

Social trajectories and the evolution of social behavior

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Current research on the evolution of sociality seeks to integrate a wealth of species-specific studies to draw more generalized conclusions. Developing a unified theory of social evolution has been a challenging process, hampered by the inherent complexity of social systems. By viewing a species' social structure as the result of a series, or "trajectory", of decisions individuals make about whether or not to disperse from their natal territory, whether to co-breed or refrain from breeding, and whether or not to provide alloparental care, we can more easily evaluate whether selective factors influencing each social decision are similar across taxa. At the same time, the social trajectory framework highlights the interrelationships among different social decisions, both throughout the life of an individual and over evolutionary time. There are likely to be multiple unifying themes within sociality research; we hope that the simple framework outlined here will promote exchange between researchers across taxonomic disciplines to begin to identify common principles.

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Individuals in social groups often perform actions whose benefits are not immediately apparent. The occurrence and diversity of seemingly paradoxical traits such as alloparental care, group foraging, or suicidal predator defense has generated considerable research into the evolution of sociality. Such research has traditionally followed taxonomic lines, as evidenced by several recent reviews (Stacey and Koenig 1990, Choe and Crespi 1997, Solomon and French 1997). For social insects, the role of within-group genetic structure has been a particularly important avenue of research since Hamilton (1964) introduced the concept of kin selection. The consequences of kin structure and relatedness asymmetries continue to be a strong focus in social insect research (Bourke and Franks 1995, Crozier and Pamilo 1996, Queller and Strassmann 1998, Chapuisat and Keller 1999). Nevertheless, ecological considerations have also received attention, especially for

colony founding in wasps and ants (Rissing and Pollock 1988, Strassmann and Queller 1989, Field et al. 1998a).

Vertebrate studies have traditionally focused on the ecological factors promoting sociality. The lack of breeding sites has been hypothesized to be an important factor selecting for cooperative breeding in birds (e.g., Brown 1974, Koenig et al. 1992, Cockburn 1998) and some mammals (e.g., Alexander et al. 1991). Other ecological constraints, such as harsh environments and predation pressure, may also be important in social evolution (Rasa 1987, Arnold 1988). With the advent of genetic techniques that clarify family structure, genetic relationships and their social consequences have also become important in the study of vertebrate social systems (Emlen 1996).

As the approaches of these disciplines converge, it is becoming increasingly clear that comparison between

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taxa can provide valuable insights for the study of social evolution in general (Emlen et al. 1991, Brockmann 1997). The desire for a more unified approach, as originally championed by Wilson (1975), has been echoed recently by authors working with many different taxonomic groups (Emlen 1996, Brockmann 1997, McRae et al. 1997, Mumme 1997, Blumstein and Armitage 1998). However, developing a unified theory of social evolution has been a challenging process, hampered both by differences in vocabulary and by the inherent complexity in studying social systems. Simply classifying social groups into descriptive categories has generated controversy (Crespi and Yanega 1995, Sherman et al. 1995, Costa and Fitzgerald 1996), and taxonomic differences in modes of communication, life histories and other characteristics make it difficult to identify analogous processes across groups (Jamieson 1991).

One component of social life applicable to most social groups is the extent to which certain group members monopolize reproduction, or reproductive skew. To date, reproductive skew theory has made an important contribution to our understanding of the ultimate causes of variation in reproductive partitioning within social groups (Keller and Reeve 1994). However, recent theoretical work suggests that the predictions of skew models are limited (Johnstone 2000) and often not testable (e.g., Magrath and Heinsohn 2000). In addition, reproductive skew theory has been criticized for its failure to incorporate two key components of social systems (Field et al. 1998b, Kokko and Johnstone 1999, Ragsdale 1999). First, past models of reproductive skew have considered only current fitness benefits, although reproductive decisions in natural systems are likely to be influenced by both current and future reproductive opportunities. Recent extensions of reproductive skew models have begun to incorporate lifetime fitness effects in an attempt to rectify this limitation (Kokko and Johnstone 1999, Ragsdale 1999).

