BRILL

Behaviour 152 (2015) 1–56

Behaviour
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Review

Coalitions in theory and reality: a review of pertinent variables and processes

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Accepted 22 August 2014; published online 15 October 2014

Abstract

Coalitions and alliances are ubiquitous in humans and many other mammals, being part of the fabric of complex social systems. Field biologists and ethologists have accumulated a vast amount of data on coalition and alliance formation, while theoretical biologists have developed modelling approaches. With the accumulation of empirical data and sophisticated theory, we are now potentially able to answer a host of questions about how coalitions emerge and are maintained in a population over time, and how the psychology of this type of cooperation evolved. Progress can only be achieved, however, by effectively bridging the communication gap that currently exists between

DOI:10.1163/1568539X-00003241

empiricists and theoreticians. In this paper, we aim to do so by asking three questions: (1) What are the primary questions addressed by theoreticians interested in coalition formation, and what are the main building blocks of their models? (2) Do empirical observations support the assumptions of current models, and if not, how can we improve this situation? (3) Has theoretical work led to a better understanding of coalition formation, and what are the most profitable lines of inquiry for the future? Our overarching goal is to promote the integration of theoretical and field biology by motivating empirical scientists to collect data on aspects of coalition formation that are currently poorly quantified and to encourage theoreticians to develop a comprehensive theory of coalition formation that is testable under real-world conditions.

Keywords
alliances, mathematical models, empirical data, primates, recruitment, fitness, dominance, co-operation.

1. Introduction

Ideally, theory and empirical data should build on each other in a series of mutually reinforcing cycles, generating ever more powerful predictive models that could be tested empirically under a wide range of laboratory and field conditions. The greater precision of our models, and the more focused data sets that would then accumulate, would enable us to identify the key elements underlying a particular behavioural phenomenon. This ideal is rarely met, however, and theoreticians and empirical scientists all too often talk past one another. Part of the reason is a difference in the generality of issues under study: many animal behaviour researchers stay close to the empirical material they gather, often focusing on just one or two groups of animals for practical reasons, while asking quite specific questions regarding the observed patterns. In contrast, theoreticians often use formal description to arrive at more general underlying principles of a given phenomenon that can be broadly applied across a variety of taxa and social systems. They do not generally formulate their models in a way that facilitates empirical investigation via precise operationalization.

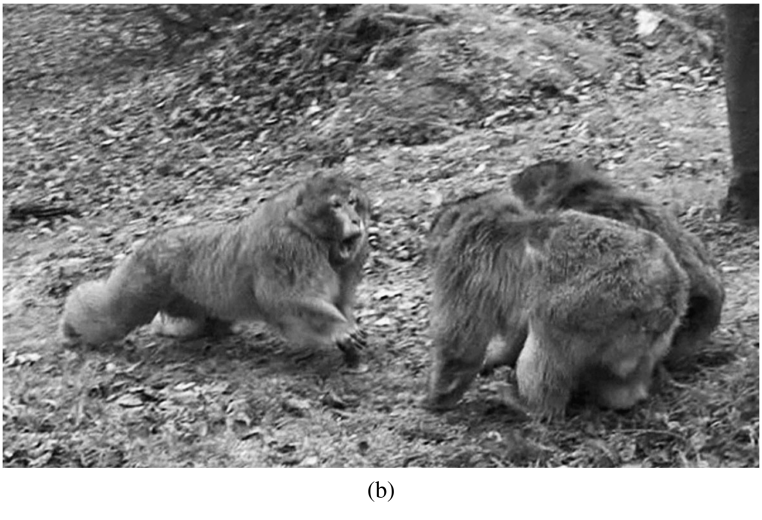
Here we consider the case of coalition formation, an active area of research that seems ready for mathematical modelling. Naturalistic observations are crucial for documenting its distribution across taxa, the variety of forms it takes, the function it serves, and the degree of cognitive complexity it requires. As we will discuss, however, the complexity of the patterns and processes revealed by these naturalistic studies demonstrates the need for a formal theoretical framework to fully understand the evolution and maintenance of coalition formation across the animal kingdom. There is currently a whole suite of modelling approaches available to address such fundamental questions as: Why do some species commonly form coalitions whereas others do not? What are the potential fitness consequences of not participating in all possible coalition opportunities? Can apparently 'cognitively complex' coalitionary behaviour emerge from simple behavioural rules? Unfortunately, as noted above, the exchange of ideas between empiricists and theoreticians is often hindered by their different goals, background, and use of terminology (Leimar & Hammerstein, 2006; Mesterton-Gibbons et al., 2011). Here, we attempt to forge an alliance between theoretical and empirical approaches as the first step toward the long-term goal of achieving a more comprehensive theory of coalition formation.

