene vs paternal gene, male vs. female, queen vs. worker, worker vs. worker, breeder vs. breeder, or breeder vs. helper, and these diverse forms of conflict should evolve under common general rules (Queller 1994b; Cant 2006). The degree to which conflict resolution or persistence is predictable across taxa, compared, for example, to the predictability of ecological effects, remains to be determined, but repression of competition by force or coercion has proven, wide-scale predictive ability (Frank 2003), as does simple dominance based on resource-holding potential (Parker 1974).

Skew modeling has also made clear the central importance of life history and demography in social evolution, which can now be extended to incorporate various patterns of life-history tradeoffs that may characterize convergent social patterns across broad or narrow taxonomic groups. Once mechanisms and processes of social control are better understood, and the life-historical architecture of social-reproductive interactions and systems has been sketched out, skew models may again become an approach of choice to structure the search for causes of social convergence and divergence. We can thus seek to develop unified theories of social evolution as grand and general as nature happens to have made them, yet no more.

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Table 1. Methods for the analysis of reproductive skew and social evolution at different taxonomic and phylogenetic scales exhibit complementary strengths and weaknesses with regard to the their feasibility, inferential power and generality.

Approach	Within populations, within species	Among populations, within species	Fine-scale phylogenetic divergence	Broad-scale analysis of convergence
Description	Collection of data on behavior, skew and other traits in single populations	Collection of same data on behavior, skew and other traits from two or more populations	Collection of data from complete sets of closely-related species, in phylogenetic context	Collection of data from large numbers of species in phylogenetic context
Strengths	Allows for experimental tests and explicit tests of model assumptions and predictions; high feasibility; can measure many traits	Allows for inference of how some social traits covary, with other traits held more or less constant; high feasibility if such variation exists; can measure many traits	Allows for inference of trajectories of change in sets of traits, which can be used to infer causation; moderate generality of results	Allows for robust statistical inference of convergences; high generality of results; high feasibility of data collection if few traits are included
Weaknesses	Low generality of results	Low to moderate generality of results, hard to infer cause and effect without data on directionality, or experiments	Moderate feasibility; can measure only low to moderate numbers of traits for each species	Difficult to include many traits for all species; large, robust phylogeny needed

Figure 1. Animals with cooperative breeding or eusociality can be categorized into three main modes, that differ in the major selective forces and evolutionary responses that underly transitions between social systems. Birds and mammals are highly heterogeneous, but only one evolutionary scenario is provided here, for simplicity.

