Teams in animal societies

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We review the existence of teams in animal societies. Teams have previously been dismissed in all but a tiny minority of insect societies. "Team" is a term not generally used in studies of vertebrates. We propose a new rigorous definition of a team that may be applied to both vertebrate and invertebrate societies. We reconsider what it means to work as a team or group and suggest that there are many more teams in insect societies than previously thought. A team task requires different subtasks to be performed concurrently for successful completion. There is a division of labor within a team. Contrary to previous reviews of teams in social insects, we do not constrain teams to consist of members of different castes and argue that team members may be interchangeable. Consequently, we suggest that a team is simply the set of individuals that performs a team task. We contrast teams with groups and suggest that a group task requires the simultaneous performance and cooperation of two or more individuals for successful completion. In a group, there is no division of labor—each individual performs the same task. We also contrast vertebrate and invertebrate teams and find that vertebrate teams tend to be associated with hunting and are based on individual recognition. Invertebrate teams occur in societies characterized by a great deal of redundancy, and we predict that teams in insect societies are more likely to be found in large polymorphic ("complex") societies than in small monomorphic ("simple") societies. *Key words:* animal societies, cooperation, division of labor, groups, invertebrates, task types, teams, vertebrates. *[Behav Ecol 12:534–540 (2001)]*

The evolution of organized groups, such as insect societies, is one of the major evolutionary transitions (Maynard Smith and Szathmáry, 1995). In the evolution of animal societies, as in many of the other great evolutionary transitions, selection has acted to promote efficiency through a division of labor (Sendova-Franks and Franks, 1999). All eusocial animal groups exhibit some form of division of labor. Indeed, the tremendous ecological success of social insects is hard to attribute to anything other than the advantages of a division of labor (Wilson, 1990). Unfortunately, however, there are few unambiguous ways to measure and rigorously compare the degree of behavioral coordination in different animal societies. This problem is greater when we compare vertebrate and invertebrate societies.

Divisions of labor can occur through individuals specializing in different tasks and thereafter working for extended periods largely independently of one another (e.g., Field et al., 1999). However, with the evolution of eusociality came the opportunity to exploit a new organizational method: highly cooperative and relatively unselfish groups of individuals who, collectively, are able to tackle tasks far beyond the abilities of the individuals themselves (i.e., groups and teams). These collective abilities, such as the construction of relatively large nests and the ability to overpower prey much larger than themselves, have been well documented in insect societies (e.g., Bonabeau et al., 1997, 1998; Camazine et al., 2001; Franks, 1989; Seeley, 1995). In addition, insect societies provide a bewildering variety of forms, ergonomic organization, and social complexity (Anderson and McShea, 2001; Bourke, 1999; Bourke and Franks, 1995). It is especially surprising, there-

fore, that groups and teams in insect societies have received relatively little attention.

In this review, we pose the following question: are there reliable measures of behavioral complexity that correlate well with ecology and social evolution? We focus on the analysis of cooperative tasks in animal societies, the extreme form of which is the existence of teams, for which we propose a new rigorous definition. We demonstrate that a variety of functional adaptive units exist at an intermediate level between the individual and colony in insect societies. We reconsider what it means to work as a group or team in animal societies and show that there are many more teams in insect societies than previously thought (e.g., Hölldobler and Wilson, 1990; Oster and Wilson, 1978). The adaptive value of groups and teams, and their evolution and importance in insect societies, is considered. We compare teams in vertebrates and invertebrates and highlight a number of important differences.

Tasks and subtasks

Before examining groups and teams in animal societies, it is important to understand both the nature of work and tasks. A task is "a set of behaviors that must be performed to achieve some purpose of the colony [animal society]" (Oster and Wilson, 1978: 326). A task is an item of work that potentially makes a positive contribution, however small, to inclusive fitness (i.e., direct and indirect fitness; Table 1). Sometimes a subset of the behaviors required to complete a task may appear as a discrete unit but will not enhance fitness unless other individuals complete their own additional work units; we call these work units "subtasks." For instance, when killing intruding ants, a group of *Pheidole pallidula* ants will work together to immobilize, or pin down, the intruder (Detrain and Pasteels, 1992). However, this is classed as a subtask because if it is not followed by the separate act of killing (i.e., decapitation by a major), then it makes no contribution to colony fitness.