We start by briefly describing patterns of coalition formation within and across species. We next summarize the primary questions addressed by theoreticians, and identify the main building blocks of their models. Then we selectively review the literature on coalition formation with the explicit aim of contrasting empirical data with the assumptions made by theoretical models, pinpointing where these might be overly simplistic, and identifying important parameters that have been poorly quantified in the field. As the literature in this area remains heavily skewed toward the primates (Smith et al., 2010), the empirical data presented here are derived mainly from this taxon. Finally, we propose some profitable lines of inquiry for future theoretical and empirical research on coalition formation.

2. A brief primer on coalition formation

The term 'coalition' is used in various ways (e.g., an alliance between political parties, Mann, 1993) but, in ethology and behavioural biology, the term typically refers to two (or more) individuals acting together against a third party in an aggressive or competitive context (Harcourt & de Waal, 1992; Figure 1). The term 'alliance', on the other hand, generally refers to a long term relationship characterized by repeated coalitions and high levels of association between the partners, which means that when one partner is in trouble, his or her ally is often nearby and able to help ('alliance behaviour based on coalitions': cf., Feh, 1999; de Waal & Harcourt, 1992). Human coalitions and alliances range from cooperation within a single family to acts of support between nation-states (Chagnon, 1988; Bowles, 2009; Apicella et al., 2012). On a smaller scale, coalitions and alliances are common in our

(a)



(b)

Figure 1. Examples of primate coalitions. (a) Three adult male chimpanzees on the left unite against the male on the right. Photograph by John Mitani. (b) A Barbary macaque male counter-attacks a coalition of two older males. Photograph by Annie Bissonnette. (c) White-faced capuchin monkeys stack on top of each other in an ‘overlord’ while both threaten a third monkey. Photograph by Susan Perry. (d) Yanomami men prepare for a raid on a neighbouring community. Photograph by Napoleon Chagnon.

(c)

(d)

Figure 1. (Continued.)

closest relatives, including for example the chimpanzee (*Pan troglodytes*, review in Muller & Mitani, 2005), as well as a number of non-primate species (reviewed by Harcourt & de Waal, 1992; Smith et al., 2010).

Animal coalitions and alliances are variable in duration and stability. Coalitions can occur opportunistically on a case-by-case basis (e.g., Bissonnette, 2009; Smith et al., 2010), or they can be observed frequently among the same partners as part of an enduring, long-term relationship (e.g., de Waal, 1982; Packer & Pusey, 1982; Smuts, 1985; Goodall, 1986; Noë, 1986b; Caro & Collins, 1987; Connor et al., 1992, 2001; Feh, 1999; Boesch & Boesch-Achermann, 2000; Boinski et al., 2005; Schülke et al., 2010). One individual may establish year-long, stable alliances with one or a few partners and also participate in opportunistic coalitions with other group members in which loyalties change regularly (Riss & Goodall, 1977; de Waal, 1982; Goodall, 1986; Noë, 1990; Uehara et al., 1994; Connor et al., 2000; Sijtsema et al., 2010). For example, Nishida (1983) and de Waal (1984) have argued that male chimpanzees intervene opportunistically in 'political' conflicts and may turn against former allies when it is beneficial to do so.

