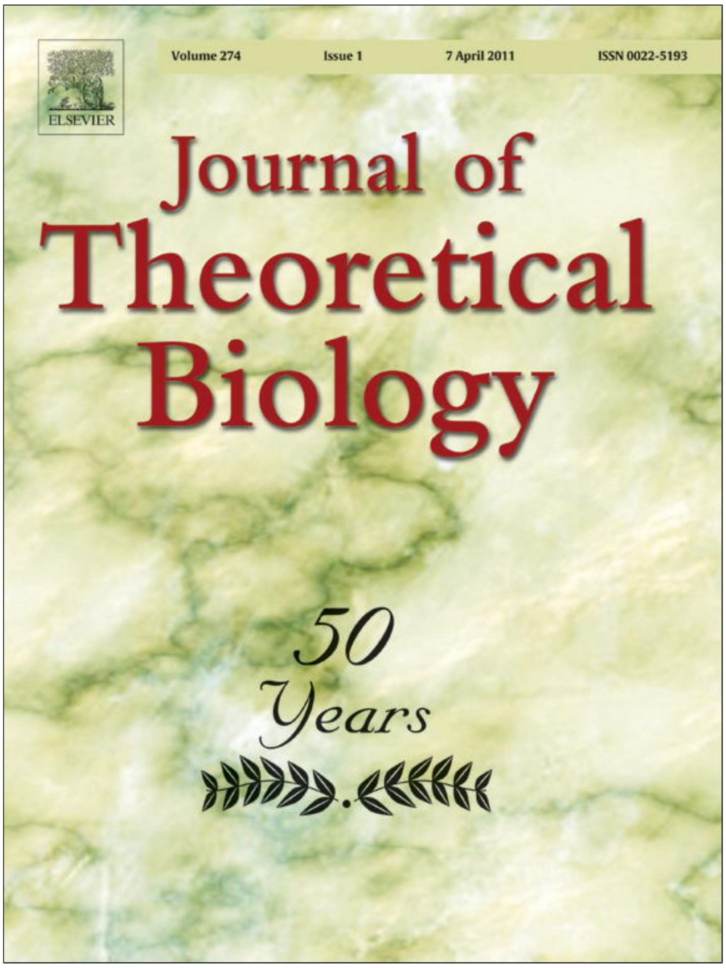
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50th Anniversary Year Review

Models of coalition or alliance formation

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ABSTRACT

More than half a century has now elapsed since coalition or alliance formation theory (CAFT) was first developed. During that time, researchers have amassed a vast amount of detailed and high-quality data on coalitions or alliances among primates and other animals. But models have not kept pace, and more relevant theory is needed. In particular, even though CAFT is primarily an exercise in polyadic game theory, game theorists have devoted relatively little attention to questions that motivate field research, and much remains largely unexplored. The state of the art is both a challenge and an opportunity. In this review we describe a variety of game-theoretic and related modelling approaches that have much untapped potential to address the questions that field biologists ask.

Contents

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1. Introduction

Coalition and alliance formation is the essence of political society, both in humans (Riker, 1962; Rubin, 2002) and in other primates (Maestripieri, 2007). It is a fundamentally strategic process, and so one would expect the theory of games to have much to say about it—especially the theory of cooperative games, because it is in this context that the word coalition has most been used by game theorists. The truth, however, is rather the opposite: game theorists have devoted relatively little attention to questions motivating field research on coalition or alliance formation among primates and other animals, and cooperative game theory has arguably had least to say. More relevant theory is needed, and in this review we describe the challenge. Throughout, we will find it convenient to refer to coalition or alliance formation theory as CAFT for short.

Coalition means different things to different people (e.g., Baker, 1981). In ethology, a coalition is usually defined as a joint aggression between at least two individuals against a common target, with alliance reserved for longer term relationships within which coalitions may occur (Noë, 1986; de Waal and Harcourt, 1992): alliances may overlap, whereas coalitions are mutually exclusive. In sociology, Gamson (1961), who regarded coalitions as "temporary, means oriented, alliances," defined a coalition more broadly as "the joint use of resources by two or more social units." Either way, a de facto difference between coalitions and alliances is in how long they last, and the essence of both is cooperating to contest or defend a resource against conspecifics. This article is primarily about coalition or alliance formation in the ethological sense. Such collaborations have now been observed in numerous mammalian taxa including primates (de Waal 1998a,b; Perry, 2008), cetaceans (Mann et al., 2000) and social carnivores (Zabel et al., 1992; Smith et al., 2010), typically for access to females among males but to food among females. On the other hand, there are also taxa, e.g., horses (Feh, 1999) and birds (Duval, 2007), in which observed alliances may conform more readily to the sociological definition.

Many coalitions form among non-kin, and these are the primary focus of our review. In primates, for example, where there is strong bias towards female philopatry, most adult males are unrelated. Even in chimpanzees, where females disperse, coalition partners are not very likely to be related (Langergraber et al., 2007); and primates anyhow have limited kin discrimination (Noë, 1986; Chapais, 1995). We are most interested in coalitions whose targets belong to the same social group, as is typical for mammalian taxa. Coalitions in other taxa more likely involve neighbors allying for joint defense against an intruder, for example, in passerines (Elfström, 1997) or crustaceans (Backwell and Jennions, 2004; Detto et al., 2010).

Coalition formation is cooperation with conspecifics, but it is also cooperation against conspecifics, in contests of one form or another (Konrad, 2009). Accordingly, we do not cover the vast literature on the evolution of cooperation, which primarily discusses cooperation against heterospecifics or the environment in terms of mutualism versus reciprocity or other categories (Doebeli and Hauert, 2005; Dugatkin, 1997; Frank, 1998; Lehmann and Keller, 2006; Mesterton-Gibbons and Dugatkin, 1997; Taylor and Nowak, 2009; West et al., 2006, 2007). There is now fairly widespread agreement that opportunistic coalition formation is supported by mutualism, with little scope for free riding (Clutton-Brock, 2009; Tomasello, 2009); even long-term alliances may be more realistically interpreted as mutualistic than as examples of direct reciprocity (de Waal, 1991, pp. 152–153; Chapais, 1995, p. 130; Clutton-Brock, 2009, p. 54). We align ourselves with this consensus. In other words, we largely assume that fitness benefits are direct (Hammerstein and Leimar, 2006).

To predict how coalition structure depends on an initial distribution of strength has been a primary goal of CAFT ever since pioneering work on triads by Caplow (1956, 1959) and later Gamson (1961) in sociology. We describe this work in Section 2. Caplow and Gamson had humans largely in mind, but Caplow (1968, pp. 41–48) also discussed the "apish tricks" of rhesus monkeys and baboons. Both scientists were thoroughly au fait with the game theory of their day, yet did not use it to reach their predictions. Nevertheless, their predictions have subsequently been incorporated into the framework of cooperative game theory, as we describe in Section 6.4.1.

From our perspective, it is useful to have a single word or phrase that stands for strength or skill or fighting ability, or whatever it is that varies among individuals and primarily determines an individual's ability to control a resource. For this purpose, we follow Parker (1974) in using the term resource holding potential, or RHP for short, but we also extend its usage from individuals to coalitions. Thus the first primary goal of CAFT has been to predict how coalition structure within a group depends on the initial RHP distribution of the group's constituent members.

Animals observed forming coalitions are typically embedded in social hierarchies. Thus a second and related primary goal of theory has been to predict how coalition structure depends on rank. Three kinds of coalition have been singled out for special attention, usually but not invariably involving a pair of animals against a lone target. In the terminology of van Schaik et al. (2006), they are all-up coalitions, which pit subordinates against animals of higher rank; all-down coalitions, which pit animals of high rank against subordinates; and bridging coalitions, which pit animals against those of intermediate rank. In the terminology of Chapais (1995), the same three kinds of coalition are called revolutionary, conservative and bridging, respectively. Either way, a second primary goal of CAFT has been to predict the factors that favor these three kinds of coalition. Because an all-up coalition need not change the rank of the target (Alberts et al., 2003), however, we prefer the terminology of van Schaik et al.

More generally, the goal of CAFT is to predict coalitional structure as a function of key ecological factors, of which RHP and rank are merely the two most salient. Relevant models can be roughly categorized as verbal, back-of-the-envelope (Swartz, 2003), analytical, or computational, and it is convenient for us here to adopt this categorization, despite its imperfections. Each kind of model is suited to a different purpose, and each has its own advantages and limitations. As Noë (1990, p. 79) has long recognized, encounters among individuals in conflict over a resource have at least three phases: an associative phase, an antagonistic (but potentially collaborative) phase, and an allocative phase (which may involve bargaining). Adding a dissociative phase would create a four-phase process, but we prefer to think in terms of a single dynamics of association and dissociation, in which the other two phases can be embedded. Any of the phases may involve strategic behavior. But incorporating all three into a single model is difficult, and has not yet been found conducive to tractable analytical models. For that reason, analytical models have tended to focus on a particular phase, whereas computational models have tended to be less constrained.

The above considerations are reflected in the structure of our review. In Section 2, we discuss verbal models, before proceeding to back-of-the-envelope models (Section 3) and a discussion of polyadic games in general (Section 4). Thereafter, we discuss analytical models of the antagonistic (Section 5), allocative (Section 6) and associative (Section 7) phases, before proceeding to a discussion of computational models (Section 8). Section 9 looks to the future.

2. Verbal models of coalition formation: early CAFT

Theory of coalition formation begins with the study of the triad. If X, Y and Z are the RHPs, in non-increasing order, of three individuals A, B and C, respectively, then four possible orderings are $X=Y=Z$, $X=Y>Z$, $X>Y=Z$ and $X>Y>Z$; in the last two cases, X may be either greater than, less than, or equal to $Y+Z$, so that in all there are eight types of triad. The five possible coalition structures are B and C against A, denoted BC; A and C against B, denoted AC; A and B against C, denoted AB; three unallied individuals, denoted by I; and a "grand coalition" of three, denoted G. To predict which of these structures emerges in the long run, Caplow (1956, 1959) assumed in essence that a stronger party can control a weaker party and seeks to do so; that all individuals prefer more control to less, and are indifferent between "internal" and "external" control (see below); that RHPs are additive; and that I is the initial configuration.

Consider, for example, Case 6 of Table 1, where $X>Y>Z$ and $X<Y+Z$. Individuals can be dominated either internally, i.e., within a coalition, or externally, i.e., as the target of a coalition that is stronger than the individual. In Case 6 no individual can externally dominate the other two, and no individual can be internally dominated within I, hence an alternative to I is preferred by each individual. In G, A would internally dominate both B and C; however, to prevent external domination by B and C acting jointly, A prefers either AB or AC to G, but is otherwise indifferent. Likewise, C is indifferent between AC and BC; either is preferable to G, because externally dominating one individual while being internally controlled by the other is better than being internally controlled by both. But B has a distinct preference: BC gives B both internal control over C (because $Y>Z$) and external control over A (because $Y+Z>X$), whereas either AB or G leaves B dominated by A, despite control over C. Thus AB will not emerge, because A's preference for it is not reciprocated by B; however, C's preference for AC or BC is reciprocated by, respectively, A or B, so that either AC or BC is to be expected. Caplow effectively assumes that both are equally likely. Hence, if ρ denotes a vector of probabilities for coalition structures I, BC, AC, AB and G, respectively, then Caplow's predicted outcome for Case 6 is $\rho=(0,\frac{1}{2},\frac{1}{2},0,0)$. Similarly for the other seven cases. A conclusion that Caplow drew from his theory is that surprisingly often weakness is strength.

Table 1
Coalition structure probability vectors predicted by Caplow's theory. BC denotes a coalition of the (two weakest) individuals B and C, whose RHPs are Y and Z, respectively, against the (strongest) individual A whose RHP is X, and similarly for AC and AB; I denotes three unallied individuals, i.e., no true coalition; and G denotes the "grand" coalition of all three individuals. Note that in Cases 5 and 8, A is a dictator. The last column indicates the labelling used by Caplow (1959, p. 490), which differs from ours. Caplow (1956) formulated his original theory for what he subsequently called "continuous" triads, where the object is "to control the joint activity" of an enduring triad and "to secure control over rewards which are found within the situation itself" (Caplow, 1959). In effect, Caplow first formulated a theory of alliances. He later revised his theory to account for "episodic" or "terminal" triads, and drew different conclusions for one or the other in Cases 2–4, 6 and 7. From our point of view, his revision merely emphasizes that coalition formation is highly context-dependent.