The distinction between tasks and subtasks is clear when a task is partitioned (Jeanne, 1986; reviewed by Ratnieks and Anderson, 1999). In this situation, a number of sequential

Table 1
General definitions

Term	Definition
Task	A task is an item of work that contributes potentially to fitness
Subtask	A subtask makes a potential fitness contribution only if other subtasks are completed
Group task	A group task requires multiple individuals to perform the same activity concurrently
Team task	A team task requires different subtasks to be performed concurrently

Figure 1
Switching between different task types in the ant *Colobopsis truncatus*: (a) when under attack, an individual can use her specially shaped (phragmotic) head to block a small nest entrance herself. This is an individual task. (b) In larger nest entrances, several workers combine together to form a living plug, thus blocking the entrance. This is a group task. (c) When a second row of workers is present, they may perform a different subtask to those in the front row (e.g., act as a keystone lock). If this is the case, then this is a team task (adapted from an original drawing in Szabó-Patay, 1928).
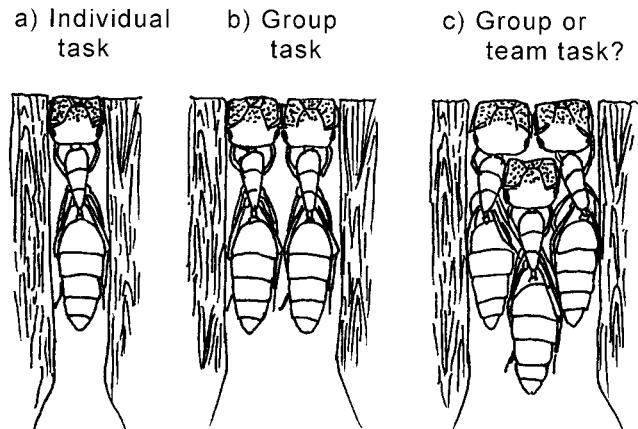
stages occur in which material is passed from worker to worker (Table 2). For instance, in the termite *Hodotermes mossambicus,* one set of workers climbs up grass stems, cuts off pieces of grass, and drops them to the ground below (subtask 1), while a second set of workers transports the material back to the nest (subtask 2; Leuthold et al., 1976). Thus, the different subtasks (cutting and transportation) are clearly distinguished by the act of transfer, regardless of whether transfer is direct or indirect.

We propose that four types of tasks exist in animal societies: individual, group, partitioned, and team (Table 2). Within our scheme of classification, subtasks do not occur within individual or group tasks; hence the subtasks that occur within team and partitioned tasks must be performed by different individuals. We define individual tasks as tasks that can be performed satisfactorily by an individual, and suggest that they account for the majority of tasks in animal societies. An example of an individual task is honey bee nurses that put their heads into cells to regurgitate to the growing larvae; they do not need help from others to perform their task. Task partitioning (defined above) is reviewed by Ratnieks and Anderson (1999). Group and team tasks are defined and considered in detail below.

Groups

A group task requires the concurrent performance and cooperation of two or more individuals for successful task completion (Table 2). There is no division of labor within the group; each individual performs the same task. Group tasks are found in many animal societies (Dugatkin, 1997; Wilson, 1975) and appear to fall into two broad categories. First, in insect societies a physical structure is formed from the bodies of many individuals. These structures are termed "self-assemblages" (Anderson C, Theraulaz G, and Deneubourg J-L, unpublished manuscript), and various types are observed, including bridges and bivouacs in *Eciton* army ants, living curtains to protect brood in *Apis dorsata* and *A. florea* bees, and rafts in *Solenopsis* ants. A particularly interesting example occurs in the ant *Colobopsis truncatus*. When these ants are attacked, two or more workers combine to form a living "plug" in the nest entrance to seal off the nest from attackers (Szabó-Patay, 1928; Figure 1). Later we suggest that *C. truncatus* plugs may sometimes be teams.