In group-living species, coalitions and alliances are important in both intergroup and intragroup competition. Coalitions for competition against conspecifics from other groups (hereafter 'group-wide coalitions') occur when the opponents belong to different social groups (or family units, e.g., Scheiber et al., 2005), whereas within-group coalitions occur when two or more members of the same group compete against at least one other 'in-group' member. Group-wide coalitions can be offensive if individuals join forces to oust incumbent male(s) and take over a group (e.g., Pope, 1990; Rood, 1990; Packer et al., 1991; Waser et al., 1994; Ostner & Kappeler, 2004), or to conduct a lethal attack on members of a neighbouring group (reviewed by Wrangham, 1999; Wilson et al., 2014). They can also be defensive, as when group members form a coalition to repel single challengers and/or an out-group coalition (e.g., Feh, 1999). Group-wide coalitions can be very large (e.g., average size in chimpanzees: 13, Watts & Mitani, 2001; hyenas: 14, Smith et al., 2010; human band and tribal level raiding parties range from 10 to 100: Mathew & Boyd, 2011; Walker & Bailey, 2013), in contrast to within-group coalitions, which often involve only two or three partners (reviewed by Smith et al., 2010). It seems likely that group-wide coalition formation provides the only context in which the opposing parties are not mutually dependent on each other (except in dolphins and especially humans, where interdependence extends beyond the level of the group, e.g., Connor et al., 2001; Walker et al., 2011): they usually occur in a clear and unambiguous competitive context and thus are predictably hostile, in contrast to the interactions that occur within groups (Connor et al., 1992; Harcourt, 1992; see below). Group-wide and within-group coalitions, however, are not mutually exclusive phenomena: for example, the need for in-group members to cooperate during between-group encounters is known to profoundly affect the social dynamics of groups, and hence the formation of within-group coalitions (humans: Alexander, 1990, 2014; Flinn et al., 2005; Choi & Bowles, 2007; Bowles, 2009; Rusch, 2014; other animals: Watts & Mitani, 2001). Group-wide coalitions have also been suggested as one possible evolutionary precursor of within-group coalitions in animals (Harcourt, 1992), although a formal test of this hypothesis is lacking. Despite the likely interdependence between intra- and inter-group coalition formation, the emphasis of this review is on within-group coalitions, as these have received much more attention both theoretically and empirically.

Research on within-group coalitions has historically focused on primates (Kawai, 1958; Kawamura, 1958; Hall & DeVore, 1965; Kummer, 1967; Packer, 1977; Riss & Goodall, 1977; de Waal, 1978). More recent empirical work, however, has revealed that a wide range of mammalian species and some birds engage in coalitionary behaviour (reviewed by Smith et al., 2010), including several social carnivores (e.g., hyenas, *Crocuta crocuta*: Zabel et al., 1992; Engh et al., 2002; Wahaj et al., 2004; ring-tailed coatis, *Nasua nasua*: Romero & Aureli, 2008; African wild dog, *Lycaon pictus*: de Villiers et al., 2003; Domestic dogs, *Canis lupus familiaris*: Ward et al., 2009), some artiodactyls (e.g., fallow deer, *Dama dama*: Jennings et al., 2009; feral sheep, *Ovis aries*: Rowell & Rowell, 1993), some perissodactyls (e.g., plain zebra, *Equus quagga*: Schilder, 1990), one proboscid (African elephant, *Loxondonta africana*: Lee, 1987), and some birds (e.g., rooks, *Corvus frugilegus*: Seed et al., 2007; ravens, *Corvus corax*: Fraser & Bugnyar, 2012).

The pattern of within-group coalition formation most commonly reported in the literature is that of one individual intervening in an on-going conflict and aligning itself with one of the original opponents (variously referred as ‘agonistic intervention’, ‘agonistic aid’, ‘fight interference’, ‘support choice’, de Waal & Harcourt, 1992). Individuals also sometimes join forces to simultaneously attack the same target prior to the initiation of a conflict with that target (i.e., instantaneous or parallel coalitions, cf., Noë, 1986b; e.g., de Waal, 1982; Bissonnette, 2009). For example, most chimpanzee male coalitions at Ngogo formed spontaneously or when the males jointly retaliated after another male displayed in the vicinity (Watts, 2002). The term coalition covers both of these interaction patterns, but excludes cases where an intervening animal breaks up an agonistic interaction between two others without siding or 'acting together' with either putative combatant (referred to as 'pacifying', 'neutral', 'policing', 'peaceful' or 'impartial' interventions, e.g., Bernstein, 1964; Boehm, 1994; Petit & Thierry, 1994; Roeder et al., 2002; Flack et al., 2006; Rudolf von Rohr et al., 2012).

Three configurations of within-group coalitions formed by two partners against a single target have been recognized (cf., Chapais, 1995; van Schaik et al., 2006; see Chapais, 1995 for various examples in primates):

(i) 'all-down' (or 'conservative') when the coalition members outrank their target;

(ii) 'bridging' when one partner ranks above and one partner ranks below the target;

(iii) 'all-up' (or 'revolutionary') when both partners rank below their target.