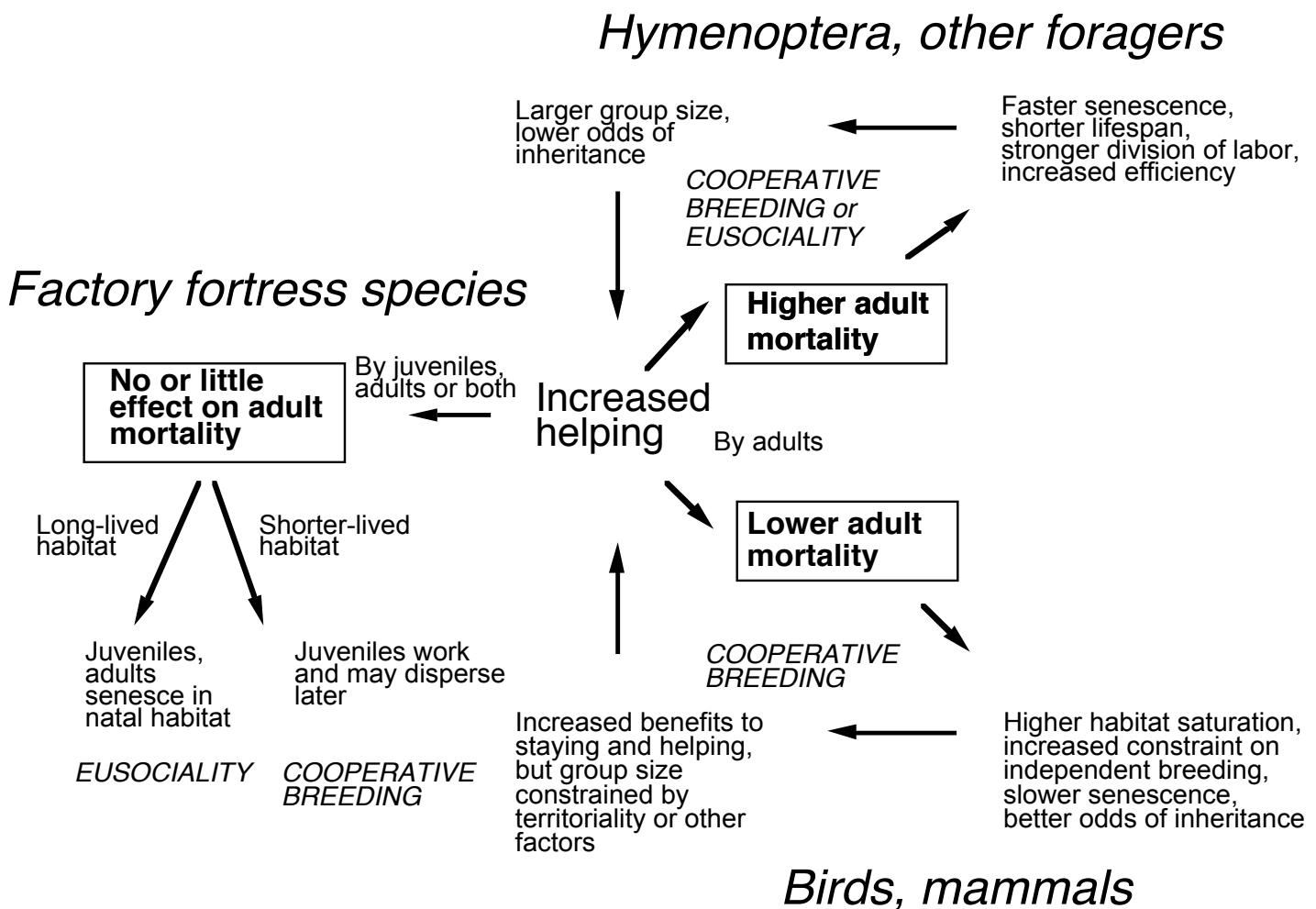


Figure 2. An increase in the prevalence and strength of alloparental care may have driven some of the major changes concomitant to the origin of modern humans. One result of this suite of changes has been the concentration of female fertility into a relatively short, 'queenlike' interval of concentrated reproduction. Under this model, population expansion and increased levels of competition and cooperation are postulated to coevolve with the entire suite of behavioral and demographic traits shown on the right. This model is consistent with hypotheses for selective forces underlying the origin of modern humans developed by Alexander (1989), Kaplan (2000), and Flinn et al. (2005), yet it also posits a central role for increased alloparental care, under low female reproductive skew, allowing female humans to reduce the strength of life-history tradeoffs that formerly constrained high reproductive output under conditions of high investment in each offspring.