Groups may harness greater power or work output from the combined abilities of their members. For instance, they are used to overpower prey (e.g., army ant predation; Gotwald, 1995), increase local prey density (e.g., white pelican group-fishing; Cottam et al., 1942), intimidate intruders and competitors (e.g., *Oecophylla* ants; Hölldobler, 1977, 1983), or construct a home (e.g., Camazine et al., 2001). Swarm-raiding army ants use the combined power of many individuals to overpower the prey in their path (Franks and Partridge,

1993). *Azteca* ants not only overpower prey as groups, but they stealthily ambush prey by lining themselves along the underside margin of leaves and waiting for prey to land on the upper side of the leaf (Morais, 1994). The defensive display of *Myrmecocystus* (honeypot) ants during intraspecific territorial confrontations is a group task. Numerous individuals are engaged to form an intimidating line of workers in front of the opposing colony. This signals to the competing colony the size and strength of the defenders. This is a group task because it is necessary that many individuals perform the same activity (display at the edge of the territory) simultaneously (Hölldobler, 1977, 1983).

Groups of individuals often work in parallel to construct a seasonal or permanent nest, especially in large insect societies. This may be out of necessity—large natural nesting cavities may be limiting (Jeanne, 1991)—or large colonies may simply have the resources (i.e., a large pool of workers) to construct their own tailor-made nests (Anderson and McShea, 2001). Either way, construction requires collective work output, usually as a group but occasionally as a team. However, even in species that do use some natural crevice, important nest structures may be built by groups of workers, as in wax combs in the honey bee. In certain of the cases above, a necessary division of labor may occur within the task. If division of labor is shown, these tasks will be reclassified as team tasks.

Teams

Teams require more structured cooperation than groups. Individuals not only have to work concurrently, they must also coordinate their different contributions. Additionally, individuals usually remain faithful to their subtask, or be substituted, for the whole task to be completed. Concurrent activity is crucial to the successful completion of a team task because different individuals tackle different "interlocking" subtasks (Table 2). Team tasks are not necessarily more complex behaviorally than partitioned tasks simply because they require concurrent, rather than sequential, activity. We suggest that team and partitioned tasks are on the same complexity level, which

Table 2

Characteristics of various task types

Task type	No. of individuals	Divided into subtasks?	Organization of subtasks
Individual task	Single	No	—
Group task	Multiple	No[a]	—
Partitioned task	Multiple	Yes	Sequential
Team task	Multiple	Yes	Concurrent

This table fully defines the various task types. For instance, a team task requires a number of individuals (column 2) performing two or more subtasks (column 3) concurrently (column 4).

[a] Concurrent activity is required.

Figure 2
Examples of some team tasks: (a) during nest construction, an *Oecophylla smaragdina* worker uses a larva as a silk-producing shuttle to bond leaves together (redrawn from Figure 4 of Hölldobler and Wilson, 1983). (b) In the vampire bat *Desmodus rotundus,* two bats may form a ''buddy system'' in which they both attempt to feed each night but will share a blood meal if one of the bats is unsuccessful in the expectation that this will be reciprocated at some future date (redrawn from Wilkinson, 1990; courtesy of P.J. Wynne).

is higher than that for group tasks, which in turn is higher than that for individual tasks (Anderson et al., in press).

Oecophylla weaver ants form nests by gluing leaves together (Hölldobler and Wilson, 1977, 1983). Three subtasks are needed. First, groups of individuals must pull leaves together and hold them in place. Second, a form of glue (silk produced by larvae) must be produced. Third, a group of workers must hold the larvae and use them like a tube of glue to bond the leaves together (Figure 2a). Thus, this is a team task for *Oecophylla* because all three tasks—holding leaves together, glue production, and gluing—must be performed simultaneously for successful task completion.
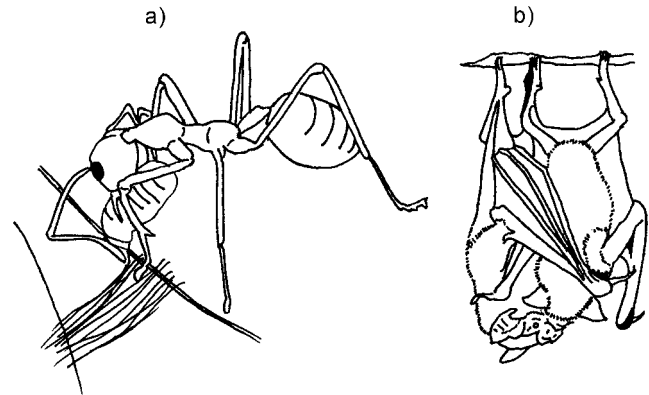
Although concurrency is required for a team task, it is not necessary that the different groups of workers start and finish their subtasks at the same time. For instance, *Oecophylla* workers pulling the leaves together must start their subtask before gluing can commence. In a team, all that is required is that at some point during the task execution, two or more subtasks must be performed simultaneously for successful task completion.