Second, reproductive skew models ignore variation in performance of non-reproductive behaviors such as foraging, defense, nest construction and maintenance. Performance of these tasks can ultimately affect group survival and productivity, usually expressed in reproductive skew models as the benefit of grouping, k (Reeve and Ratnieks 1993, Keller and Reeve 1994). This benefit is generally considered a constant property of a social group (but see Ragsdale 1999); however, both overall task performance and the distribution of tasks among group members can vary, with significant fitness consequences for individual survival and/or reproductive potential as well as for group productivity. Non-reproductive behaviors are particularly important to consider for groups in which reproduction does not occur, such as in "foraging groups" of insects and arachnids (Costa and Pierce 1997, Whitehouse and Lubin 1999), and for groups containing juveniles

(Queller 1989, Solomon 1991). Indeed, the exclusion of such behaviors from reproductive skew models has led to the suggestion that reproductive and non-reproductive social groups may operate under fundamentally different rules (Whitehouse and Lubin 1999).

An alternative approach to understanding social systems has been developed, but has received little attention in the wake of rapid development in reproductive skew models. Decision theory treats social behaviors as a series of decisions made throughout an individual's lifetime, each of which influences fitness in some way. For any given set of decisions, the lifetime inclusive fitness can be calculated and compared to other potential sets of decisions to determine the optimal social strategy (Emlen and Wrege 1994). In their studies of white-fronted bee-eater behavior, Emlen and Wrege (1994) used decision theory to predict the optimal behavioral options for male and female birds of varying status and compared those predictions to the birds' actual behaviors. This approach incorporated future fitness effects into the model, and explicitly included non-reproductive behaviors as a component of social decisions. Decision theory has been used successfully in other taxa as well (e.g., Nonacs and Reeve 1995, Creel and Waser 1997); however, the range of social options considered in each case was highly taxon-specific, making it difficult to use such an approach to compare species with disparate life-histories. In this paper we expand and generalize this previous work (Emlen and Wrege 1994, Emlen et al. 1995) to encompass a wider range of taxa. We develop a conceptual decision framework that emphasizes the common decision points faced by individuals in all social species in both reproductive and non-reproductive contexts. By framing sociality in this way, we can examine the number and types of evolutionary shifts in a trajectory that lead to different social systems, and identify key areas where interspecific comparisons would be most informative. Although not a mathematical treatment of social evolution, we feel that the integrative approach we advocate can provide a bridge between empirical studies and mathematical modeling of the evolution and maintenance of social systems.

The social trajectory

Social groups are collections of individuals in which reproduction may or may not occur. Groups vary widely in their composition and in the behavioral repertoire of their members. In many societies, reproduction is unequally distributed, with some individuals forgoing breeding and helping to rear other individuals' offspring. In all cases, individuals are presumed to act to maximize their inclusive fitness.

From an individual's perspective, becoming social involves three key decisions. Two decisions have generally been considered in many studies of avian sociality: whether an individual disperses or remains in the natal territory, and whether an individual helps to raise non-descendent offspring (Stacey and Koenig 1990, Koenig et al. 1992). Studies of mammals and social insects have focused on a third decision: whether an individual attempts to breed or does not breed within a group (Keller and Reeve 1994).

We can view each of these key decisions graphically as a node in a tree of social decisions (Fig. 1). At each node, individuals weigh the costs and benefits of alternative strategies, ending up with a set of decisions that forms its current social trajectory. The first decision is whether or not to disperse. If an individual disperses, it may immediately gain a new territory and breed alone, or it may have to wait for an available territory ("floating"). This trajectory represents the ancestral, solitary breeding strategy. Alternatively, a dispersing individual can form or join a group with conspecifics. At this point, the individual can either breed or not breed. This may be a "decision" made by the individual or a constraint imposed by a dominant group member (Keller and Reeve 1994, Cant 1998). We have divided alloparental behavior into two distinct categories: if an individual forgoes breeding it can choose to help. If an individual is sharing in direct reproduction, however, and extends its own parental care to include other young, we consider that to be cooperation among equal group members rather than asymmetrical helping behavior. If group members are unrelated, the only way for non-breeding individuals to obtain direct fitness is to usurp the breeding position. In contrast, continued helping can have fitness benefits for related non-breeders.

If an individual does not disperse, it must interact with its parents or siblings who are reproducing in the territory. The individual may forgo or share breeding. If the individual does not breed, it then must decide whether to help the breeding group member(s). This may lead to permanent helping, eventual usurpation, territory inheritance, or delayed dispersal. If the individual shares breeding, it must then decide whether to cooperate in parental care. Individuals failing to cooperate can remain within the group as social parasites (Buschinger 1986) or disperse after reproduction, as occurs in egg-dumping insects (Tallamy 1985), salamanders (Harris et al. 1995), and birds (Yom-Tov 1980).