Case	Ordering	Sign of $X-Y-Z$	Probabilities (ρ)					Caplow type
			I	BC	AC	AB	G	
1	$X=Y=Z$	–	0	$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{3}$	0	1
2	$X=Y>Z$	–	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	3
3	$X>Y=Z$	–	0	1	0	0	0	2
4		0	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	8
5		+	1	0	0	0	0	4
6	$X>Y>Z$	–	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0	5
7		0	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	7
8		+	1	0	0	0	0	6

Vinacke and Arkoff (1957) devised a laboratory experiment to test Caplow's theory. Generally the results supported the theory, except in Case 6 discussed above, where $\rho=(\frac{1}{45},\frac{59}{90},\frac{2}{9},\frac{1}{10},0)$ was observed. Gamson (1961, p. 379) interpreted this outcome as support for his own theory, which predicts $\rho=(0,1,0,0,0)$ in Case 6, and in every other case agrees with Caplow. Gamson's theory assumes that participants expect others to demand a payoff share proportional to resources contributed, and that participants maximize payoff by maximizing share, which favors the cheapest winning coalition if the total payoff is held constant. In Case 6, because $X>Y$ implies both $Y+Z<X+Z$ and $Z/(Y+Z)>Z/(X+Z)$, BC both is cheaper than AC and yields a higher payoff to C.

Chertkoff (1967) argued that a revised version of Caplow's theory is superior to Gamson's, and Walker (1973) later refined the theory in accordance with Chertkoff's key observation, essentially just that it takes two to tango: formation of a coalition requires reciprocation. For reasons given above, in Case 6, if A (being indifferent) offers a coalition to each of B and C with probability $\frac{1}{2}$ and C likewise offers a coalition to each of A and B with probability $\frac{1}{2}$, while B offers a coalition to A and C with probabilities 0 and 1, respectively, then the probabilities of coalition structures AB, AC and BC are, respectively, $\frac{1}{2}\cdot 0=0$, $\frac{1}{2}\cdot\frac{1}{2}=\frac{1}{4}$ and $1\cdot\frac{1}{2}=\frac{1}{2}$. With probability $\frac{1}{4}$, however, A makes an offer to B, B to C and C to A, so that no coalition forms. Then each individual "must decide between continuing the present negotiations or switching to the other player" (Walker, 1973, p. 410); note that for B, AB is better than I, because it prevents external domination by C through AC. Because the situation is symmetrical, Walker assumes that BC, AC and AB in this "cyclic" case are equally likely to form. Thus the total probability of BC is $\frac{1}{2}+\frac{1}{3}\cdot\frac{1}{4}=\frac{7}{12}$; and similarly for the other cases, yielding $\rho=(0,\frac{7}{12},\frac{1}{3},\frac{1}{12},0)$. This prediction was remarkably close to the frequencies observed by Vinacke and Arkoff (1957).

Willis (1962) attempted to extend Caplow's theory from the triad to the tetrad, but experiments offered only limited support for the extended theory, and it has not been developed since. Of many factors limiting its scope, perhaps the most critical is that it is purely ordinal and thus ignores the magnitude of RHP differences: only the sign of $X-Y-Z$ in the third column of Table 1 is allowed to have an effect. On the one hand, it is unfortunate that this line of inquiry was abandoned so early, because Caplow and Willis framed a central issue that remains to be resolved: How should coalition structure in triads and tetrads depend on an initial RHP distribution? On the other hand, there is only so far one can go with verbal theory. Significant further development depends on mathematization—and hence on game theory, which we review in context in Section 4. We revisit Caplow's theory in Section 6.4.1.

3. Back-of-the-envelope models: identifying key determinants

Very simple analytical models can identify key determinants of coalition formation with minimal calculation. For example, to establish as expeditiously as possible that variance in a Caplovian triad is too important to neglect, we can proceed from Section 2 as follows. Suppose that the benefits of occupying the alpha, beta and gamma roles in a dominance hierarchy are 1, b and 0, respectively, where $b<1$; and that initially these roles are taken by Players 1, 2 and 3, respectively. Assume that there is zero cost to bargaining, and that the cost c of fighting as one of a pair against the remaining individual is independent of RHP. Also assume that Player 1 will always accept an offer from Player 2 to exclude Player 3, or—if Player 2 is unwilling to make a pact—from Player 3 to exclude Player 2. This assumption enables us to focus directly on the following question: when is it strategically stable for Players 2 and 3 to unite against Player 1?

First suppose that relative ranks within coalitions are fixed, with Player i outranking Player j for all $i<j$. Let Player 2 offer the coalition {2,3} to Player 3, and let p_1^{23} denote the probability that it defeats Player 1. If Player 3 accepts, then with probability p_1^{23} Player 2 becomes an alpha individual, Player 3 the beta individual, and Player 1 the gamma individual; whereas with probability $p_{23}^1=1-p_1^{23}$ Player 1 remains the alpha, Player 2 the beta and Player 3 the gamma. Thus the reward to Player 3 from coalition {2,3} is $p_1^{23}(b-c)$ + $p_{23}^1(0-c)=$ $p_1^{23}b-c$. If Player 3 were instead to accept the offer of coalition {1,3} from Player 1 (whose offer of {1,2} to Player 2 is implicitly rejected by Player 2's offer of {2,3} to Player 3), then, using analogous notation, with probability p_2^{13} Player 1 remains the alpha, Player 3 becomes the beta and Player 2 the gamma; whereas with probability $p_{13}^2=$ $1-p_2^{13}$ Player 2 becomes the alpha, Player 1 the beta and Player 3 the gamma. Thus the reward to Player 3 from coalition {1,3} would be $p_2^{13}(b\ -c)$ + $p_{13}^2(0-c)=$ $p_2^{13}b\ -c$. Clearly, Player 3 should agree to {2,3} only if $p_1^{23}>p_2^{13}$. But it is reasonable to assume that this condition never holds, e.g., if probabilities are proportional to RHP, so that

$$p_1^{23}=\frac{Y+Z}{X+Y+Z},\quad p_2^{13}=\frac{X+Z}{X+Y+Z}. \tag{1}$$

Now suppose, by contrast, that relative ranks within coalitions are not fixed, and that Player 2 offers to share coalitional benefits evenly with Player 3; but continue to assume, for the sake of simplicity, that Player 1 makes no such offer. Then the rewards to Player 3 from coalitions {2,3} and {1,3} become $p_1^{23}(\frac{1}{2}\{1+b\}-c)+p_{23}^1(\frac{1}{2}\,b-c)=\frac{1}{2}\,p_1^{23}+\frac{1}{2}b-c$ and $p_2^{13}(b-c)+p_{13}^2(0-c)=p_2^{13}b-c$, respectively, from which Player 3 should form a coalition with Player 2 if $b<(Y+Z)/(X-Y+Z)$ by (1). Similarly, Player 2 should form a coalition with Player 3 if $b<(Y+Z)/(X-Z+Y)$. The second of these inequalities implies the first. Hence {2,3} is strategically stable if $b<(Y+Z)/(X-Z+Y)$. The smaller the variance, or the smaller the value of b, the more readily this condition is satisfied; in particular (because $b<1$), it must be satisfied if the strongest individual is less than twice as strong as the weakest. (If Player 2's offer to Player 3 is the proportion $Z/(Y+Z)$ instead of $\frac{1}{2}$, then the condition instead becomes $b<(Z(Y+Z))/XY$, which requires a lower b, but is again always satisfied if $X<2Z$.) The model also incidentally demonstrates that if costs are assumed to be independent of RHP, then the result is the same as if costs are assumed to be zero.

Other key determinants of coalition formation can be likewise identified through back-of-the-envelope models. For example, for a model that focuses on rates of encounter during resource utilization, Connor and Whitehead (2005) have established that alliance formation can be favored only if the proportion of an animal's resources obtained competitively is at least $\frac{1}{2}$, and likely much higher. They exploit their result to argue that alliances should start to form when the mean number of animals competing for a resource increases above about 0.7–2.0, and that differences in encounter rate or resource utilization time can explain why alliances are more widespread among males than among females in odontocete fission–fusion societies.

4. Polyadic games

A game in the mathematician's sense is a model of strategic interaction, which arises when the outcome of one individual's actions depends on actions taken by others. From this definition we readily infer what the main ingredients of a game must be. We discuss each in turn and in context. For further discussion of game-theoretic concepts see, e.g., Mesterton-Gibbons (2001), Webb (2007), Peters (2008) or Sigmund (2010).

4.1. The players

The first main ingredient is a set of n interacting individuals, of whom m ($\leq n$) could form a coalition. These individuals are the players; the set of all players is usually denoted by N, i.e., $N=\{1,\ \ldots,\ n\}$. Players may be either actors with specific RHPs and (possibly) other individual characteristics, or individuals whose RHPs and other characteristics are randomly drawn from a large population. In the latter case, the game is called a population game. There does not seem to be a standard phrase to distinguish the former case; but such a phrase would be useful, and so here we refer to games among specific actors as community games. Broadly speaking, community games are more the province of economic game theory (Myerson, 1991; Peters, 2008), and population games are more the province of evolutionary game theory (Maynard Smith, 1982; Hofbauer and Sigmund, 1998; Mesterton-Gibbons, 2001; Sigmund, 2010; Szabó and Fáth, 2007).

Much of evolutionary game theory assumes that interaction among individuals is either dyadic ($n=2$) or effectively so; for example, in some spatial games, effects of interacting with several neighbors are captured by comparing the outcomes of independent dyadic interactions with each neighbor (Nowak, 2006; Sigmund, 2010). However, any theory of coalition formation must allow for the possibility that $1<m<n$ (without precluding $m=1$ or $m=n$). Accordingly, we restrict our scope to interaction in polyads (groups of more than two), assuming throughout that $n\geq 3$.

4.2. Strategies

A second main ingredient is a strategy set, through which players interact. A strategy set implies an information structure; for example, individuals can base decisions to be aggressive on one another's RHP only to the extent that RHP is observable. A strategy set must be consistent with the cognitive ability of players, for example, whether they show ‘‘triadic awareness’’ (de Waal, 1998a; Perry et al., 2004; DeDeo et al., 2010).

Because different strategies—i.e., different plans for conditioning behavior on available information—can lead to the same action, strategies in nature are not in general observable, although we can still observe the outcomes to which strategy combinations lead. Moreover, in some game-theoretic models, strategy is only implicit: the spotlight instead shines directly on outcomes. In games of coalition formation, the outcomes of interest are coalition structures.

Tractable models require tractable strategy sets (regardless of whether the models are analytical or computational). There is fortunately now considerable evidence that humans and other animals tend to use ‘‘fast and frugal’’ heuristics (Gigerenzer, 2008), as opposed to very sophisticated strategies, for strategic interaction. Plausible strategy sets for the antagonistic phase are typically based on broad regularities or ‘‘stylized facts’’ (Kaldor, 1963; Gächter and Herrmann, 2006) distilled from empirical evidence; for example, evidence that players of lower RHP are more likely to form coalitions has been found in both chimpanzees (Watts, 1998) and humans (Benenson et al., 2009), and can be used to justify threshold strategies of the type assumed in Section 5.2 below. Recently, DeDeo et al. (2010) have pioneered inductive game theory, through which plausible strategies for the associative phase can be inferred directly from time-series data.

4.3. Rewards

The third main ingredient is a reward function, which defines the reward to each individual from every possible outcome—hence, in games of coalition formation, from every possible coalition structure. A reward function not only may depend on combinations of strategies, but also is based on various assumptions about several key components.

4.3.1. Pattern of interaction

A reward function is always predicated on a pattern of interaction. For example, if no coalitions have formed among n individuals contesting a resource, then it may be assumed that their conflict is settled by a single polyadic scramble resulting in outright victory for one of the individuals (Skaperdas, 1998; Tan and Wang, 2010); or that it is settled by a round-robin tournament of dyadic fights (Mesterton-Gibbons and Sherratt, 2007; Stamatopoulos et al., 2009); or that all multi-player fights start with a dyadic conflict, but other individuals may subsequently side with one ‘‘initiator’’ or the other (Gavrilets et al., 2008).