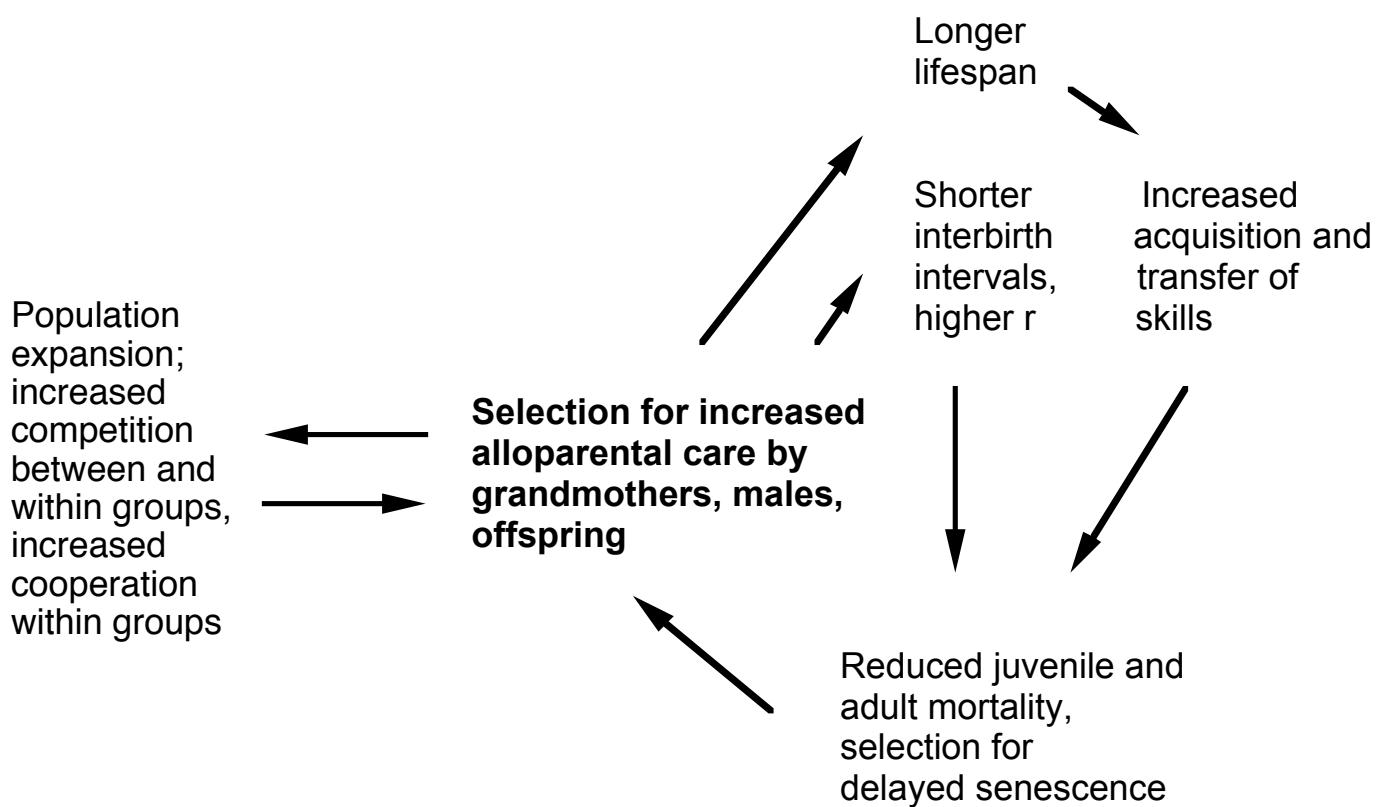


Figure 3. Higher male than female mortality rates, and the tendency for males to reproduce with females younger than themselves, create conditions where the mate of a female relatively-commonly dies when she has more or less grown offspring yet remains capable of further child-bearing. These circumstances are expected to generate conflict between the female (in a rectangle) and her son (circled) over whether the female either: (a) foregoes personal reproduction and engages in alloparental care of the son's children (dashed line), or (b) pairs with another male and produces more of her own children, who will be her son's maternal half sibs. Resolution or persistence of this conflict should be mediated by the ability of each party to persuade, coerce, or force the other, and by the forms of the life-history tradeoffs that determine the relative costs and benefits of alternative behaviors related to helping, maintenance, and current vs future reproduction. Under scenario (a), older females gain a form of 'assured fitness returns', as in some eusocial Hymenoptera (Queller 1989; Gadagkar 1990), in that high-benefit investment opportunities are available in the absence of personal reproduction, and parental investment in relatives will continue after their death. To the degree that sons are philopatric (Cant and Johnstone 2008) and can commonly 'win' in such conflicts, the selective forces represented by this scenario should, like relatedness asymmetries under common family resources (Cant and Johnstone 2008, this volume), favor the evolution of menopause and long lifespan along the lineage leading to modern humans.