Although some variation within- and across species has been reported (e.g., Harcourt, 1992; Boesch & Boesch-Achermann, 2000; Young et al., 2014), all-down coalitions appear to be the most common coalitionary pattern observed in animals when the beneficiary is not related to the supporter (e.g., Harcourt & Stewart, 1989; Silk, 1993; Smith et al., 2010).

As we will see below, coalitions can serve different functions (van Schaik et al., 2006); they can be observed among different sex and age classes (reviewed in Chapais, 1995); they can involve kin (e.g., Riss & Goodall, 1977; Chagnon & Bugos, 1979; Wahaj et al., 2004), non-kin (e.g., Vigilant et al., 2001; Langergraber et al., 2007; Schülke et al., 2010), and friends or acquaintances (Hruschka & Henrich, 2006; Hruschka, 2010). As this brief review makes clear, coalitionary patterns are varied, and understanding this diversity would be greatly enhanced by formal modelling that would allow us to identify the general conditions under which coalition formation is expected to evolve, characterize the degree of variability expected, and predict when coalitions should, and should not, occur. Below, we summarize existing modelling approaches and highlight their main findings and predictions to date.

3. Modelling coalitions and alliances

3.1. General theoretical perspectives

There exist four major mathematical theories that can provide insight into how coalitions and alliances work (for more technical details see a recent review by Mesterton-Gibbons et al., 2011). Of these, two have been most commonly applied to coalition formation. First, the theory of endogenous coalition formation has been developed in the economics literature (Tullock, 1980; Skaperdas, 1996, 1998; Noh, 2002; Esteban & Sákovics, 2003; Garfinkel, 2004; Bloch et al., 2006; Sánchez-Pagés, 2007; Konrad & Kovenock, 2009; Stamatopoulos et al., 2009; Tan & Wang, 2010). This theory aims to predict coalitionary strategies that maximize individual fitness given a particular (ecological) situation, the costs and benefits of different actions, and the information available to individuals. Most existing models of coalition formation in animals belong to this general framework, which overlaps with evolutionary game theory (Noë, 1990, 1992, 1994; Pandit & van Schaik, 2003; van Schaik et al., 2004, 2006; Connor & Whitehead, 2005; Whitehead & Connor, 2005; Mesterton-Gibbons & Sherratt, 2007; Broom et al., 2009; Okasha, 2009). We will discuss a number of these models in more detail below.

Second, the theory of cooperative games models situations where players that have pooled their resources attempt to come to an agreement on how to divide the spoils (von Newmann & Morgenstern, 1947; Kahan & Rapoport, 1984; Myerson, 1991; Ray, 2007; Gilles, 2010). Coalitionary theory using this perspective on cooperation predicts which coalitions can form and how the benefits are distributed. Cooperative game theory proved to be useful in the study of human behaviour, but has rarely been applied to coalitions in non-human animals. This is at least partly because it remains unclear how animals could negotiate without language and how any agreement could be enforced (McNamara et al., 2006; Akcay & Roughgarden, 2007; Binmore, 2010). One notable exception is Noë (1990), who used a veto game from cooperative game theory to explain patterns of coalition formation among adult males in a group of wild baboons. In the veto game, there is a single 'strong' player who is able to claim (i.e., without negotiating) most of the spoils by playing other individuals against each other. The power of a veto player may also be based on a unique skill, or possession of a unique resource. A key player playing off of two partners against each other is a situation that has been described for both captive and wild male chimpanzees (de Waal, 1982; Nishida, 1983; Muller & Mitani, 2005), and primate negotiation without language is discussed by de Waal (1996) and Melis et al. (2009).

Third, the theory of dynamic linking and network formation focuses on dyadic or polyadic games played by individuals in which the outcomes of previous interactions determine who interacts with whom in the future

(Skyrms & Pemantle, 2000; Pemantle & Skyrms, 2004a, b; Hruschka & Henrich, 2006; Pacheco et al., 2006, 2008; Santos et al., 2006; Gavrilets et al., 2008; Aktipis, 2011). We discuss one application of this theory below.

Fourth, coagulation-fragmentation theory studies the dynamics of the population structure given some simple rules concerning the mechanisms by which individuals join and leave groups (which in our context can be thought of as representing coalitions). Its origins go back to a 1917 study of polymers by Smoluchowski (Wattis, 2006), and have only recently found a way into the social sciences (Euguíluz & Zimmermann, 2000; Bohorquez et al., 2009; but see Cohen, 1972). This promising approach will not be discussed further in this paper because it has not yet been applied to coalitionary behaviour in animals.