A generalization of Section 2's two-to-tango rule, namely, that a coalition forms if and only if all parties agree to it, is a standard assumption; however, it is not universal (Yi, 1997). Various restrictions on fission and fusion are possible. For example, Ray and Vohra (1997) allow coalitions to break up into smaller subcoalitions; whereas Tan and Wang (2010) assume that a coalition cannot break up, once formed, although existing coalitions (including singletons) can agglomerate.

4.3.2. Synergy rules

In games of coalition formation, the reward function requires a synergy rule for pooling RHPs. Let S be the RHP of a coalition that forms among m individuals of mean RHP $\overline{s}=m^{-1}(s_1+\cdots+s_m)$, where s_i is the RHP of Player i. Throughout the biological, economic and sociological literatures, the most widely adopted rule is that $S=m\overline{s}$, i.e., the RHP of the coalition is the sum of the RHPs of its members (e.g., Caplow, 1959; Skaperdas, 1998; Tan and Wang, 2010; van Schaik et al., 2004, 2006; Whitehead and Connor, 2005). A non-trivial generalization is that $S=qm\overline{s}$ (Mesterton-Gibbons and Sherratt, 2007), where $q-1$ may be either positive (for synergy) or negative (for antergy). Although $q=1$ is so commonly assumed, there is at least some evidence that $q\neq 1$, e.g., $q<1$ for male savanna baboons (Noë, 1994, p. 212).

A different generalization is that $S=m^{\alpha}\overline{s}$, where $\alpha>0$ (Gavrilets et al., 2008). This rule reflects what is largely still called a modified or generalized Lanchester model (Adams and Mesterton-Gibbons, 2003; Plowes and Adams, 2005; Tanner, 2006), although it is now becoming known that Lanchester's laws (Lanchester, 1956; Kingman, 2002; Lepingwell, 1987) were independently discovered by Osipov (Helmbold, 1993; Osipov, 1995).

None of these rules allows for synergy to be spatially heterogeneous. Yet it is known that small groups are able to defeat larger groups near the center of their home range (Crofoot et al., 2008). Such effects could perhaps be modelled by allowing q or α in the synergy rules above to depend on location.

4.3.3. Allocation rules

In games of coalition formation, the reward function usually requires allocation rules for apportioning the costs and benefits of a coalition to its members. In principle, a rule need not be the same for costs as for benefits; for example, in Camargue stallion pairs guarding mares, a subordinate bears more of the costs of engaging rivals and a dominant obtains more of the mating benefits (Feh, 1999). In practice, however, either the same rule is used in both cases; or costs are assumed to be zero, so that the issue becomes moot.

A general form of the allocation rule adopted throughout the literature is

$$\delta_i=\frac{1}{m}\left\{\lambda+(1-\lambda)\frac{s_i}{\overline{s}}\right\}, \tag{2}$$

where $0\le\lambda\le 1$ and δ_i is the proportion of benefit allocated to Player i. Various desirable properties that this rule satisfies have been characterized by Moulin (1987). If $\lambda=1$ (e.g., Bloch et al., 2007; Gavrilets et al., 2008; Mesterton-Gibbons and Sherratt, 2007; Sánchez-Pagés, 2007a), then the division of spoils is egalitarian. If $\lambda=0$ (e.g., Garfinkel, 2004; Whitehead and Connor, 2005; Stamatopoulos et al., 2009; Tan and Wang, 2010), then the division of spoils is proportional to RHP. Finally, if $0<\lambda<1$ (e.g., Nitzan, 1991; Noh, 2002; Sánchez-Pagés, 2007b), then the rule yields a compromise, with proportion λ allocated on egalitarian grounds, e.g., $\lambda=\frac{1}{2}$ (Komorita and Chertkoff, 1973, p. 153).

An exception to the need for allocation rules arises where a contested resource is assumed indivisible and costs of fighting are assumed to be zero (as in Section 5.1).

4.3.4. Costs of fighting

For the sake of tractability, costs of fighting may be either completely absent from the reward function (e.g., Noh, 2002; Sánchez-Pagés, 2007b; Skaperdas, 1998; Stamatopoulos et al., 2009; Tan and Wang, 2010) or chosen primarily for analytical convenience in framing a theoretical issue (e.g., Esteban and Sákovics, 2003). Nevertheless, as in the case of strategies, typically costs are based on stylized facts distilled from empirical evidence.

Among such stylized facts are that fights among more evenly matched opponents take longer to settle (Enquist and Leimar, 1983), and fights between mismatched opponents tend to be of short duration (Morrell et al., 2005). If Δs denotes the RHP difference between two parties in conflict, then the aforementioned regularities support the assumption that the cost of fighting has the form $c(\Delta s)$, and decreases nonlinearly with $|\Delta s|$ at a rate determined by a parameter k measuring sensitivity of cost to RHP difference (Mesterton-Gibbons and Sherratt, 2007, 2009b).

A related idea is that predictable fighting outcomes are less costly to all participants. For Gavrilets et al. (2010), this observation justifies costs that are proportional to the probability of a loss for the eventual winner.

Both ansatzes implicitly assume that costs of fighting are primarily energetic, or at least that injuries are not serious. Neither ansatz need apply to potentially lethal fighting between neighboring groups of chimpanzees (Wilson and Wrangham, 2003). Where a coalition of size m_1 confronts another of size $m_2 \le m_1$, there is evidence that the chance of a fatality in—and hence the fighting costs of—the smaller group increases with the extent $m_1 - m_2$ to which it is outnumbered, injury being rare if $m_1 \approx m_2$ (Wilson et al., 2001).

4.3.5. Victory odds

A further component of the reward function is an assumption about the complementary probabilities of victory in a contest between opposing parties. The simplest choice is that the higher RHP always wins (Whitehead and Connor, 2005; Konrad and Kovenock, 2009). Again, however, the standard approach is to base the assumption on stylized facts distilled from empirical evidence. One such assumption is that the probabilities are $p(\pm\Delta s)$, where p is a sigmoidal function of RHP difference Δs with $p(0) = \frac{1}{2}$ and $p(\Delta s) + p(-\Delta s) = 1$; and where p also has a parametric dependence on a quantity r measuring the reliability of RHP difference as a predictor of fight outcome, in such a way that $p \to \frac{1}{2}$ as $r \to 0$, whereas the higher RHP always wins as $r \to \infty$. For example, if RHP is distributed over $(0,\infty)$, then one of several suitable choices is the logistic function

$$p(\Delta s) = \frac{1}{1+e^{-r\Delta s}}. \tag{3}$$

In the past, evidence for the assumption that p is a sigmoidal function of RHP difference has come only from contests between individuals (e.g., Pratt et al., 2003, p. 949). Recently, however, Bissonnette et al. (2009b) have found evidence to support the assumption in coalitionary behavior of Barbary macaque males.

An alternative assumption would be to make p a sigmoidal function of RHP ratio, as in (5a) below. Where RHP is interpreted as resource commitment, however, Hirshleifer (1989) argues that RHP ratio has a "crucial flaw" which RHP difference avoids.

4.4. Solution concepts

The last main ingredient is a solution concept. In this regard, a theoretical distinction is usually observed between cooperative and non-cooperative play. In cooperative games, all agreements are assumed to be exogenously binding. So strategy recedes to the background, and an appropriate solution concept is a strategically stable distribution of rewards—an outcome. Possibilities are reviewed in Section 6.

By contrast, in non-cooperative games, any agreements must be self-enforcing, and strategy is front and center. Then an appropriate solution concept for community games is that of Nash equilibrium (Nash, 1951), i.e., a strategy combination from which no individual has a unilateral incentive to depart. Equivalently, a Nash equilibrium is a vector of mutual best replies. If a game has several stages or subgames, then each is required to preserve the best-reply property of Nash equilibrium, which accordingly is said to be subgame-perfect. (A sequence of best replies over several stages is obtained by use of backward induction.)

Correspondingly, an appropriate solution concept for population games is that of evolutionarily stable strategy, or ESS (Maynard Smith, 1982). Population strategy v is an ESS if it does not pay a potential mutant to switch from v to any other strategy; v is a strong ESS if it is also uniquely the best reply to itself, and a weak ESS if there is at least one alternative best reply, say u, but v is better reply than u to all such u. Usually, an ESS is not directly observable, but we can observe associated outcomes; for an illustration of this point, see Mesterton-Gibbons and Sherratt (2009b, pp. 270–272).

All of the above solution concepts are for analytical models. Solution concepts for computational models are more ad hoc, but are usually devised to capture emergent patterns or long-term average behavior, in some appropriate sense. In computational games of coalition formation, a reasonable goal is to obtain a probability distribution over all possible coalition structures by numerical experiment.

5. Analytical models of the antagonistic phase: mainly triadic games

To make predictions about coalition formation within a group of n individuals, one must obtain expressions for the reward to each individual from every conceivable coalition structure, i.e., from every partition of the player set N. These expressions depend upon specific assumptions about the pattern of interaction, including informational ones. Here we describe three different choices that have each led to tractable analytical models. For the sake of clarity, we focus on a particular model of each type. In all three cases, individuals contest a resource whose value is 1. The resource may be either indivisible or divisible, depending on the model. Which is more appropriate, even for males fighting over females, is an open question: paternity is indivisible, but probability of paternity is not.

5.1. Full information with RHP explicit

The first possibility, which is that players have full information about one another's RHPs, gives rise to a community game, i.e., a game among specific actors. A model developed by Tan and Wang (2010) exemplifies the approach. This model, which builds on earlier work by Skaperdas (1998), is the most recently published scion of a venerable pedigree in the economics literature. It descends from Olson and Zeckhauser (1966) and Tullock (1980) and includes Bloch (1996), Noh (2002), Esteban and Sákovics (2003), Garfinkel (2004), Bloch et al. (2007) and Sánchez-Pagés (2007a), among others. Earlier contributions are reviewed by Sandler (1993).

Tan and Wang (2010) assume that players sort themselves into coalitions to fight for control of an indivisible resource, and that members of the winning coalition further sort themselves for further fighting, until a single individual has won. If $\{C_1, \ldots, C_k\}$ is a coalition structure, i.e., if the player set N is partitioned into k disjoint subsets as $N = C_1 \cup C_2 \cup \cdots \cup C_k$, then the probability of victory for coalition C_i is assumed to be

$$p_i = \frac{h(S_i)}{\sum_{j=1}^{k} h(S_j)}, \tag{4}$$

where h is a contest success function (Skaperdas, 1996), assumed positive and increasing, and S_j is the RHP of C_j, assumed equal to the sum of the RHPs of its members.

Assumptions about the pattern of interaction are specified by Tan and Wang (2010) for arbitrary n and include that a coalition, once formed, must fight as a unit unless, and until, it becomes the winning coalition. For our purposes here, the key point is that these assumptions allow every possible initial coalition structure to be associated with a reward to each player from every such partition. These rewards can then be compared to determine whether a coalition structure is strategically stable.

Let π_{ij} denote the reward to Player j from coalition structure i. Because the indivisibility of the resource precludes a grand coalition,

Table 2
The reward matrix π.

Case i	Coalition structure	Reward to player j		
		$j=1$	$j=2$	$j=3$
1	{{1},{2,3}}	$\frac{h(X)}{h(X)+h(Y+Z)}$	$\frac{h(Y+Z)}{h(X)+h(Y+Z)}\frac{h(Y)}{h(Y)+h(Z)}$	$\frac{h(Y+Z)}{h(X)+h(Y+Z)}\frac{h(Z)}{h(Y)+h(Z)}$
2	{{2},{1,3}}	$\frac{h(X+Z)}{h(X+Z)+h(Y)}\frac{h(X)}{h(X)+h(Z)}$	$\frac{h(Y)}{h(X+Z)+h(Y)}$	$\frac{h(X+Z)}{h(X+Z)+h(Y)}\frac{h(Z)}{h(X)+h(Z)}$
3	{{3},{1,2}}	$\frac{h(X+Y)}{h(X+Y)+h(Z)}\frac{h(X)}{h(X)+h(Y)}$	$\frac{h(X+Y)}{h(X+Y)+h(Z)}\frac{h(Y)}{h(X)+h(Y)}$	$\frac{h(Z)}{h(X+Y)+h(Z)}$
4	{{1},{2},{3}}	$\frac{h(X)}{h(X)+h(Y)+h(Z)}$	$\frac{h(Y)}{h(X)+h(Y)+h(Z)}$	$\frac{h(Z)}{h(X)+h(Y)+h(Z)}$

Table 3
Two examples of the reward matrix π with $X=0.7$, $Y=0.6$ and $Z=0.2$.