One possible problem with our scheme of classification is that it might be taken to imply that the whole colony is a team, and thus be used as evidence of the weakness of our classification by showing that it is too inclusive. We reject this potential criticism. Our definition of a team task explicitly states the absolute necessity for concurrent activity. Many colony activities that will potentially enhance fitness occur concurrently, but the majority will not need to occur concurrently. For example, an ant colony may need, at some time, to rebuild parts of its nest and at other times it will need to forage. Rebuilding and foraging may occur concurrently, but this is not absolutely necessary for the colony to be successful. Therefore, we conclude that whole colonies will not usually be teams according to our classification.

Interchangeability of team members
Conspicuously absent from our definition of a team task is any reference to castes. Unlike Hölldobler and Wilson (1990), we do not constrain teams to consist of members of different castes. We reject this particular constraint and suggest that a team is simply the set of individuals that performs a team task. Individuals are interchangeable within a team if they can switch between one subtask and another quickly. However, in the same way that a sports team may contain members that could swap positions, but tend not to, specialization of particular individuals or castes (morphological, behavioral, or physiological) upon certain subtasks may well be favored by selection. Thus, a worker may perform a certain subtask repeatedly to benefit from learning and enhanced performance efficiency (Jeanne, 1986; Seeley, 1982).

Pheidole pallidula ants act as a team during colony defense.

A group of minors pins down an intruder, and one of the majors, who have larger and stronger mandibles than minors, is recruited to decapitate the intruder (Detrain and Pasteels, 1992). Pinning down and decapitating the intruder must be performed concurrently or the intruder cannot be killed. Although it is mostly the minors that do the pinning down, majors may also help. Minors with smaller mandibles, however, do not have the power to decapitate. Thus, in this example, interchangeability of caste members is limited.

Reciprocal altruism provides examples of teams in which frequent switching between subtasks is necessary for teams to persist (Trivers, 1971). The two most well-known examples are the formation of coalitions in male olive baboons *Papio anubis* during sneaky matings (Packer, 1977), and blood-meal sharing in the vampire bat *Desmodus rotundus* (DeNault and McFarlane, 1995; Wilkinson, 1984; Figure 2b). In olive baboons, two lower ranking males sometimes form a team to gain access to estrous females. The troop's dominant male usually escorts such females. One low-ranking male keeps the alpha male busy, by causing a fight, while the other male goes off with the female. Later, the males switch subtasks. This is clearly an instance of a team. Both subtasks, keeping the dominant male occupied, and mating with the female, must be performed concurrently. The task is to achieve a mating for one of the members of the team.

In vampire bats, approximately 8% of adults fail to feed successfully on a given night (Wilkinson, 1984), and starvation can result in as little as 48–72 h of food deprivation (McNab, 1973). It is crucial that all bats attempt to forage concurrently each night, but in some cases reciprocal food sharing takes place between consistent pairs of bats (a team), who are usually relatives or frequent roost neighbors. Thus, if one of the two bats has failed to feed that evening, its teammate may donate a blood meal to its hungry partner. Accordingly, there are three subtasks: forage, regurgitate when necessary, and receive blood within the team task ''promote your own long-term survival by helping your partner survive.''

Such teams are composed of reciprocal altruists (Trivers, 1971). This term indicates the functional mechanism for team formation and has profound implications for the willingness of an individual to form a coalition in the first place (i.e., individual recognition is required; discussed further below).

Also, this term encompasses the concept that, although two or more individuals may be working together in a team, they may only be acting on their own selfish interests.