It is important to note that these decisions may not always be absolute or dichotomous. For instance, once an individual decides to help or reproduce, the extent of such actions may vary. Thus, these divisions represent endpoints of a continuum of social decisions, analogous to that of the eusociality continuum (Sherman et al. 1995), and quantifiable by the eusociality index (Keller and Perrin 1995). We have divided up breeding systems into three commonly used categories: solitary breeding, in which no non-reproducing individuals of the same sex are present, singular breeding, in which there is one breeding individual and at least one non-reproducing group member of the same sex, and plural breeding, in which two or more same-sex individuals breed within the group (Brown 1987). These divisions are made to allow simple distinctions among systems that are characterized by different levels of reproductive skew. In practice, natural groups display a continuum of reproductive partitioning that makes classification difficult. We do not make distinctions that incorporate both male and female breeding behavior simultaneously, such as singular polyandrous breeding. Instead, we feel that these categories can be used from the perspective of either sex, keeping in mind that the same social

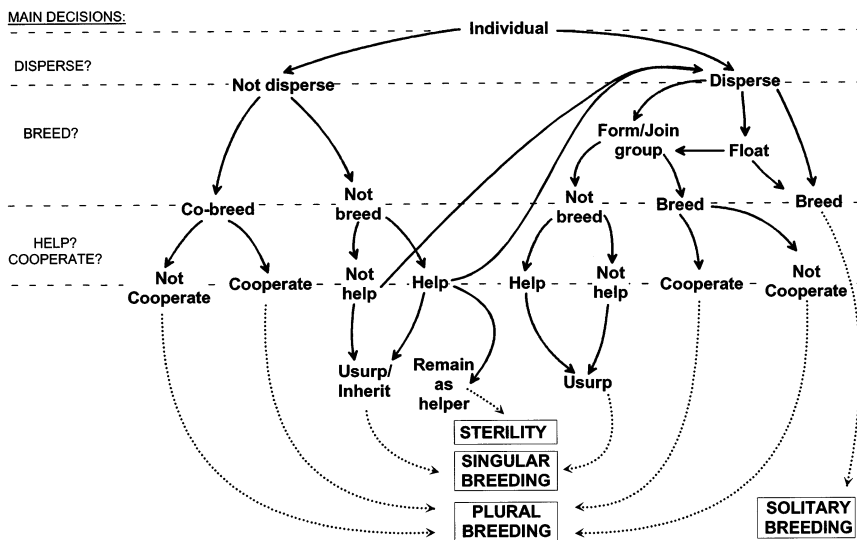


Fig. 1. Schematic representation of the range of social decisions available during an individual's lifetime. Each set of decisions, moving from dispersal to cooperation, defines a "social trajectory". Solid arrows indicate the order of decisions over time. Dotted lines connect trajectories with the breeding systems (terms in boxes) in which individuals displaying those trajectories may participate.

system may be singular breeding with respect to females but plural breeding for males.

The optimal social strategy is likely to change over the life of an individual with changes in ecological conditions, group structure or membership, and individual age, condition or experience. Young Seychelles warblers (*Acrocephalus sechellensis*), for example, show extreme dispersal flexibility, quickly shifting from helping to dispersing if a quality territory becomes available (Komdeur 1992). However, the consequences of initial decisions may constrain an individual's later social options, so realized trajectories may not always reflect the optimum. In most ant species and some bees and wasps, initially bipotent offspring are canalized into specific reproductive roles during development and cannot alter their reproductive trajectory after this point is reached (Wheeler 1986, Hölldobler and Wilson 1990). Similarly, decisions such as dispersal substantially reduce the potential for helping relatives even if conditions for helping subsequently become optimal (Emlen and Wrege 1994).

Clearly, not all options are available in any particular species or in all individuals within a species. Social animals have evolved away from the ancestral non-social trajectory at one or more decision points, and over evolutionary time, individuals may gain or lose the ability to make certain decisions. Shifts toward sociality may result in adaptations that fix particular social trajectories, such as delayed maturation or hormonal changes for certain helping behaviors (Brown and Vleck 1998, Rasa 1997). Even if individuals cannot make certain decisions during their lifetimes, however, the decision tree represents the range of social trajectories possible, should conditions favor them, via adaptive changes in morphology, physiology or behavior. By visualizing the points at which species have added additional social options or permanently altered their trajectories, we can use the decision tree to trace the evolution of social behavior as well as to understand individual fitness considerations.