Coalition structure	Rewards to players 1, 2 and 3, respectively					
	(a) $h(s)=\sinh(s^{0.95})$			(b) $h(s)=e^{0.5s}-1$		
{{1},{2,3}}	0.462	0.403	0.134	0.460	0.415	0.125
{{2},{1,3}}	0.477	0.388	0.135	0.495	0.381	0.124
{{3},{1,2}}	0.479	0.405	0.116	0.489	0.408	0.103
{{1},{2},{3}}	0.470	0.398	0.133	0.479	0.400	0.120

for $n=3$ the only possible coalition structures are those shown in the second column of Table 2. Denoting the RHPs of Players 1, 2 and 3 by X, Y and Z, respectively, from (4) we obtain the 4×3 matrix π in the last three columns of Table 2. For example, if the coalition structure is {{3},{1,2}}, then Player 3 fights alone against the coalition {1,2} and wins with probability $\pi_{33}=h(Z)/(h(X+Y)+h(Z))$, by (4). If the coalition wins, with probability $1-\pi_{33}$, then Player 1 fights Player 2 and wins with probability $h(X)/(h(X)+h(Y))$, again by (4). This conditional probability must be multiplied by $1-\pi_{33}$ to obtain the probability π_{31} that Player 1 obtains the resource, and similarly for other cases.

The strategic implications of the reward matrix π are most readily appreciated by choosing a particular form for h and particular values for X, Y and Z. Two examples are given in Table 3. In (a), if the opportunity to form coalition {2, 3} presents itself to Players 2 and 3, then Player 3 will reject it because a coalition with Player 1 is preferable ($\pi_{23}=0.135>\pi_{13}=0.134$); and if the opportunity to form coalition {1, 3} presents itself to Players 1 and 3, then Player 1 will reject it because a coalition with Player 2 is preferable ($\pi_{31}=0.479>\pi_{21}=0.477$). However, if the opportunity to form coalition {1, 2} now presents itself to Players 1 and 2, then both will accept, Player 1 because $\pi_{31}=0.479$ is the highest reward in the first column of the matrix, and Player 2 because $\pi_{32}=0.405$ is the highest reward in the second. So {{3},{1,2}} is the unique equilibrium coalition structure. The model thus predicts an all-down coalition (assuming that rank is correlated with RHP). The strongest individual is still most likely to win, but Player 2's probability of gaining the resource has slightly increased, from 0.398 to 0.405, by virtue of the coalition. In (b), on the other hand, similar reasoning shows that the unique equilibrium coalition structure is {{1},{2,3}}: the model predicts an all-up coalition. Note the important point that these outcomes are independent of the order in which opportunities for coalition formation present themselves to players.

The essential difference between these two outcomes is that although h is increasing and satisfies $h(0)=0$ in both cases, in (b) h is always a convex function, whereas in (a) h fails to be convex for small (positive) values of its argument. Tan and Wang (2010) have shown more generally that for any contest success function either of the form

$$h(s)=s^r, \tag{5a}$$

where r exceeds 1 and measures the reliability of RHP ratio (Section 4.3.5), or of the form

$$h(s)=e^{\gamma s}-1, \tag{5b}$$

with γ positive, if $X>\max(Y,Z)$, then {{1},{2,3}} is the unique equilibrium coalition structure (by straightforward algebra; e.g., with $h(s)=e^{\gamma s}-1$ in Table 2, $\pi_{12}-\pi_{32}$ equals $(e^{\gamma X}-1)e^{\gamma Y}(e^{\gamma Y}-1)^2(e^{\gamma Z}-1)(e^{\gamma X}-e^{\gamma Z})$ divided by a positive denominator, and the numerator is positive because $X>Z$). However, the function h for (a) in Table 3 is not included in the class of functions defined by (5).

Tan and Wang (2010) proceed to establish a handful of further results for the given h, some for $n=4$, some for $n\geq 3$. For example, for $n=4$, when X, Y, Z and W, the respective RHPs of Players 1–4, satisfy $X>Y>Z>W$, Tan and Wang (2010) show that if $X>Z+W$, then the unique equilibrium coalition structure is {{{2},{3,4}},{1}}; note that if the coalition defeats Player 1, then the two weakest players are committed to taking on Player 2 as a unit. If instead $X<Z+W$, however, then the equilibrium coalition structure is indeterminate (i.e., more sensitively dependent on h), although it must exist and consist of two pairs. Again, for $n\geq 5$, Tan and Wang (2010) show that convexity of h with $h(0)=0$ guarantees that every player prefers some coalition to fighting alone (so that the last row in Table 2 is always dominated by one of the preceding rows), and that any equilibrium coalition structure will contain only two coalitions (a result that is strongly dependent on both the constant-sum reward structure and the assumption that a larger coalition preserves any smaller coalitions from which it is formed). However, as Tan and Wang (2010) remark, "the exact characterization of the equilibrium coalition structure is very difficult."

The model developed by Stamatopoulos et al. (2009) is a further example of the approach just described. The main differences are as follows. First, the model is purely triadic. Second, the resource is divisible and is shared by a winning coalition, proportionally to RHP. Third, if no coalition forms, then the resource is contested by a sequence of dyadic fights (as opposed to a scramble). Finally, assuming $X>Y>Z$, the complementary probabilities of victory for a contest between two coalitions are determined by (3) with $r=1/Z$, as opposed to (4). The model predicts that the unique equilibrium coalition structure is {{1},{2,3}} if X is sufficiently large; {{1,2}, {3}} if X and Y are both sufficiently small (i.e., sufficiently close to Z, given $X>Y>Z$); and otherwise {{1,3}, {2}}. Thus (assuming rank to be correlated with RHP) all-up, all-down and bridging coalitions are all possible.

On the one hand, these are clear predictions. On the other hand, they are based on very special assumptions. In general, it is best for costs and victory odds to depend on a "tunable" parameter that is independent of RHP and can be matched to different ecologies (using maximum-likelihood estimation or otherwise). For tractability, however, Stamatopoulos et al. (2009) assume that costs are zero or at least independent of RHP (Section 3), while acknowledging that it is better for the cost of a fight to be "an increasing function of the strength of the opponent;" and they choose $r=1/Z$ in (3), precluding a tunable reliability parameter that is independent of RHP. They may be right to suppose that other choices will lead to qualitatively similar results, but to us it seems unlikely that the coalition structure would be independent of r.

5.2. Partial information with RHP explicit

The second possibility, that players have only partial information about one another's RHPs, gives rise to a continuous population game in which a strategy is an RHP threshold, below which an individual seeks to enter a coalition with others. A model developed by Mesterton-Gibbons and Sherratt (2007, 2009a) exemplifies this approach. It assumes that each member of a triad knows only its own RHP, but that all three RHPs are drawn independently from a common distribution with density g on [0,1]. Let $f(u,v)$ denote the reward to a focal u-strategist in a population of v-strategists. For all (u,v), the joint sample space $[0,1]^3$ can be decomposed into a finite number K of mutually exclusive events, each associated with a coalition structure. Let $\Omega_i(u,v)$ denote the i-th such event; and let $P_i(X,Y,Z)$ denote the corresponding payoff to the focal individual, where X, Y and Z again denote the RHPs of Players 1, 2 and 3, respectively. Then

$$f(u,v) = \sum_{i=1}^{K} \iiint_{(x,y,z)\,\in\,\Omega_i(u,v)} P_i(x,y,z)g(x)g(y)g(z)\,dx\,dy\,dz. \tag{6}$$

Assumptions about the pattern of interaction are as follows. Stronger animals tend to escalate when involved in a fight, weaker animals tend not to escalate. If an animal considers itself too weak to have a chance of being the top-ranking individual in a dominance hierarchy that controls access to the resource, then it attempts to form a coalition with both others: coalition means a mutual defense pact and an equal share of benefits. As a proportion of total group fitness 1, it costs θ (≥ 0) to attempt a coalition; the attempt may not be successful, but if all agree to it, then there are no fights.

If there is a dominance hierarchy with three distinct ranks after fighting, then the alpha individual gets α ($>\frac{1}{2}$), the beta individual gets $1-\alpha$ and the gamma individual gets zero. If there is a three-way coalition or if the animals fight one another and end up winning and losing a fight apiece, then each gets $\frac{1}{3}$; however, in the second case they also incur a fighting cost. If a coalition of two defeats the third individual, then each member of the pair obtains $\frac{1}{2}$ while the individual obtains zero; and if the individual defeats the pair, then it obtains α while each member of the pair obtains $\frac{1}{2}(1-\alpha)$. There is at least potentially a synergistic effect, so that the RHP of a coalition of two whose individual RHPs are S_1 and S_2 is $q\{S_1+S_2\}$, where q need not equal 1.

Fighting costs are specified as in Section 4.3.4 and are equally borne by all members of a coalition. Victory odds are specified as in Section 4.3.5, except that an incomplete Beta function is used in place of (3), because RHP is distributed over [0,1].

Let u be the coalition threshold for a potential mutant (the focal individual), whose RHP is X: if X fails to exceed u, then it attempts to make a mutual defense pact with each of its conspecifics. Let v be the corresponding threshold for the other two members of a triad, whose RHPs are Y and Z. Then the set of mutually exclusive events with associated coalition structures and payoffs is as shown in Table 4, and the reward follows from (6) with $K=8$.

For this game, an ESS is a strong ESS, i.e., a strategy v that is uniquely the best reply to itself ($f(v,v)>f(u,v)$ for all $u \neq v$). The evolutionarily stable strategy set depends on seven parameters, namely, c_0 (maximum fighting cost), q (synergy multiplier), θ (pact cost), α (proportion of group fitness to a dominant), r (reliability of RHP difference as predictor of fight outcome), k (sensitivity of cost to RHP difference) and σ^2 (variance of distribution, assumed symmetric). It is a complicated dependence, but it enables us to calculate, among other things, the probability of an all-up coalition, i.e., the probability that the two weakest animals will ally against the strongest in an ESS population. An initially counterintuitive prediction is that this probability is higher when $q<1$—that is, when there exists a degree of antergy in combining RHPs—than when $q>1$ (synergy); and it is especially high when σ^2 and r are both high. These are conditions that appear to characterize coalitions found in primate societies (Mesterton-Gibbons and Sherratt, 2007, pp. 284–285).

Potentially just as important, however, is the model's prediction that low values of α, c_0 or r and high values of k or θ all tend to preclude the formation of a coalition at the ESS, and that no coalition may form at the ESS even if $\theta=0$ (Mesterton-Gibbons and Sherratt, 2007, p. 281). There are indeed some species of primate in which coalition formation is known to be rare, e.g., chacma baboons (Barrett and Henzi, 2006).

Coalitions between neighbors to deter an intruder have also been modelled by the approach described above, with the modified assumption that neighbors know one another's RHPs, but not the RHP of an intruder, and vice versa (Mesterton-Gibbons and Sherratt, 2009b). So far, the approach has been limited to triads; but it should be possible to extend it to higher values of n, in particular to $n=4$. A particular reason for these extensions to be of interest is that the number of essential ecological parameters increases far more slowly than the number of possible coalition structures with n: the first number increases by only 1 (for a new fitness-proportion parameter) whenever n increases by 1, whereas the second number is the n-th Bell number (Bell, 1934, p. 417).