Superefficieny and nonrandom team membership
Until now, the only accepted teams in insect societies were those performing prey retrieval in the army ants *Eciton burchelli* (Franks, 1986, 1987) and *Dorylus wilverthi* (Franks et al., 1999). In these teams there are just two subtasks: front-running, involving a single ant at the front, and following, involving one or more ants bringing up the rear (Franks et al., in press). This distinction might seem almost absurdly obvious and trivial, but it is not, as is clear from considering prey retrieval groups such as *Formica* wood ants that habitually pull in different directions when they attempt jointly to carry a large prey item (Sudd, 1963, 1965). In *Formica,* subtasks within the prey retrieval group are absent, each ant continues to try to take the lead, and they are notoriously inefficient. Uniquely, army ants straddle items they carry and can therefore face in the same direction as they run along carrying a prey item between them; hence, team members can work together well. In principle, two army ants might straddle the same item but face and pull in opposite directions, but this is never observed. This implies that the group has a distinct structure in which cooperation is maximized by a simple division of labor between those at the front and those at the rear.

This organizational structure is likely the reason for the teams' ''superefficiency,'' meaning they carry much more weight than would be predicted by summing the typical weights carried by all its team members if they were carrying items alone. (Superefficient groups or teams may also exist in *Novomessor cockerelli* [Hölldobler et al., 1978] and *Pheidolegeton diversus* ants [Moffett, 1987, 1988], but further investigation of these cases under natural conditions is needed.) One possible explanation for this ergonomic synergism is that when two ants pick up either end of a bulky item, rotational forces disappear (Franks, 1986).

These teams contain a nonrandom membership of workers: a front-runner is an especially large individual (in relation to the size distribution of available workers), and followers are especially small (Franks et al., in press). This disparity appears to be a result of the way that such teams form and probably helps establish the division of labor within the team: At first, a prey item is surrounded by a group of ants. After a variable period, a sufficiently large ant, usually a submajor, comes along that can get the item in motion. Then other ants join the team until the item is being carried at the standard retrieval speed—a speed at which the item is no longer an obstacle to the smooth flow of traffic along the trail (Franks et al., 1999). Three important characteristics of this process are that first, the initial ant to get the item moving becomes the ant at the front of the team; second, such an ant is almost invariably the largest member of the team; and third, following ants are most often considerably smaller than the ant at the front of the team (Franks et al., in press).

We believe that it is deeply misleading to refer to the ant at the front of the team as a leader in any sense that implies the special role of organizational leadership. Nor is such an individual an ''organizer'' or a ''key individual'' (sensu Robson and Traniello, 1999). To put this in perspective, we imagine that all of the individuals that form a team in army ants are initially using exactly the same rules of thumb. Indeed, occasionally, though very rarely, teams in *E. burchelli* can be formed solely by several submajors (see Wilson, 1971: Figure 4–19). The composition of these teams depends on a sampling process from a highly skewed distribution combined with the rule of more ants joining a team only until the item is moving at the standard retrieval speed. Thus, teams of four or more submajors are expected but only rarely. Even though all the members of such a team are from the same caste, they still have different roles: one is a front-runner, while the rest are followers (Franks et al., in press).

Hunting in teams
With the exception of the sneaky matings in olive baboons described earlier, teams in vertebrates tend to be associated with feeding and hunting. In vertebrates, individuals usually coordinate efforts so that one or more individuals chase the prey, or flush it from hiding, while others prevent escape (reviewed by Dugatkin, 1997). For instance, in chimpanzees (*Pan troglodytes*), some individuals chase and surround the prey (usually a juvenile baboon), forcing it to climb a tree while other chimpanzees climb adjacent trees ready to capture the prey when it attempts to leap to safety (van Lawick-Goodall, 1968). In African wild dogs (*Lycaon pictus*), some individuals will chase the prey, and may even change leaders during the chase. However, ''a dog at the rear sometimes will cut corners in an attempt to head off prey'' (McFarland, 1985: 136–137). Thus, there may be different subtasks, ''chase'' and ''head off.'' Attack from different directions is also found in cooperatively hunting lions (*Panthera leo*). Some lions are habitual ''wingers,'' individuals who always tend to go around the prey and approach it from the front or side, while others act repeatedly as ''centers,'' individuals who remain chasing directly behind the prey (Stander, 1992). Thus, there are clearly different subtasks.