Using the decision tree

When an individual decision tree is constructed, it becomes clear that the evolution of sociality is not infinitely complex. There are a limited number of decisions that all social animals face. The overall structure of the decision tree appears applicable to a wide range of organisms. Social ambrosia beetles (*Austroplatypus incompertus*), for instance, do not disperse from the parental tunnel. They do not breed, but help their parents maintain and enlarge the tunnel, then eventually disperse to found a new tunnel to breed solitarily (Kent and Simpson 1992, Kirkendall et al. 1997). Social cichlid fish (*Lamprologus* spp.) follow the same trajec-

tory, though young dispersers will often float for some time before growing large enough to claim a territory (Taborsky 1994). The list of possible species to test against the tree is virtually endless; there may be other pathways that we have not identified, but inclusion of some additional trajectories would still not make the decision tree overly complex. Thus, we believe it is possible to construct a relatively simple model that encompasses the evolution of all social organisms.

This generality makes the social trajectory framework a potentially useful tool for evaluating and comparing social evolution within and among different taxonomic groups. By isolating different components of social evolution, the inherent complexity of social systems becomes more tractable and amenable to direct tests. This is the paradigm used historically in field studies, in which the causes of specific social decisions are investigated (Table 1). Past theoretical treatments have also given separate consideration to group joining, reproduction, and cooperation (see below).

Dispersal

The decision whether or not to disperse depends on ecological constraints preventing independent breeding, and direct or indirect benefits of group living (Stacey and Ligon 1991; Table 1). These two components have been integrated in the "dispersal threshold model", which incorporates the relative merits of breeding in an average vacant territory and those of delaying dispersal from the parents' territory (Koenig et al. 1992, Emlen 1994). It is most likely that a combination of constraints and benefits is responsible for dispersal decisions in many organisms (Koenig et al. 1992, Komdeur 1992, 1994), and these same issues appear important in post-dispersal group formation despite potential differences in the relatedness and age structures of such groups (McCorquodale 1989, Strassmann and Queller 1989, Bernasconi and Strassmann 1999). This approach has been used successfully by Brockmann (1997), who compared the importance of ecological constraints for dispersal decisions in wasps and vertebrates. She found that, as in vertebrates, high costs of independent reproduction appear to favor wasp foundress associations, although the specific types of constraints may differ for the two taxa. However, there was little evidence that these factors directly influenced breeding or helping decisions, leading her to suggest that separate comparative treatments of these decision points were needed.

Because the success of independent breeding is highly dependent on ecological conditions, dispersal may be the decision most sensitive to environmental factors such as resource availability, population density or predation risk. Such factors appear to have promoted delayed dispersal in desert isopods and beetles, as well as in African cichlids (Shachak and Newton 1985,

Table 1. Examples of selective factors empirically suggested to influence social decision points.