5.3. Full information with RHP implicit: models of intervention

The third possibility, which is that RHP is not explicitly modelled but players have full information about probabilities of victory, has

Table 4
Payoff to a focal u-strategist, Player 1, of RHP X whose partners, Players 2 and 3, are v-strategists of RHPs Y and Z, respectively, with $\Delta=q\{X+Z\}-Y$ and $\zeta(X,Y,Z)=\alpha p(X-Y)p(X-Z)+\frac{1}{3}\{p(X-Y)p(Z-X)p(Y-Z)+p(X-Z)p(Y-X)p(Z-Y)\}+(1-\alpha)\{p(X-Y)p(Z-X)p(Z-Y)+p(X-Z)p(Y-X)p(Y-Z)\}$.

Case i	Coalition structure	Event $\Omega_i(u,v)$	Payoff $P_i(X,Y,Z)$
1	{{1,2,3}}	$X<u, Y<v, Z<v$	$\frac{1}{3}-\theta$
2	{{1,3},{2}}	$X<u, Y>v, Z<v$	$\frac{1}{2}\{\alpha p(\Delta)+1-\alpha-2\theta-c(\Delta)\}$
3	{{1,2},{3}}	$X<u, Y<v, Z>v$	$P_2(X,Z,Y)$
4	{{1},{2,3}}	$X>u, Y<v, Z<v$	$\alpha p(X-q\{Y+Z\})-c(X-q\{Y+Z\})$
5	{{1},{2},{3}}	$X<u, Y>v, Z>v$	$-\theta$
6	{{1},{2},{3}}	$X>u, Y>v, Z<v$	$(2\alpha-1)p(X-Y)+1-\alpha-c(X-Y)$
7	{{1},{2},{3}}	$X>u, Y<v, Z>v$	$(2\alpha-1)p(X-Z)+1-\alpha-c(X-Z)$
8	{{1},{2},{3}}	$X>u, Y>v, Z>v$	$\zeta(X,Y,Z)-c(X-Y)-c(X-Z)$

been used to model interventions and gives rise to a discrete population game. A model developed by Johnstone and Dugatkin (2000), which builds on earlier work by Dugatkin (1998), exemplifies this approach.

Let Player 1 be the focal individual in a triad whose other members are Players 2 and 3. Assumptions about the pattern of interaction are as follows. Player 1 observes a fight between the others and may or may not intervene, with a view to the effect on its next fight, for which Players 2 and 3 are equally likely opponents. The effect is mediated through winner and loser effects (Rutte et al., 2006): a probability p of victory against an untested opponent is raised to $V(p)$ after a victory but lowered to $L(p)$ after a loss. If Player 1 decides to intervene on behalf of, say, Player 2, then Player 2 is guaranteed to win against Player 3 (and vice versa); moreover, Player 2 willingly accepts the help, and there is no possibility of a coalition {2,3} against {1}. Thus, in modifying Table 2 for present purposes, the first thing we do is delete its first row: {{1},{2,3}} cannot arise, the only coalition structures being those listed in Table 5. Let the benefit of victory (to Player 1 from its next fight) be 1, and let c be the cost of intervention. Then, as in Section 5.1, we can associate a reward to each individual from every possible coalition structure. Because this is a population game, however, we are interested only in rewards to the focal individual, Player 1. So, instead of a reward matrix as in Table 2, we obtain the reward vector π in Table 5, whose entries can be compared to determine whether intervention pays; here p_2 or p_3, p_{23} and p_{32} denote the probabilities that Player 2 or Player 3 defeats Player 1, Player 2 defeats Player 3 and Player 3 defeats Player 2, respectively, absent winner and loser effects. Because $p_{23}+p_{32}=1$, it follows that

$$\pi_1-\pi_3=\tfrac{1}{2}\,p_{32}\{D(p_3)-D(p_2)\}-c,\ \pi_2-\pi_3=\tfrac{1}{2}p_{23}\{D(p_2)-D(p_3)\}-c, \tag{7}$$

symmetrically, where $D(p)=V(p)-L(p)$ in essence implicitly measures the difference in confidence between winning and losing as a function of prior RHP. If D is a decreasing function, then it pays to intervene only on behalf of the stronger of the other two players (a conservative coalition if Player 1 is the alpha), and only if c is not too large; whereas if D an increasing function, then it pays to intervene only on behalf of the weaker (a bridging coalition if Player 1 is the alpha, an all-up coalition if Player 1 is the beta). This is an intriguing result, but as Johnstone and Dugatkin (2000) point out, the empirical literature offers essentially no guidance as to whether D should be increasing or decreasing—if either.

Despite many differences of detail, a recent model by Broom et al. (2009) is essentially a further example of the approach just described: a triadic model of intervention. Two big differences are as follows. First, potential benefits of intervention derive from relatedness between actors, as opposed to prior-experience effects. Second, it is no longer assumed that an intervention is guaranteed to be successful, i.e., two always beat one, against which now there is solid evidence (Bissonnette et al., 2009b). Instead, Broom et al. (2009) model the observed fight as a Hawk-Dove contest, which a supported contestant is more likely to win. The analysis turns out to be rather complicated, despite numerous simplifying assumptions. But the model yields several intriguing predictions, most notably that it is variance of relatedness within a group—as opposed to degree of relatedness itself—that seems to drive the likelihood of coalitions of this type.

Table 5
The reward vector π. The benefit to the focal individual from its next fight is 1 if it wins, 0 if it loses. Hence all benefits have the form $\sum_l\sum_{j\neq k}q_{kl}p_{kj}\omega_l$ for $2\le j,k,l\le 3$, where ω_l is the probability that Player l is the next opponent, p_{kj} is the probability that Player k won against Player j, and q_{kl} is the conditional probability that Player l loses against Player 1 if k won against j. It is assumed that $\omega_2=\frac{1}{2}=\omega_3$ with $p_{32}=0$ in Case 1 and $p_{23}=0$ in Case 2.

Case i	Coalition structure	Reward to focal individual
1	{{1,2},{3}}	$\frac{1}{2}\{1-V(p_2)\}+\frac{1}{2}\{1-L(p_3)\}-c$
2	{{1,3},{2}}	$\frac{1}{2}\{1-L(p_2)\}+\frac{1}{2}\{1-V(p_3)\}-c$
3	{{1},{2},{3}}	$\frac{1}{2}\{p_{23}\{1-V(p_2)\}+p_{32}\{1-L(p_2)\}\}$ $+\frac{1}{2}\{p_{23}\{1-L(p_3)\}+p_{32}\{1-V(p_3)\}\}$

6. Cooperative games: the allocative phase

Cooperative game theory is essentially a framework for division of spoils among individuals who have already agreed to pool their resources (Gilles, 2010; Kahan and Rapoport, 1984; Mesterton-Gibbons, 2001; Myerson, 1991; Osborne and Rubinstein, 1994; Owen, 1995; Peters, 2008; Ray, 2007). Here we assess the potential relevance of this theory to models of coalition formation among animals, as advocated, e.g., by Noë (1990).

The central concept is the characteristic function, introduced by von Neumann and Morgenstern (1953), and usually denoted by v. To each possible subset S of the player set $N=\{1, 2, \ldots, n\}$, v assigns a reward $v(S)$ that coalition S can somehow guarantee for itself, even if all other players have formed a coalition against it; this reward is assumed to be freely redistributable among the members of S, yielding a cooperative game with "transferable utility" or CGTU. Thus $v(S)$ is determined by the RHP of S. Nevertheless, a "grand coalition" of all n players is assumed to have formed (perhaps voluntarily, perhaps enforced by an external agent or circumstance); and within it, subcoalitions of fewer than n players can use as bargaining leverage the RHP they would have had without the others, if the others were not there. For games of biological interest, after subtracting out the rewards that individuals can guarantee for themselves, v can be "0–1 normalized" (Aumann, 1989), so that $v(N)=1$ and $v(\{i\})=0$ for all $i\in N$. Let us define an imputation to be a reward vector $x=(x_1, x_2, \ldots, x_n)$ such that

$$x_i\ge 0\quad\text{for all } i\in N, \tag{8a}$$

$$x_1+x_2+\cdots+x_n=1. \tag{8b}$$

Here (8a) expresses individual rationality and (8b) expresses group rationality (also called unimprovability or Pareto-optimality): by (8b), no player's allocation can be increased without decreasing another's. Then a solution to a cooperative game is an imputation satisfying various additional desiderata, corresponding to different notions of what comprises a stable division of rewards.

6.1. Constraints on excess

One such desideratum is that the excess

$$e(S,x)=v(S)-\sum_{i\in S}x_i \tag{9}$$

of coalition S at imputation x be as low as possible to minimize player dissatisfaction. In particular, it is desirable that the excess be nonpositive for all possible S; that is

$$\sum_{i\in S}x_i\ge v(S)\quad\text{for all } S\subset N. \tag{10}$$

When (10) holds, x allocates to each coalition at least as much inside the grand coalition as it could have guaranteed outside it. The set of all such imputations is said to form the core. The core need not exist, which Herbers (1979) has used to argue that sex ratios of progeny in mound-building ant species exhibit fluctuations because the sex ratio is not in evolutionary equilibrium; and when the core does exist, for which sufficient conditions are known (Aumann, 1989; Bondareva, 1963; Shapley, 1967), it need not contain a single imputation. Either way, the maximum excess over all coalitions can be minimized to yield a "higher order core," called the nucleolus, which contains a unique imputation that belongs to the core if the core exists.

Because the grand coalition is assumed to have formed, however, the nucleolus is essentially incapable of predicting the formation of a true coalition. To illustrate for $n=3$, consider three males of RHPs X, Y and Z in competition with a rival fourth male of RHP W over the indivisible resource of a female in estrus, with $W>X>Y>Z$ and $\min(X+Y,X+Z)>W>Y+Z$. Assume synergicity $q=1$ (Section 4.3.2). Because the coalition $\{2,3\}$ is weaker than the rival, whereas either $\{1,2\}$ or $\{1,3\}$ is stronger, it is reasonable to assume that $v(\{2,3\})=0$ with $v(\{1,2\})=v(\{1,3\})=1$. Thus Player 1 is a veto player (Kahan and Rapoport, 1984; Noë, 1990), essential for a successful coalition in this game. The core contains a unique imputation, namely, $x=(1,0,0)$. It predicts that all the benefits go to Player 1; however, it cannot predict how. Intuition suggests that the benefits should accrue to Player 1 through $\{1,2\}$ or $\{1,3\}$, but neither of these true coalitions can be predicted, because $\{1,2,3\}$ is assumed to have formed.

The above example is closely based on behavior that Noë (1990) observed in three male yellow baboons, called H5 (Player 1), H6 (Player 2) and H7 (Player 3). H5 did indeed obtain most of the benefits, and 60% of all coalitions included H5 and one other; however, H5 did not monopolize benefits, and all possible coalitions formed some of the time. In particular, H6 and H7 paired up about 20% of the time, and on one occasion this coalition was successful. The key point is that CGTUs are principally concerned with distributing the benefits of a pie that all have agreed somehow to share, and so have relatively little to say about coalition formation per se.

Similar remarks also apply to other cooperative game solution concepts.

6.2. Constraints on unreasonableness

Another desideratum involves a consideration of all possible orders in which the grand coalition could be assembled, one player at a time. If, in any such order, $S-\{i\}$ denotes the coalition that Player i joins to form coalition S, then $v(S)-v(S-\{i\})$ is Player i's marginal worth to S. It is desirable that no player's allocation at imputation x should exceed that player's greatest possible marginal worth from a possible order of formation:

$$x_i \le \max_{S\in\Pi^i}\{v(S)-v(S-\{i\})\} \quad \text{for all } i\in N, \tag{11}$$

where Π^i denotes the set of all possible coalitions containing Player i. The set of all such imputations is called the reasonable set. Because marginal worth is a random variable over all possible orders of formation, its expected value for each player can be used to select a specific imputation from the reasonable set as the solution concept. If all orders of formation are equally likely, then that imputation is the Shapley (1953) value, for which x is defined by

$$x_i = \frac{1}{n!}\sum_{S\in\Pi^i}(\#(S)-1)!(n-\#(S))!\{v(S)-v(S-\{i\})\}, \tag{12}$$

where $\#(S)$ denotes number of players in S.