3.2. Specific goals of theoretical models

From a biological perspective, there are three major sets of questions that modellers aim to answer. First, which strategies maximize individual fitness? Second, which coalitionary patterns are expected to emerge, and how do they affect individual fitness and behaviour? Third, how do the behavioural rules used by individuals evolve and what are the individual and group level consequences of such evolution? To illustrate how theoreticians address these questions, we discuss several recent models in more detail and present their central assumptions in Table 1.

3.2.1. Fitness maximization

An overwhelming majority of coalitionary models focuses on determining which of a possible set of coalitionary strategies maximizes individual fitness, given specific assumptions about the costs and benefits to individuals, as well as the group composition and the information available to individuals. Typically these models involve only three individuals. One of the oldest models is the one of ‘minimally winning coalitions’ of Riker (1962), i.e., rational players form coalitions in which the pooled resources are as small as possible yet sufficient to win. In a more detailed analysis, Stamatopoulos et al. (2009) investigated how differences in strength between three individuals competing for a unit of divisible resource affect whether coalitions of two against one will emerge and which individuals will form them. In their model, they assumed that: (a) the strength of a coalition is given by the sum of the strengths of its participants, (b) the probability of winning a fight (and thus obtaining the resource) is given by a logistic function of the difference

Table 1.
Example of key assumptions underlying six representative models of coalition formation (see text for more details).

Reference	Model synopsis	Allocation rules		Victory odds and synergy	Rules of partner choice	Empirical test[b]
		Benefits	Costs			
Dugatkin (1998); Johnstone & Dugaktin (2000)	A coalition of two against one with winner and/or loser effects	Keeping or improving the position in a hierarchy	Risk of injury, energy expenditure, etc.	Coalitions are always successful against a single target	Help if helping leads to an incremental increase in fitness	Jennings et al. (2009)
Pandit & van Schaik (2003)[a]	A coalition of an arbitrary number of individuals of adjacent rank against a single target	Rank-dependent division of spoils; Coalitions introduce some levelling of the hierarchy	Opportunity costs equal for all participants; Risk of injury related to rank and coalition size; Coordination costs relative to coalition size	Coalition strength equals the sum of the payoffs of its members (it is assumed that fighting ability determines rank, which in turn determines payoffs); Stronger coalition always wins	A coalition forms if it is feasible (i.e., strong enough to beat its target) and profitable (i.e., increases the players' payoff)	Jones (2005); Bissonnette (2009); Bissonnette et al. (2009a); Higham & Mastripieri (2010); Berghänel et al. (2010); Young et al. (2014)

Table 1.
(Continued.)

Reference	Model synopsis	Allocation rules		Victory odds and synergy	Rules of partner choice	Empirical test[b]
		Benefits	Costs			
Whitehead & Connor (2005)	Multiple coalitions of arbitrary sizes; Individuals can join coalitions that maximize their fitness	Division of spoils according to resource holding potential (RHP, cf., Parker, 1974)	Coordination costs relative to coalition size; Costs of switching coalitions	Coalition strength equals the sum of the fighting abilities of its members; Stronger coalition always wins	An individual joins the alliance within which he gains the maximum expected reproductive success	No
Mesterton-Gibbons & Sherratt (2007)	A coalition of two against one. Analysis of evolutionary stable behavioural rules for joining coalitions	Rank-dependent division of spoils	Cost of fighting related to difference in resource holding potential (RHP)	Coalition strength equals: $s_{ij} = q(s_i + s_j)$, where q represents the degree of coordination or synergy; Probability of winning is an incomplete Beta function of the difference in strengths	Each individual seeks partners if her strength is below a threshold; the thresholds are controlled genetically and can evolve	No

Table 1.
(Continued.)