Slave-making ants, such as *Protomognathus* (= *Harpagoxenus*) *americanus* and *Leptothorax* (= *Myrafant*) *duloticus,* sometimes work as a hunting team during a raid. Slave makers enter the host nest to steal brood (subtask 1). Host workers, however, take their brood and attempt to flee. To prevent this and thus ensure that there is brood left to steal (subtask 2), a slave-maker guard stays at the nest entrance and prevents host workers escaping with brood. Efficient concurrent functioning of both the guard and brood stealers is necessary to complete the task of stealing brood (Alloway, 1979; Foitzik et al., 2001). See Anderson and McShea (in press) for other insect team tasks.

In the vertebrate hunting examples above, killing the prey may be performed by any of the individuals in the team. In contrast, Galapagos and Harris's hawks have a much more discrete division of labor (Faaborg and Bednarz, 1990). The hawks hunt cooperatively with several birds simultaneously swooping on their prey, which consists of woodrats, jackrabbits, and other birds. However, if the prey finds cover, some birds land and surround it, while one or two hawks walk or fly into the vegetation to kill the prey. Later all the birds feed together. (Cooperative hunting in raptors is reviewed by Ellis et al., 1983.) A similar strategy may occur in lions: ''Sometimes a lioness or two will leave the other members of a group lying in ambush. They will then circle conspicuously around a herd of game animals and drive them back toward their fellow ambushers'' (Alcock, 1979: 320).

Alaskan humpback whales (*Megaptera novaengliae*), when hunting Pacific herring, sometimes work as a team to perform two basic subtasks: prey herding and bubble blowing. Most whales perform the herding subtask and search along the sea bottom for herring schools above them. The group then initiates an attack by rushing the prey while issuing loud calls. The herring swim upward in an attempt to escape, but at the same time another whale, the bubble blower, swims in a circle above the school and deploys a curtain of air which both traps the prey and channels them to the surface, whereupon all the whales feed on the herring. Interestingly, this strategy not only involves precise spatiotemporal coordination between the

herders and bubble blower, but the bubble blower, vocalizer(s), and herders all appear to specialize in their subtasks (Sharpe, 2000).

Teams, cliques, and persistent groups

A number of examples of teams have been claimed on the basis of a consistent group membership—that is, the same individuals interact with each other repeatedly. This is not to be confused with the term "clique," defined by Hölldobler and Wilson (1990: 343) as a "group of workers whose members recognize one another as individuals to accomplish some task." Kolmes (1985) cites two examples of "teams." First, he cites the existence of "dance groups" in the honey bee in which there is a correlation between the size of dancers and their recruits, thereby implying a reasonably consistent scout-recruit membership, at least over several days (von Frisch, 1967; Waddington, 1989). Second, he cites the study by Sommeijer et al. (1982) of the stingless bee *Melipona favosa,* in which groups of workers build larval cells and subsequently provision them as teams. Persistent groups are not necessarily teams, however, and it is unlikely in these cases that individuals recognize each other, and so it is doubtful that these are examples of cliques.

Reznikova and Ryabko (1996; see also Reznikova, 1999; Ryabko and Reznikova, 1996) cite the existence of teams in *Formica* and *Camponotus* ants in which it appears that scouts recruit a particular and consistent set of individuals to exploit a resource. However, the temporal separation between the first subtask, finding the food source, and the second subtask, exploitation of the resource by the recruits, means that they are not, according to our definition, a team. It can also be argued that the scouts and recruits perform two different tasks: "find food and recruit others" and "exploit resource," respectively. In effect, by the time the recruits arrive at the source, the scout's task is finished and the recruits are only just starting theirs. Of course, recruitment, and indeed all coordination activity and information flow, requires at least momentary concurrency (for a signal to be effective it must be sent and received), but this should not be confused with a team task.

In vertebrates, individual recognition has been clearly demonstrated (e.g., Wilson, 1975, and references therein) and is an important factor in team membership. It is, for instance, a significant factor in the formation of teams, which are also examples of reciprocal altruism (e.g., Packer, 1977). We suggest that vertebrate teams are also likely to be cliques.