Decision	Factor	Taxon	Reference	
Dispersal/ Group joining	Constraints: Territory availability	Seychelles warbler	Komdeur 1992	
		Sponge-dwelling shrimp	Duffy 1996	
		<i>Leptothorax</i> ants	Herbers 1986	
	Predation risk	European badger (<i>Meles meles</i>)	Woodroffe and Macdonald 2000	
		Dwarf mongoose	Rasa 1987	
	Intraspecific competition	<i>Augochlorella striata</i> (bee)	Mueller 1996	
		Ant foundresses	Bartz and Hölldobler 1982 Tschinkel and Howard 1983	
	Nest construction costs	African lions (females)	Packer et al. 1990	
		Ambrosia beetles	Kirkendall et al. 1997	
		Naked mole rats	Brett 1991	
	Low/unpredictable resources	Red-cockaded woodpecker (<i>Picoides borealis</i>)	Walters et al. 1992	
		<i>Cerceris</i> wasps	McCorquodale 1989	
		Desert isopod (<i>Hemilepistus reamuri</i>)	Shachak and Newton 1985	
	Usurpation risk	Leaf-cutter ant (<i>Acromyrmex versicolor</i>)	Cahan and Julian 1999	
		<i>Polistes</i> wasps	Gamboa 1978 Nonacs and Reeve 1995	
	Physiological condition/ reserves	African lions (male coalitions)	Bygott et al. 1979	
		Wood ant queens (<i>Formica truncorum</i>)	Sundström 1995	
	Benefits:	Territory quality	Seychelles warblers	Komdeur 1992
			Hover wasps	Field et al. 1998a
		Thermoregulation	Alpine marmots	Arnold 1988
Hissing-Cockroach				
Desiccation resistance		(<i>Gromphadorhina portentosa</i>)	Yoder and Grojean 1997	
		Tenebrionid beetle	Rasa 1997	
		Larval Lepidoptera	Costa and Pierce 1997	
Foraging efficiency		White-nosed coatis	Gompper 1996	
		<i>Dugesia</i> flatworm	Cash et al. 1993	
		Parrotfish	Clifton 1990	
	Colonial web-building spiders	Uetz and Hieber 1997		
Reproduction	Relatedness	<i>Polistes</i> wasps	Reeve et al. 2000	
	Cost of offspring Production	Callitrichid primates	French 1997	
	Resource unit size	<i>Nicrophorus</i> beetles	Scott 1997	
	Incest Avoidance	Bark and Ambrosia beetles	Kirkendall et al. 1997	
		Damaraland mole-rat	Cooney and Bennett 2000	
Helping/ Cooperation	Risk of eviction	Acorn woodpecker	Koenig et al. 1998	
		Cichlids	Taborsky 1984	
	Resource defensibility	gall-forming thrips	Crespi and Mound 1997	
		White-winged chough	Heinsohn and Cockburn 1994	
	Energetic costs of helping	Rifleman birds	Sherley 1990	
		Attracting a mate	Pied kingfisher (<i>Ceryle rudis</i>)	Reyer 1984
	Increased offspring production	White-throated magpie-jay	Innes and Johnston 1996	
		African wild dog (<i>Lycaon pictus</i>)	Malcolm and Marten 1982	
		Seychelles warbler	Komdeur 1996	
	Parental experience	Bats	Wilkinson 1992	
		Increase group-size effects	Brown hyena	Owens and Owens 1984
	Relatedness	Argentine ant (<i>Iridomyrmex humilis</i>)	Aron et al. 1994	
Big-headed ant (<i>Pheidole desertorum</i>)		Helms et al. 2000		
Risk of punishment	<i>Polistes</i> wasps	West-Eberhard 1977		

Taborsky 1994, Rasa 1997). In the dwarf mongoose and in polygynous ant species, low dispersal success has caused permanent failure to disperse from the parental colony (Creel and Waser 1994, Keller 1995).

The dispersal decision is also strongly influenced by social interactions among individuals co-habiting the

home territory. Social dominants, often the parents, can either promote or discourage offspring dispersal through the level of aggression directed toward subordinates. At the extremes, this can result in forced eviction (Taborsky 1994) or recruitment as helpers (Emlen and Wrege 1992).

Reproduction

The decision of whether or not to attempt reproduction has received by far the most attention in recent literature on social evolution (e.g., Nonacs and Reeve 1995, Reeve and Keller 1996, Cant 1998, Emlen et al. 1998, Koenig et al. 1998, Reeve et al. 1998, Cant and Johnstone 1999, Johnstone et al. 1999, Cooney and Bennett 2000, Clutton-Brock et al. 2001). This is for good reason, as fitness is ultimately measured in number of offspring produced either by the individual or its relatives. For solitary individuals, breeding decisions are based on current body condition, resource, mate or territory availability, the probability of survival to the next breeding season and other ecological considerations. Within social groups, these considerations are still present but their effects are complicated by two additional social factors: relatedness to potential mates within the group and competition for reproductive opportunities with other same-sex group members.