Because of the fundamental tension between power and equity already reflected in (2), the nucleolus and the Shapley value almost never coincide; for example, the Shapley value of the veto game described in Section 6.1 would be the imputation $(\frac{2}{3},\frac{1}{6},\frac{1}{6})$. Broadly speaking, the first solution concept gives priority to the most dissatisfied coalitions, whereas the second grants all coalitions equal status.

The expected marginal worth of a player has an especially appealing interpretation in so-called simple games (Taylor and Zwicker, 1999), where every coalition is either winning or losing, so that $v(S)=0$ or $v(S)=1$ for every S. Such games arise naturally in the context of voting for or against a status quo; the veto game discussed above is also a simple game. Let P^i denote the set of coalitions in which Player i's resources are crucial to victory, i.e., the coalitions that would become losing if Player i were removed. Then (12) becomes the Shapley–Shubik power index

$$x_i = \frac{1}{n!}\sum_{S\in P^i}(\#(S)-1)!\;(n-\#(S))! \tag{13}$$

(Shapley and Shubik, 1954), which is the probability that Player i's vote is pivotal (in forming some coalition). It is, therefore, a measure of Player i's voting power; for example, the first baboon in the veto game can be viewed as possessing $\frac{2}{3}$ of the power to change the status quo (from no female access to access for the coalition).

The index above has been generalized, and numerous other power indices have since been constructed (Holler and Owen, 2001). We revisit this topic in Section 6.4.1.

6.3. Constraints on transferable utility and negotiation

Transferable utility within a CGTU allows players to bargain as subcoalitions within the grand coalition (as opposed to individuals). It effectively assumes that a unit of reward is worth the same to every player. By contrast, the Nash bargaining solution (Nash, 1953) or NBS for short, which is the vector x that maximizes the product $x_1x_2\,\ldots x_n$ in (8), does not assume transferable utility and thus allows rewards to be measured in different currencies: it has the property of "scale invariance." So it may sometimes yield a more appropriate division of spoils when favors of different kinds are being traded; however, the desirability of scale invariance in general is controversial (Binmore, 2010, p. 1359).

At least partly because it is unclear how animals can negotiate without language, controversy likewise surrounds the defensibility of the assumption of binding agreements that underpins cooperative game theory (McNamara et al., 2006; Akçay and Roughgarden, 2007b). In at least some cases, however, such agreements can be enforced by simple mechanisms requiring only a basic capacity to remember and punish defections; and in other cases they can be supported by various non-cooperative bargaining procedures (Binmore et al., 1986; Rubinstein, 1982; Binmore, 2010).

Roughgarden et al. (2006), Akçay and Roughgarden (2007a), Roughgarden (2009) and Akçay et al. (2009) have proposed using the NBS to study social behavior in animals more generally. This framework has potential to become polyadic. Nevertheless, it has so far been developed only for the dyadic case and thus falls largely outside our purview (Section 4.1), although the NBS can be used as a submodel for dividing the spoils inside a dyadic coalition that forms within a polyad.

6.4. Potential for application

A special difficulty with the characteristic function is that assigned worths are assumed to be independent of coalition structure; for example, in a group of four players, $v(\{1,2\})$ would be the same, regardless of whether the coalition $\{1,2\}$ were embedded in the coalition structure $\{\{1,2\},\ \{3,4\}\}$ with a "counter-coalition" {3,4} or in the coalition structure {{1,2}, {3}, {4}} with a pair of singletons. Moreover, as remarked above, cooperative game theory has relatively little to say about coalition formation per se, being principally concerned with distribution of benefits.

6.4.1. Generalized power indices

Nevertheless, what limits the applicability of cooperative game theory to coalition formation is not its concern with a distribution of benefits to individuals—which, as we have seen, in simple games can be interpreted as an index of power—but rather that this index of power is associated with a particular coalition structure, namely, the grand coalition. If instead an index of power can be associated with each possible coalition structure, then a comparison of these indices can be used to identify transitions between coalition structures.

Consider once more Case 6 of Table 1 (Section 2), and let *A*, *B* and *C* be Players 1, 2 and 3, respectively. Shenoy (1978, pp. 182–191) has devised a Caplow power index, which is the vector of proportions of all dominances a player achieves in a given coalition structure. The relevant five vectors are listed as the columns of Table 6(a); for example, in coalition structure *BC*, *A* dominates no other, *B* dominates *A* (externally) and *C* (internally), and *C* dominates *A* (externally), so that the proportions of all dominances for *A*, *B* and *C* are 0, $\frac{2}{3}$ and $\frac{1}{3}$, respectively. Suppose that *I* is an initial configuration (as Caplow did). If coalition structure *AC* is now offered, then it will be accepted by both *A* (because $\frac{2}{3} > 0$) and *C* (because $\frac{1}{3} > 0$), which makes *B*'s preferences irrelevant. Thus *I* is dominated by *AC* through {1,3}. No movement from *AC* is possible, so *AC* is the final outcome. Likewise, *I* is dominated by *AB* through {1,2}; however, *AB* in turn is dominated by *BC* through {2,3}. Because no movement from *BC* is possible, this time *BC* is the final outcome. Thus *AC* and *BC*, i.e., Caplow's predictions for Case 6, are the only undominated coalition structures in a sense made precise by Shenoy (1978, 1979, 1980), who in this way recovers all of Caplow's predictions within the framework of game theory.

Table 6
Power indices for Case 6 of Table 1. For $i \in \{A,B,C\}$ and $j \in \{I,BC,AC,AB,G\}$, the term in row *i* and column *j* of each matrix is the power of individual *i* in coalition structure *j*. (a) The Caplow power indices. (b) The Gamson power indices (Shenoy, 1978, pp. 192–193) are based on the result that many (but not all) simple games have a weighted-majority representation of the form $[Q;\, w_1, w_2, \ldots, w_n]$, where w_i is the weight attached to Player *i* and a coalition is winning if the sum of its members' weights equals or exceeds the quota *Q*; for example, the veto game in Section 6.1 has representation [3; 2, 1, 1], and the game considered in this table has representation [5; 4, 3, 2]. The Gamson index is defined using these weights as proportion of power in a winning coalition and otherwise zero. (c) The Shapley–Shubik power indices.

	I	*BC*	*AC*	*AB*	*G*
(a) *The Caplow indices*					
A	0	0	$\frac{2}{3}$	$\frac{2}{3}$	$\frac{2}{3}$
B	0	$\frac{2}{3}$	0	$\frac{1}{3}$	$\frac{1}{3}$
C	0	$\frac{1}{3}$	$\frac{1}{3}$	0	0
(b) *The Gamson indices*					
A	0	0	$\frac{2}{3}$	$\frac{4}{7}$	$\frac{4}{9}$
B	0	$\frac{3}{5}$	0	$\frac{3}{7}$	$\frac{1}{3}$
C	0	$\frac{2}{5}$	$\frac{1}{3}$	0	$\frac{2}{9}$
(c) *The Shapley–Shubik indices*					
A	0	0	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{3}$
B	0	$\frac{1}{2}$	0	$\frac{1}{2}$	$\frac{1}{3}$
C	0	$\frac{1}{2}$	$\frac{1}{2}$	0	$\frac{1}{3}$

Shenoy's approach is quite general: it identifies the undominated coalition structures associated with any power index. In particular, Shenoy has also devised an index to recover Gamson's theory; for Case 6 of Table 1, its unique prediction is *BC*, as confirmed by Table 6(b). Also, for simple games, (13) generalizes to the idea that individual power in any coalition structure (not just the grand coalition) equals probability of being pivotal in reaching it (Aumann and Dreze, 1974; Shenoy, 1979). This generalized Shapley–Shubik index yields yet another prediction for Case 6 of Table 1, namely, that any configuration except *I* or *G* is to be expected; see Table 6(c). Here the underlying rationale is strategic symmetry of external control (with an implicit assumption that internal dominance is not an issue because players can bargain it away through a binding agreement): if any two players can succeed in wresting a prize from a third, then it should not matter who is one's partner. Gamson (1961, p. 378) refers to this prediction as "strict rationality theory."

6.4.2. van Schaik et al.'s model

The above considerations show that although cooperative game theory is by no means an off-the-shelf tool for predicting coalition formation, it has served to bring coherence to verbal theory. It can also serve as a useful point of departure for other models.

For example, van Schaik et al. (2004, 2006) applied excess-minded thinking to a group of primate males ranked 1 through *n* in a linear dominance hierarchy and competing for access to females in estrus. Building upon earlier work by Pandit and van Schaik (2003), van Schaik et al. assumed (8) to hold with $x_i = (1-\beta)x_{i-1}$ for $0 \le \beta \le 1$, so that reward—in terms of proportion of fertilizations—decreases with rank more rapidly when the "environmentally determined degree of despotism" β is larger. With *x* thus determined, they define *v* so that (10) holds with equality, and so every imputation belongs to the core.

To progress from here, van Schaik et al. (2004, 2006) assumed such a high correlation of RHP with rank (Alberts et al., 2003) that the RHP of coalition *S* is proportional to $v(S) = \sum_{i \in S} x_i$. They were thus able to explore the "profitability and feasibility" of a coalition of individuals occupying adjacent ranks against a lone target. Such a coalition *S* is profitable for Player *i* if $x_t - x_i$ exceeds the cost of coalition formation, where *t* is "the targeted rank, i.e., the rank individual *i* would occupy as a result of a successful coalition;" the coalition is feasible if $v(S) - x_t$ is sufficiently large; and because $x_1, \ldots, x_n$ are now readily calculated in terms of β, *m*, *n* and a (highly idealized) cost parameter *C*, it is possible to identify regions of parameter space where coalitions are viable, that is, both feasible and profitable. The model yields a variety of interesting predictions. For example, rank-changing all-up coalitions should arise only if $\beta \le \frac{1}{2}$; moreover, they should be small (dyads or triads), target the top ranker, and involve individuals ranking just below it.

Both van Schaik et al. (2004) and Jones (2005, 2006) found a relatively good fit between the model and data existing in the literature. On the other hand, the model also predicts that rank-changing bridging coalitions are not profitable at low β, contradicting behavior recently observed in Barbary macaques (Berghänel et al., 2010, p. 4). Furthermore, the model is predicated on the assumption that x_i decreases with *i*, contradicting recently obtained results on chimpanzee paternity (Newton-Fisher et al., 2010, p. 423, Fig. 3).

7. Analytical models of the associative phase: alliance formation

There is no universal agreement on where to draw the line between alliance and coalition, or even whether different words are necessary; for example, Chapais (1995) and Duval (2007) use alliance in either case, whereas Öst et al. (2003) and Olson and Blumstein (2009) use coalition. In our lexicon, however, an alliance is a longer-term relationship within which coalitions may occur; and a key distinction is that alliances may overlap, whereas coalitions are mutually exclusive. A further de facto distinction is that alliances may develop through affinities of age, gender, location, personality, shared interest or any other quality that are independent of RHP. In other words, an alliance in its purest form is a product of affinitive association or dissociation. In principle, there need be no source of internal conflict. In practice, conflict may arise, precipitating the formation of coalitions within or across alliances. (Of course, coalitions may also form in the absence of alliances, and members of alliances may cooperate in ways that we would not call coalition formation.)

The associative phase of strategic interaction, which deals with how individuals enter or exit interactions with collaborative potential, is the one that has received least attention from game theorists, not only in the context of CAFT (DeDeo et al., 2010) but also more generally (Jasper, 2006). Nevertheless, there exist two literatures on models of association and dissociation from which much of relevance can be drawn. Our purpose here is a brief introduction that suggests their potential. For further discussion of terms we use from network theory see, e.g., Jackson (2008) or Newman (2010).

7.1. Models of coagulation and fragmentation

The first literature originates with a 1916 study of polymers by Smoluchowski (Wattis, 2006). If coalitions may form either unintentionally or intentionally (Wilke, 1985), then models of coagulation and fragmentation are arguably those which embody the least intentionality, and can thus serve as null models, to which other models are compared. They have already found their way into the social sciences (Eguíluz and Zimmermann, 2000; Bohorquez et al., 2009; Zhao et al., 2009) and should be attractive models in biology as well, at least as minimal models or building blocks. But so far their applications have been few (Gueron and Levin, 1995).