DISCUSSION

The evolution of cooperation can arise through several routes, such as repeated interactions with the same individuals (Axelrod, 1994; Trivers, 1971) or through haplodiploidy and increased relatedness between cooperating individuals (Bourke and Franks, 1995). Either way, the result is cooperative, functional, and adaptive assemblages. We have defined these aggregations as "groups" when, to achieve successful task completion, each individual must perform the same task concurrently, and "teams" when individuals must perform different subtasks concurrently. By our definition, it is clear that teams do indeed exist in animal societies and can play an important role in social life.

Oster and Wilson (1978) defined a team as a group of noninterchangeable individuals who recognize each other as individuals and who move around the colony as a single group. Under this extreme definition they dismissed the existence of teams in insect societies. Later, Hölldobler and Wilson (1990) recognized Franks's (1986) demonstration of superefficient

teams in *Eciton* army ants. If individuals were to be noninterchangeable and move around as a team as defined by Oster and Wilson (1978), loss of just one individual would most likely affect efficiency and effectiveness of task performance or speed of response if they have to recruit another worker to fill the place. This organizational approach would therefore compromise the colony's behavioral flexibility (Oster and Wilson, 1978). Consequently, we predict that teams in social insects only form in immediate response to the stimulus of a team task.

Vertebrate teams have been given a number of different names, such as groups, coalitions, and reciprocal altruists. These terms recognize the reasons and/or the mechanisms by which the teams form. Here we have explored the functional organization of teams. We encourage other researchers to recognize the organizational and functional parallels between these teams and those in other taxa. Why teams form is an important consideration. In vertebrates, these reasons have been subject of much discussion (e.g., Axelrod, 1984; Dugatkin, 1997; Wilson, 1975) but little has been said of teams in insect societies. Specialization, learning, and overall enhanced performance efficiency (Jeanne, 1986; Seeley, 1982) will enhance the ergonomic efficiency of a team. Thus, we predict that teams in insect societies are most likely to be found in polymorphic species with large colonies and high tempo—in other words, complex societies (Anderson and McShea, 2001; Bourke, 1999; Oster and Wilson, 1978). Polymorphism implies inherent differences among individuals in their abilities to perform different (sub)tasks (Wilson, 1984), whereas large colony size is likely to be associated with relatively greater homeostatic properties of the colony and greater system redundancy (replication of parts). That is, the loss of an individual in a large society has less of an effect on colony operations and ergonomics than it does in small societies.

Certain clear differences are found between vertebrate and invertebrate teams. In vertebrates, teams appear to be based on individual recognition. Hence, most, if not all, teams in vertebrates are also cliques. As yet, there is no evidence for individual recognition in social insects. All of the vertebrate team examples involve a degree of trust between individuals and are potentially prone to cheats. During team hunting, for example, often a single individual kills the prey. The other individuals have to trust that the spoils will be shared between all the team members after the kill. When reciprocal altruism is involved, individuals anticipate that the act will be reciprocated. In vampire bat teams, social grooming, which makes up 5% of their day, appears to be an important factor in both roost-mate recognition and as a prelude to regurgitation. Thus, individual recognition is crucial for team formation in vertebrates (at least in nonhumans). This is much less of a problem with viscous, single-family societies, such as in certain ants, bees, wasps, termites, and mole rats. In such societies, individuals are often relatively much less selfish and may essentially work for the same goal (Bourke and Franks, 1995; Wilson, 1971; but see Ratnieks, 1988; Ratnieks and Reeve, 1992).

Vertebrate societies are often much smaller than insect societies. The degree of redundancy in vertebrate societies is very low; usually there are no "spare" individuals. This is in stark contrast to most insect societies where redundancy is generally high (Herbers, 1981; Oster and Wilson, 1978), often with many individuals in the immediate vicinity that could be recruited to perform one of the teams' subtasks. However, there are many insect societies, such as ponerine ants and primitively eusocial wasps, in which colony size is small and intracolony conflict is relatively high (Bourke, 1999; Peeters, 1997; Ross and Matthews, 1991). Here, we predict the existence of vertebrate style teams if individuals can recognize one

another, or the absence of teams altogether (Anderson and McShea, 2001) if they cannot.