The intensity and outcome of social reproductive competition depends on many factors. The value of current direct reproduction for both dominants and subordinates varies as a function of longevity, the degree and symmetry of relatedness between group members, and the likelihood of future territory inheritance (Keller and Reeve 1994, Kokko and Johnstone 1999, Ragsdale 1999). In addition, the intensity of competition depends on the relative costs to dominants and subordinates of producing the extra offspring that can be raised as a result of grouping (Cant and Johnstone 1999). As dominant individuals reach the limits of their reproductive capacity, the magnitude of competition for remaining resources decreases. This is particularly likely when resources are clumped into separate high-quality patches, such that groups defend more resources than are required for the maximal number of offspring of a single female (Macdonald 1983). For example, burying beetles (*Nicrophorus tomentosus*) defending medium-sized carcasses (the food source for developing larvae) tend to show reproductive skew toward the larger female, but on large carcasses that a single female cannot fully utilize, reproduction is equally shared (Scott 1997). In callitrichid primates, high resource levels are also often associated with plural breeding, presumably because there are more resources available than a single female can convert into offspring (French 1997).

Even if a single individual could theoretically monopolize reproduction, it must have the means to restrict the reproductive activities of other group members. Whether dominants completely control reproduction, and the impact of such control on reproductive skew, have been explored in two types of models. Optimal skew models assume that dominants control reproduction (Vehrencamp 1983, Reeve and Ratnieks 1993, Reeve and Keller 1995), while in Incomplete control

models subordinates can claim shares of available reproduction against the interests of dominants (Cant 1998). The true extent of a dominant's ability to detect and prevent or terminate breeding attempts impacts both the occurrence of co-breeding and the mechanism of reproductive suppression (Jennions and MacDonald 1994, Johnstone and Cant 1999). Which model most closely corresponds to natural social groups is not yet settled; it is most likely that each model is appropriate in some cases (Clutton-Brock 1998a, b, Emlen et al. 1998, Field et al. 1998b, Reeve et al. 1998).

Helping/cooperating

Historically, the evolution and maintenance of helping behavior has been examined in two ways. Researchers studying cooperative breeding systems investigated activities of helpers but rarely considered this decision as independent of dispersal (e.g., Koenig et al. 1992). At the same time, a large body of theory was being developed on the evolution of cooperation between unrelated individuals (Trivers 1971, Axelrod 1984, Connor 1995a). Integration of these two approaches, at either an empirical or theoretical level, has scarcely begun (Clements and Stephens 1995, Connor 1995b, Mesterson-Gibbons and Dugatkin 1997). Part of the difficulty is that non-reproductive behavior encompasses so many different types of activities whose energetic costs and social functions vary widely. Some behaviors, such as aggregation and group hibernation, require little individual investment but have significant benefits including predator dilution and increased thermoregulatory ability, desiccation resistance, and nest attendance (Solomon 1991, Blumstein and Armitage 1999, Cahan 1999). Without individual costs acting to modulate the performance of such behaviors, they can be considered automatic benefits of grouping, akin to the grouping benefit k in reproductive skew models (Reeve and Ratnieks 1993, Jennions and MacDonald 1994).

Non-reproductive behaviors that require individual investment, whether or not they are offspring-directed, are helping or cooperative behaviors whose costs and benefits (direct and indirect) can be investigated in a similar conceptual framework. Unlike automatic benefits, the benefits of helping are not invariant and individuals may adjust their effort to increase fitness. Even members of the same social group may differentially weigh the costs and benefits of helping as a function of a variety of factors (e.g., probability of survival, future reproduction, or relatedness; Cockburn 1998).

Individuals make a large number of helping decisions in their daily lives; thus, the helping/cooperation node may be the most likely route for individuals to test the strength of dominance or control relationships within social groups through small reductions in their coopera-

tive investment. However, assigning a fitness benefit to helping can be problematic. Because each act of helping may have little effect, helping benefits are generally measured at a gross scale that includes all helping activities performed over a set period of time, such as a single reproductive season. The usual method is to compare reproductive success with and without helpers, but this method is often confounded by other differences among groups and often cannot determine long-term effects on productivity (Magrath and Yezerinac 1997, Woodroffe and Macdonald 2000).

Compared to helping benefits, the fitness costs of helping have been addressed in relatively few systems (reviewed in Heinsohn and Legge 1999), and even when measured, there is little quantitative information on the relationship between short-term costs in terms of time and energy and lifetime reproductive success. A clear understanding of this relationship is sorely needed if we are to combine reproductive and helping decisions within a single modeling framework.