To describe these models in context, we start with n unconnected individuals. They start to form coalitions, which coalesce and fragment according to the following constraints: The network is determined by binary bonds between individuals, and coalitions are connected components in which every pair is connected (i.e., "cliques"); coalitions merge due to random contact between them; coalitions fragment for various reasons; and fragmenting and coalescence of coalitions is instantaneous.

7.1.1. Merging

To specify the merging of coalitions we posit that a pair of coalitions of sizes r and s merges into one of size $r+s$ at rate m_{rs}. Typical assumptions (Aldous, 1999; Collet, 2004; Wattis, 2006) are as follows:

(i) $m_{rs} = \text{constant}$ (the Kingman coalescent). Coalitions merge by contact with specific individuals, usually leaders or other appointed representatives.
(ii) $m_{rs} \propto rs$ (multiplicative, or Erdös–Renyi, coalescent). Coalitions merge due to random contact between arbitrary members. This is the most common assumption.
(iii) $m_{rs} \propto r^{\gamma} + s^{\gamma}$. The parameter $\gamma \in [0,2]$ measures the degree of homogeneity or hierarchical structure in a typical coalition.

7.1.2. Fragmentation

The easiest assumption is that coalitions fragment at random, on the same time scale as they are formed. The crucial ingredient is the fragmentation function, i.e., the distribution of the number and sizes of the smaller coalitions that result. Some possibilities are as follows:

(i) All smaller coalitions are singletons (Eguíluz and Zimmermann, 2000). We call this model the EZ model. It was introduced to study herding behavior on a stock market, and a more involved version is used in the study of insurgency groups (Bohorquez et al., 2009). At rate v, a random individual is chosen and its group fragmented into individuals, while at rate $1-v$ two individuals are chosen at random from two different groups, and their groups are merged.
(ii) Splits are into two smaller coalitions, chosen at random among available choices (Gueron and Levin, 1995). We call this model the GL model.
(iii) A random number ϕ of fragments is chosen, and any individual chooses at random which fragment to join. This may be called a multinomial model.
(iv) From isolated individuals a coalescing model is run on a faster time scale.

7.1.3. Smoluchowski equations

The main analytical tool is the Smoluchowski coagulation–fragmentation equation for n_s, the average number of coalitions of size s. With large n, and ignoring stochastic fluctuations, for the EZ model in (i) above we obtain

$$\frac{dn_s}{dt} = -\frac{vsn_s}{n} + \frac{(1-v)}{n^2}\sum_{r=1}^{s-1} rn_r(s-r)\, n_{s-r} - \frac{2(1-v)sn_s}{n^2}\sum_{r\geq 1} rn_r \tag{14a}$$

when $s \geq 2$ with

$$\frac{dn_1}{dt} = \frac{v}{n}\sum_{r\geq 2} r^2 n_r - \frac{2(1-v)\, n_1}{n^2}\sum_{r\geq 1} rn_r \tag{14b}$$

(Wattis, 2006). At equilibrium ($dn_s/dt = 0$) the equations can be solved analytically, and for large n and small v one obtains a power law:

$$n_s \sim ne^{-(1/4)sv^2} s^{-5/2}$$

(D'Hulst and Rogers, 2000). This power law is the same as for a model with no fragmentation, observed at time about n, i.e., the critical Erdös–Renyi random graph (Durrett, 2007). Interestingly, the $\frac{5}{2}$ scaling law has been observed in the empirical data on sizes of insurgency groups (Bohorquez et al., 2009), although there are also significant deviations.

The Smoluchowski coagulation–fragmentation equation for the GL model has different analytic properties (Ruszczycki et al., 2009).

7.2. Affinitive network dynamics

A common assumption in evolutionary games is that individuals meet one another at random, whether in an infinitely large or in a finite—but well mixed—population; in a spatially extended system; or on a graph (Nowak, 2006; Szabó and Fáth, 2007; Sigmund, 2010). Such individuals would be as unallied as possible. An alternative assumption is that individuals meet assortatively, selecting their partners through various rules that can be interpreted in terms of various degrees of intentionality.

For a group of n players interacting in dyads, Skyrms and Pemantle (2000) operationalize this assumption by introducing a matrix of what they called relative weights, but which we call affinities. If the matrix is A, then a_{ij} is interpreted as the affinity of Player i for Player j, and the probability that Player i is paired with Player j in a dyadic interaction is made to depend on A. The simplest such rule is

$$\text{Prob(Player } i \text{ is paired to Player } j) = \frac{a_{ij}}{\sum_{k=1}^{n} a_{ik}}, \qquad (15)$$

but Skyrms and Pemantle (2000) incorporate discounting of the past by continuously decreasing the affinities a_{ij} with time, and various other possibilities have now been explored as well (Skyrms, 2009). A separate rule allows players to be influenced—e.g., through imitation—by the strategies that other players are using, so that choice of partner and choice of strategy co-evolve.

Each dyadic interaction is a subgame generating payoffs, which are used to increment the affinities of the involved players through a procedure analogous to reinforcement learning (Kaelbling et al., 1996; Macy and Flache, 2002). As a consequence, players learn to associate with partners yielding better payoffs and to dissociate from partners yielding worse payoffs. In this way, the model predicts the formation within a group of certain clusters and networks, which may be interpreted as alliances.

Important insights emerge from this work. One is that the rate at which partner choice evolves relative to that at which strategy choice evolves is a critical parameter, and cooperation is favored in a variety of models when this parameter is large—i.e., "free association favors cooperation," a result that Skyrms (2009) regards as a robust theorem, sensu Levins (1966). Another insight is that even if the system is guaranteed to approach an equilibrium, it may not be a reliable guide to behavior observed on any reasonable time scale. A similar approach is the focus of several recent game-theoretic papers (Pemantle and Skyrms, 2004a,b; Pacheco et al., 2006, 2008; Santos et al., 2006; Hruschka and Heinrich, 2006), and some results have been obtained analytically. Nevertheless, the concept of affinities yields greatest dividends when used in conjunction with a computational model, as described in Section 8.1 below.

8. Computational models

With a computational approach the spotlight switches from triads or tetrads to polyads of arbitrary size, and it becomes possible to explore how the size distribution of coalitions or alliances varies as a function of relevant ecological parameters. Computational models are almost invariably agent-based models (Epstein, 2006; Miller and Page, 2007), in which not only the characteristics of every individual in a finite population, but also their interrelationships are known at every time step, after being drawn initially from a specified distribution and updated according to various stochastic rules.

8.1. Gavrilets et al.'s model

Gavrilets et al. (2008) have extended the approach of Section 7.2 to deal with coalitionary conflict. Now affinities, which may be positive or negative, control the probabilities of getting coalitionary support as n individuals continuously engage in competition for status and/or access to a limited resource. Individuals vary in RHP, and time is continuous.

At a constant rate α, two randomly chosen individuals, say Players i and j—the "initiators"—engage in a conflict. For all other $k \in N$, Player k is aware of this conflict with constant probability ω. For all such k, whether Player k intervenes on behalf of either initiator, or stays neutral, depends on h_{ki} and h_{kj}, where in general h_{ij} is an interference probability determined by a sigmoidal function of affinity a_{ij} that is scaled by two parameters. A baseline interference rate β controls the probability of interference on behalf of an individual towards whom the affinity is zero; β can be viewed as a measure of individual aggressiveness (i.e., readiness to interfere in a conflict). A slope parameter η controls how rapidly the probability of interference increases with affinity; it can be viewed as a measure of persuasiveness (i.e., ability to attract help).

As a result of interference, an initially dyadic conflict may transform into a conflict between two coalitions. The RHP of a coalition depends on its size and the individual RHPs of its members, e.g., as described in Section 4.3.2. The probability that one coalition prevails over another likewise depends on their respective RHPs, e.g., as described in Section 4.3.5. Following a conflict resolution, the affinities of all parties involved are updated. The affinities of winners are changed by δ_{ww}; those of losers by δ_{ll}; those of winners to losers by δ_{wl}; and those of losers to winners by δ_{lw}. These δ values reflect the effects of the costs and benefits of interference on future actions. It is natural to assume that the affinities of winners increase ($\delta_{ww} > 0$) and those of antagonists decrease ($\delta_{wl} < 0, \delta_{lw} < 0$). The change in the affinities δ_{ll} of losers can be of either sign, or zero. Coalitions are assumed to form, and conflicts to be resolved, on a time scale much faster than that of conflict initiation. Finally, to reflect a reduced importance of past events relative to more recent events in controlling affinities, they decay towards 0 at a constant rate μ (White, 2001).

Several conclusions emerge from this study. First, the model shows the emergence of coalitions of friends supporting each other in conflicts (Fig. 1). The size, RHP, and temporal stability of alliances depend on various ecological parameters, and may vary dramatically from one run to another, even with the same parameters. Individuals belonging to the same alliance have very similar social success, which is only weakly correlated with their individual RHPs. That is, the social success of a player is now determined, not by individual RHP, but rather by the size and RHP of the alliance to which that player belongs. Individuals from different alliances may have vastly different social success, so that the formation of alliances does not necessarily reduce social inequality in the group as a whole. As expected, increasing α or reducing μ promotes alliance formation. Most interestingly, some characteristics exhibit phase-transition-like behavior as certain parameters undergo small changes. In particular, Gavrilets et al.

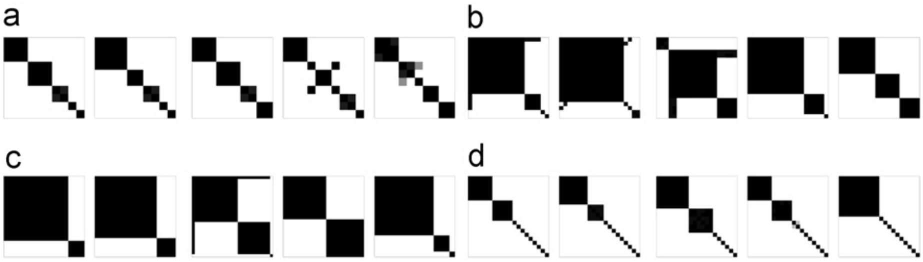

Fig. 1. Interference matrices at time 1000. Values of h_{ij} are gray-scale coded from 0 (white) to 1 (black), with diagonal elements set to black. For display purposes, alliances are ordered according to their clustering coefficients $C^{(1)}$ as in Whitehead and Connor (2005), so that stronger alliances occur first along the diagonal. Default set of parameters: $\alpha = 1$, $\beta = 0.05$, $\delta_{ww} = 1$, $\delta_{ll} = 0.05$, $\delta_{wl} = -0.05 = \delta_{lw}$, $\eta = 0.5$, $\mu = 0.5$. (a) $n=10$. (b) $n=20$. (c) $n=30$. (d) $n=20$, $\delta_{ll} = -0.05$. The interference matrices are symmetric in this illustration because δ_{wl} and δ_{lw} have been chosen equal.

(2008) have shown that including inheritance of social networks may result in the emergence of a grand coalition of all n members of the group. This behavior can be interpreted as "egalitarian revolution" sensu Boehm (1999). Gavrilets et al. (2008) have focused on the possibilities of stochastic equilibrium and cycling in their model, using (analytical) mean-field approximations to elucidate their extensive numerical simulations (Gavrilets et al., 2008, Supporting information).

A particularly attractive feature of the approach adopted by Gavrilets et al. (2008) is that it is both scalable and expandable. It is scalable in that it can be generalized to larger groups, or groups of groups, and potentially applied to modelling the origin and evolution of states (Carneiro, 1970; Wright, 1977; Turchin, 2003, 2007; Marcus, 1992; Iannone, 2002; Rubin, 2002). It is expandable in that it allows for inclusion of additional features, such as behavioral, genetic, social or cultural factors.

8.2. Other computational models

In an attempt at predicting alliance structure based on ideas from physics and chemistry, Axelrod and Bennett (1993) posited that observed configurations should minimize an "energy" $\sum_{i,j} s_i s_j a_{ij} d_{ij}(X)$ over X, where A is an affinity matrix, D is a distance matrix, s is a size vector and X is a coalition structure; here a_{ij} is the "propensity" of actor i to align with actor j, and size and distance may be broadly interpreted. This "landscape" model, which evokes the adaptive landscape of Sewall Wright (Gavrilets, 2004; Ruse, 2009), has so far has been applied only within business and politics (Axelrod, 1997). It was criticized and reformulated by Galam (1996), and does not seem to have been developed since. But we mention it for its potential relevance.