Although we have presented a precise definition of teams, discussion of currently ambiguous and borderline examples can be illuminating. In certain cases it is not yet clear whether a particular assemblage is a group or a team because there is a paucity of pertinent data. Nest-entrance plugging by groups of *Colobopsis truncatus* ants (Szabó-Patay, 1928), described earlier, is such an example. If the nest entrance is small and a single ant can block the entrance by herself, plugging is an individual task (Figure 1a). If the ants form a single layer across the entrance, then plugging is a group task; each individual is performing the same subtask (Figure 1b). However, if a second row of one worker (or more) is present, as in Figure 1c, then the worker may be performing a different subtask, perhaps acting as a keystone lock. Currently, data are lacking to determine whether *C. truncatus* workers act as groups or as teams.

A second example concerns thermoregulation in *Apis dorsata* and *A. florea*. In these two species, a group of individuals forms a living curtain around the brood (a group task), and thermoregulation is achieved by altering interindividual spacing. However, at higher ambient temperatures, nest cooling is enhanced by evaporation of water: some workers exude water droplets, while other bees fan their wings (Dyer and Seeley, 1991). Both subtasks, exuding water and fanning, must be performed simultaneously to achieve enhanced cooling. Hence, this could be considered a team task (although an individual may be able to perform both subtasks at once). However, it may simply be an example of synergy (the nest would still be cooled if the two behaviors did not occur concurrently), and the two groups may be acting independently.

A third example concerns retrieval of grass in the harvester desert termite *Anacanthotermes macrocephalus* (Kumar and Thakur, 1990). The termites cut blades of grass and transport them back to the nest. If the blade of grass is long and the termite cannot easily enter the nest entrance hole with it, the forager will push the end of the grass into the hole. Workers inside pull the grass in while the forager pushes from the outside. Are the two (or more) workers acting as a team? Here the question will only be resolved if it can be shown that an individual cannot bring the leaves in by itself because two concurrent actions, pushing and pulling, are required for successful task completion.

Clearly, tasks may be organized in a variety of ways. It is possible to imagine a certain task that an individual can accomplish by itself by performing two different subtasks concurrently. For example, a chimp might conceivably steady a nut on an anvil with one hand while using a piece of wood as a nut-cracking hammer with the other. Because only one individual is involved, this is clearly not a team task. However, a similar task could be a team task if its subtasks were performed by different individuals. Certain tasks may sometimes be performed as an individual task but at other times in a teamlike manner solely for opportunistic or synergistic reasons. For instance, *Dinoponera quadriceps* ants use a variety of behaviors to assert dominance (Monnin and Peeters, 1999). One behavior is "gaster rubbing" in which a dominant individual grabs the antenna of a lower-ranking individual and rubs it upon her gaster (part of her abdomen). This is an individual task. Sometimes, several individuals will hold down a worker (pinning down), which is a group task. However, the alpha female may take the opportunity of a pinned-down worker to reinforce her dominance and gaster rub the victim. In isolation, this may appear as a team task—"the victim must be pinned down while the dominant individual gaster rubs"—but this is not so because an individual can complete the task herself. A second example concerns geese that fly in a chev-

ron formation during migration. As in army ants, there are two subtasks, leading and following. However, in geese there is periodic switching of the leader's subtask. Flying in such a formation can extend the range of a bird considerably (e.g., by 70%; Lissaman and Shollenberger, 1970; but see Norberg, 1990). Clearly, a goose can fly alone, implying that formation flying may simply represent synergy among the birds. But, because of the additional range benefits of formation flying during migration, especially when crossing open sea, this is a team task if the task is "to travel as economically as possible," or if an individual goose cannot fly the required distance alone between refueling stops. In both these cases the birds must fly in formation and periodically switch roles to complete the task, and thus they are a team.

In summary, we have presented a precise definition of teams that can be applied to both vertebrates and invertebrates, and we argue that there are many more teams in animal societies than previously thought. We encourage researchers to report other examples of teams to facilitate comparative studies. In addition, careful behavioral studies are needed to elucidate some of the details of teams. In which societies do individuals habitually act in teams, and are such teams an important aspect of a society's economy? Further studies are required to test the prediction that insect teams are more likely to be found in large polymorphic ("complex") societies than in small monomorphic ("simple") societies.

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