Individuals participate in social activities to maximize their inclusive fitness. In this sense, the components of social decision-making that we have outlined all contribute to overall lifetime fitness and are therefore not truly independent of one another. However, considering each separately can provide important insights that may otherwise be missed because very different individual trajectories can lead to similar social structure (Fig. 1). For example, plural breeding systems can form under two distinct trajectories: when offspring fail to disperse, such as in acorn woodpeckers (*Melanerpes formicivorus*; Koenig and Mumme 1987) or female lions (*Panthera leo*; Schaller 1972); and when offspring disperse, such as in sweat bees (Kukuk and Sage 1994) or male lions (Schaller 1972). Thus, encompassing the components of social decision-making under a single "fitness" umbrella masks fundamental distinctions among groups and impedes comparative investigation of the selective pressures that cause changes in specific components of individual social behavior.

Evolutionary considerations

Although the social trajectory primarily describes social decisions made by individuals over their lifetimes, both the social context and available options change over evolutionary time. As species evolve social attributes, selective pressures may impact a decision point differently, or cause a response at a different decision point altogether. This changing relationship between individuals and their environment highlights the fact that understanding the current adaptive value of social traits does not necessarily mean that we un-

derstand the historical processes producing social systems. The selective forces producing and maintaining sociality may often be quite different, as subsequent adaptations alter the costs and benefits of social decisions at each node (Macdonald 1983). Reconstructing the evolutionary routes to sociality was once a central part of sociobiological research but this level of analysis has received less critical attention in recent years with the rising prominence of mathematical modeling to address current maintenance issues. In general, such historical reconstructions described the shifts required to go from solitary life to "complex" forms of sociality, namely eusociality in insects and cooperative breeding in vertebrates (Brown 1974, Wilson 1975). Two primary pathways were generally considered that correspond to the dispersal and non-dispersal options in the decision tree. In the subsocial route, offspring fail to disperse and form social groups with their parents. In the parasocial route, individuals form groups with individuals of the same generation, either by remaining with siblings or forming new groups with non-relatives. While this dichotomy implied subsequent changes in reproductive and helping behaviors, these behavioral decisions were not explicitly acknowledged. By formally stating the behavioral decisions under selection, our framework can provide a more complete picture of the types of evolutionary transitions involved in social evolution and bring together experimental research and phylogenetic analyses of these processes (e.g., Packer 1991, Edwards and Naeem 1993, Richards 1994, Arnold and Owens 1999, Vehrencamp 2000).

The decision tree framework highlights another important aspect of social evolution research that has recently been the subject of study. Without the social context created by group formation, individuals of solitary species do not have the opportunity to make the reproductive and cooperative decisions further down the decision tree. Because these decision points are novel, it is unclear what trajectories would be followed when these points are initially encountered by species evolving social traits. Uncovering these initial "default" trajectories is of fundamental importance in identifying the number of independent evolutionary steps involved in social evolution. Experiments on normally solitary species placed into artificial social groups suggest that many reproductive and cooperative behaviors displayed by derived social species, such as reproductive division of labor and cooperative brood care, may in fact correspond to initial states of incipient social groups rather than being separate evolutionary changes after groups were formed (Sakagami and Maeta 1987, Fewell and Page 1999, Helms Cahan 2001). This challenges the notion that group formation initially has intrinsic costs but few if any of the intrinsic benefits associated with cooperation (Alexander 1974, Emlen 1994).

Conclusions

The field of sociobiology has reached the exciting point where data are available on enough different taxonomic groups to begin to investigate general principles. In order to achieve this goal, unifying principles across disciplines have to be developed. The decision tree approach may be a productive step towards such unification. Once common transitions are identified, we can begin to examine the selection regimes that influence the choices made by organisms that differ widely in morphological, physiological, and life-history characters. When the alternative social trajectories available in a species are identified, the fitness consequences of choosing each trajectory can be quantified and compared, as was done in the white-fronted bee-eaters by Emlen and Wrege (1994).

Reproductive skew theory is a good example of comparative investigation, but it is important to remember that altering reproductive effort is not the only mechanism for increasing inclusive fitness. The decision tree suggests that the development of complementary models, focusing on dispersal and helping behaviors, could be instrumental in producing testable predictions about specific components of social behavior. In addition, the relationships between decision points provided by the social trajectory concept allow it to be used not only for understanding current social adaptations but also for reconstructing the evolutionary history of social systems, serving as a map upon which phylogenetic data sets can be meaningfully compared. Framing social groups as sets of individual social trajectories may give us new insight about variation in social systems, and clarify our understanding of how a simple set of evolutionary rules can lead to diverse and complex social dynamics.

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