Whitehead and Connor (2005) have used an agent-based model to confirm their prediction that alliances should start to form when the mean number of animals competing for a resource increases above about 0.7–2.0 (Section 3). Their simulations explored various rules for joining and leaving alliances and included costs of changing alliance, intrinsic costs of large alliances and other factors that their analytical model ignored.

Most recently, Gavrilets et al. (2010) have built an agent-based model of the evolution of societal complexity driven by warfare. In their model, agents are spatially structured autonomous local communities (e.g., villages), whereas coalitions (e.g., chiefdoms) are represented as hierarchical trees that go through processes of coagulation and fragmentation. Their model predicts continuous growth and collapse in the size and complexity of early societies.

9. A look to the future

More than half a century has now elapsed since Caplow first developed his theory. During that time, primatologists and other field biologists have amassed a vast amount of detailed and high-quality data on coalition and alliance formation (Barrett and Henzi, 2006; Bissonnette et al., 2009b; Bissonnette, 2009; Harcourt and Stewart, 2007; Mitani, 2006; Perry, 2008). But models have not kept pace. Relatively little is understood, and much remains largely unexplored. This state of the art is a golden opportunity for theoretical biologists.

Analytical models in CAFT are still overwhelmingly triadic. The reasons are partly empirical: two against one is the coalition structure most commonly observed in nature (Bercovitch, 1988; Bissonnette et al., 2009b; Smith et al., 2010), and studies exist in which most coalitions involve only the three top-ranked individuals, or in which ranks have been pooled as "high," "medium" or "low" for statistical purposes (de Villiers et al., 2003), so that a game among a population of three different types becomes the appropriate model for aligning predictions with available data. But the reasons are mainly theoretical: triads are both the simplest groups in which coalition formation can be studied and the groups beyond dyads in which analytical models of population games are most likely to be tractable, especially when allowing for intrinsic variation among individuals. Moreover, triads are large enough groups with which to address some fundamental questions. Recall from Section 2 that a triad of animals A, B and C has five possible coalition structures, namely, I, BC, AC, AB and G. If A, B and C are ranked in that order, then the five possible structures correspond, respectively, to no coalition, an all-up coalition, a bridging coalition, an all-down coalition, and universal sharing. Thus many questions of interest to biologists—frequently questions about cross-species differences in all-down versus bridging versus all-up coalitions—can be well addressed within the confines of a triad.

One such question concerns the rarity of coalitions in chacma baboons (Barrett and Henzi, 2006). An answer would require an appropriate triadic model to identify an ecological parameter regime associated with a very high probability of I, as suggested towards the end of Section 5.2. Another such question is this: What destabilizes the coalition and dominance structure of a triad, and what is predicted to replace it? Nishida (1983) has described a change in the dominance hierarchy of three adult males in an habituated group of wild chimpanzees. Before the disturbance there was a bridging coalition: the gamma male had supported the alpha. But the gamma male switched his allegiance to the beta when the beta attacked the alpha, giving rise to an all-up coalition. After the disturbance, the former beta and gamma were the new alpha and beta, respectively, with the former alpha relegated to the bottom rung. In this case, an answer to the question would require a triadic model to predict a switch from AC to BC (and ideally a concomitant cyclic permutation of ranks). This would be a dynamic prediction.

To date, only computational models of coalition formation have been explicitly dynamic, in the sense that time is an included variable. This reality reflects a wider trade-off in game theory at large. There are indeed explicitly dynamic analytical frameworks (Hofbauer and Sigmund, 1998; Nowak, 2006; Sigmund, 2010), but a typical model treats individual variation only implicitly. Likewise, there are analytical frameworks that model individual variation explicitly, such as those discussed in Section 5, but a typical model is only implicitly dynamic. Nevertheless, although dynamics are excluded from the model itself, they can still be part of the larger story that the model is used to tell. For example, in Table 3, if conditions favoring the contest success function h for (a) suddenly switched to conditions favoring h for (b), then the predicted coalition structure would suddenly switch from $\{\{3\},\{1,2\}\}$ to $\{\{1\},\{2,3\}\}$, i.e., from AB to BC; and it is not difficult to imagine that a similar model could predict a switch from AC to BC, as required above. Of course, Table 3 is merely a toy, but it illustrates the possibilities of analytical models, especially triadic ones. Their potential is far from fully exploited.

Thus triadic games have an important role to play in the development of CAFT. Indeed Shubik (1998) has observed an explicit distinction between few-person games of 4–20 individuals and three-person games, which in his view "call for a special study." It seems to us, however, that tetrads also call for a special study, because they are the smallest groups in which counter-coalitions can form. Willis (1962) attempted such a theory (Section 2) early on; but the only subsequent developments are a few results of Tan and Wang (2010) described in Section 5.1, and further results are desirable.

On the other hand, there are questions that cannot be addressed within the confines of the triad or tetrad. Larger polyads are needed, for example, to explain that the highest frequencies of coalition formation in groups of 6–17 male savanna baboons are found among males ranking directly below the top two or three (Noë, 1994, p. 212). As discussed in Section 6.4.2, van

Schaik et al. (2006) have used a polyadic model to broach such issues, but further development is desirable.

van Schaik et al.'s model is firmly rooted in cooperative game theory, whereas the models described in Section 5 all largely belong to non-cooperative game theory. To the extent that these models focus on coalition structures, however, they are also rooted in cooperative game theory. We have seen in Section 6 how this perspective has brought coherence to early verbal theory, and can also serve as a useful point of departure for other developments. But the more telling point is that effective models of coalition formation almost inevitably draw at least partly from both cooperative and non-cooperative game theory, and the distinction between them may already have outlived its usefulness for CAFT, as implicitly recognized by a growing number of researchers (Cressman et al., 2004; Ray, 2007).

That all models are now hybrids is arguably the central message of Ray (2007), whose perspective as an economist is a marriage of both traditions. Interpreting a coalition to mean a set of players "who are willing signatories to a binding agreement" and assuming agreements to be binding and—once reached—costlessly implementable, Ray proceeds to model the negotiation process leading up to such agreements as a non-cooperative game. Interestingly, his bargaining model tends to generate equal division of spoils within coalitions, i.e., $\lambda \to 1$ in (2), although it also allows for unequal division when members of the coalition have "truly different characteristics or outside options" (Ray, 2007, p. 290). In a complementary approach, Ray replaces the characteristic function of cooperative game theory by a partition function to address the difficulty that we highlighted in Section 6.4. This strand of Ray's theory, although abstract, is largely in the spirit of the ideas that underpin Section 5.1, in particular Table 2.

Least developed of all in CAFT are models that distinguish between coalitions and alliances. Neither is able to form unless its members can at least communicate (Kirman et al., 1986). Beyond that, it is easy enough to think of coalition and alliance structure as separate but overlapping networks, with coalitions corresponding to disconnnected cliques in the first, and links continuing to exist in the second network even where they are broken in the first. How two such networks interact, however, "is a complicated theoretical question—it is not even clear what the appropriate general framework may be" (Skyrms, 2009, p. 106). It is so unclear that Ray (2007, p. 297) has questioned whether an integrated theory of coalitions and networks "is possible or even desirable." It is anyhow a major challenge.

At a much more basic level, even triads are still not well understood. Consider, for example, a triad whose resource holding potentials X, Y and Z satisfy $X > Y > Z$ with $X < Y + Z$. What will be the coalition structure, assuming rank to be correlated with RHP? As we saw in Section 2, Caplow (1959) predicted either a bridging or an all-up coalition with equal frequency, but never an all-down coalition; Gamson (1961) predicted an all-up coalition with certainty; and Walker (1973) predicted an all-up coalition with probability $\frac{7}{12}$, a bridging coalition with probability $\frac{1}{3}$, and an all-down coalition with probability $\frac{1}{12}$. All of these theories are largely verbal and ignore properties of the RHP distribution, in particular its variance. But a back-of-the-envelope calculation shows that these properties make a difference (Section 3), and this result is confirmed by a variety of analytical models in Section 5. Assuming full information about RHP, Tan and Wang (2010) identify a pattern of interaction and specific contest success functions h, defined by (5), for which an all-up coalition is predicted (Section 5.1). But the result does not hold if sequential elimination of all but one contestant is replaced by proportional allocation within the winning coalition, i.e., by (2) with $\lambda = 0$; in particular, if $r = 2$ in (5a), then a bridging or an all-down coalition is predicted according to whether $X^2 > Y^2 + Z^2$ or $X^2 < Y^2 + Z^2$ (Tan and Wang, 2010, p. 290). Stamatopoulos et al. (2009), likewise assuming full information about RHP and proportional allocation but using a different pattern of interaction and contest success function, find that bridging, all-up and all-down coalitions are all possible, depending on the relative magnitudes of X, Y and Z (Section 5.1). All of these models assume costs of fighting to be zero. However, assuming partial information of RHP, Mesterton-Gibbons and Sherratt (2007) have included costs that depend on RHP difference, and they show that the probability of an all-up coalition is higher at higher variance.

These predictions are all based on RHP, thus raising the issue of its empirical basis. Early CAFT required only ordinal information about RHP (Section 2), but more recent theory requires cardinal measures. Here three remarks are in order. First, sometimes fighting ability is known, or hypothesized, to be equivalent to a single observable such as body weight or size of weaponry; in that case, although—for greatest generality—the term RHP is used in developing theory, any application of that theory adopts a specific and concrete interpretation of RHP, which accordingly is directly measurable from relevant empirical data. Second, if the factor varying among individuals that primarily determines ability to control a resource is unknown, or if there are several such factors, then there exist at least four methods for obtaining (cardinal) estimates of RHP indirectly, from information about the number and outcomes of antagonistic dyadic interactions. The earliest method was developed by Boyd and Silk (1983); it builds on Bradley and Terry (1952), and uses the method of maximum likelihood. Two more recent approaches are both Bayesian, and use either Markov chain Monte Carlo simulation (Adams, 2005; Romero and Castellanos, 2010) or approximate Bayesian computation (Csilléry et al., 2010) to approximate posterior distributions. The last of the methods is the non-parametric normalized David's score (Bissonnette et al., 2009a).

Third, if multiple factors that vary among individuals determine ability to control a resource, then in principle it is better to model these factors separately and explicitly than to aggregate them into a single measure of RHP by one of the aforementioned methods. In particular, personality, which appears to be an important factor in coalition formation (e.g., Perry, 2008), should be distinguished from size or strength: a bold individual may be weak, a strong individual may be timid. In practice, however, such multiple factors are difficult to model; in particular, and despite increasing attention to animal personality in recent literature (e.g., McNamara et al., 2009), variation in personality has yet to be incorporated into game-theoretic models. This is another major challenge for CAFT.

In the light of all the above, the only truly broad statement one can currently make about coalition or alliance formation is that it is highly context-dependent. Indeed high context dependence is intrinsic to all strategic interaction: any change to any of a game's ingredients (Section 4) can be expected to lead to a different outcome. What this means in practice is twofold. First, the future of CAFT requires close collaboration between empiricists and theoreticians. All models are predicated on reward functions (Section 4.3), and hence on specific assumptions about pattern of interaction, synergy rules, allocation rules, fighting costs, victory odds and the distribution of RHP. Even if one initially adopts an axiomatic approach (Skaperdas, 1996; Münster, 2009), one ultimately relies on empirical evidence to support the axioms, e.g., that "contests among smaller numbers of players are qualitatively similar to those among a larger number of players" according to the specific rule assumed by Skaperdas (1996, p. 286), which is controversial (Corchón, 2007, p. 74). Second, CAFT—like game theory itself—is less a theory than a diverse collection of analytical and computational tools. By using a variety of approaches, each with its own advantages and limitations, we expect to achieve a much better understanding of underlying processes and resulting patterns than is possible within a single framework. It is our belief that approaches we describe in this review have much untapped potential, and can be significantly developed in the coming years to address the questions field biologists ask.

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