Reference	Model synopsis	Allocation rules		Victory odds and synergy	Rules of partner choice	Empirical test[b]
		Benefits	Costs			
Gavrilets et al. (2008)	Multiple coalitions of arbitrary sizes; Participation in coalitions depends on affinities which change dynamically depending on conflict outcomes	Egalitarian division of spoils	Absent	Coalition I strength equals: S_I $= \bar{s}_n * n^2$, where $\bar{s}_n$ is the average fighting ability of the participants and n the number of participants; Coalition I wins against coalition J with probability S_I/(S_I + S_J)	Help is provided according to probabilities proportional to affinities	No
Stamatopoulos et al. (2009)	A coalition of two against one	Division of spoils according to resource holding potential (RHP)	Absent	Coalition strength equals the sum of the RHP of its members; Win probability is a logistic function of the difference in strengths	Partner choice is based on how the coalition affects an individuals’ share of the resource and his probability of obtaining access to the resource	No

[a] Pandit & van Schaik (2003) also present a model without costs. See van Schaik et al. (2004) for modifications and extensions of the model.
[b] Only the published papers that explicitly aimed at testing the model assumptions or predictions with empirical data are given.

in strengths, (c) a winning coalition divides the reward in proportion to the strengths of the individuals in the coalition, and (d) the costs of fighting are absent. Using additional assumptions about how the reward is divided if no coalition is formed, Stamatopoulos et al. (2009) showed that if the strongest individual is sufficiently strong relative to the weakest members, the latter should form an all-up coalition against the former. If the strengths of the two strongest members are relatively close to that of the weakest member, they should form an all-down coalition. In all other cases, the strongest and the weakest players should form a bridging coalition against the medium-strength player. Consistent with one of the model's prediction, Benenson et al. (2009) found that human subjects are increasingly willing to form coalitions as their own level of perceived strength diminishes.

Broom et al. (2009) studied the effects of coalitionary support by kin on the stability of dominance hierarchies in group-living animals. Their model considers a conflict between a high-ranking individual and a challenger seeking to replace it in the hierarchy. The conflict is observed by a third individual who can decide to help one of the two parties. Helpers derive only indirect fitness benefits as a consequence of their relatedness to the main actors. Specifying the costs and benefits of different actions, Broom et al.'s (2009) model predicts who should attack whom under which circumstances. An interesting prediction is that increased variance in relatedness within a group, but not the mean relatedness, makes formation of coalitions more plausible (i.e., if variance in relatedness is low, regardless of the mean degree of relatedness among all individuals, coalitions will not occur).

Using a similar approach, van Schaik and colleagues (Pandit & van Schaik, 2003; van Schaik et al., 2004, 2006) aimed to predict the type of coalitions formed (i.e., all-up, bridging, or all-down; rank-changing or levelling) in a group of males competing for fertilization opportunities. They considered primate males living in groups of an arbitrary size, where individuals ranked in a linear hierarchy compete over increases in ranks. van Schaik et al. (2004, 2006) assumed: (a) that the relationship between the rank and fitness pay-off is exponential, (b) that coalitions are formed only against a single target, (c) that coalition strength is given by a sum of the strengths of its participants, and (d) that the stronger party always wins. Using an idealized cost parameter, van Schaik et al. (2004, 2006) identified regions of parameter space where coalitions were both feasible (i.e., are stronger than the target) and profitable. Building on these results, van Schaik et al.

(2004, 2006) made a number of testable predictions. For example, they predicted that all-up rank-changing coalitions should (a) arise only in groups with a medium degree of despotism, (b) be a small coalition (two or three members), (c) target the top individual, and (d) involve individuals ranking just below the target. Recent empirical tests have provided support for some predictions of the Pandit/van Schaik model in primate males (Jones, 2005; Bissonnette, 2009; Higham & Maestripieri, 2010; but see Kulik et al., 2012), although important limitations of the approach have also been discussed (Bissonnette, 2009; Berghänel et al., 2010; Young et al., 2014).

There is a general criticism of the optimization approach embodied in fitness maximization models. Specifically, the applicability of this approach hinges on the assumption that the optimal strategies identified in the mathematical models are (or closely approximate) the strategies used by real individuals. How can animals know what the best strategies are? One common answer is that natural selection is able to find the best strategy so that organisms have evolved to develop an optimum 'coalitionary psychology'. Given the multiplicity and interdependence of possible behaviours and the complexity of resulting evolutionary dynamics in a coalitionary context, this answer is not entirely satisfactory (McNamara & Houston, 2009). Also, it is possible that the optimization problem has multiple alternative solutions, which means that the most relevant solution is not always obvious.

3.2.2. From behavioural rules to coalitionary patterns

An alternative approach is to predict group level coalitionary patterns and their effects on individual fitness and behaviour, given the assumptions listed above, as well as some additional assumptions about how individuals interact in dyadic and polyadic conflicts. For example, using the theory of dynamic linking, Gavrilets et al. (2008) examine the theoretical plausibility of an argument about the role of coalitions in the 'egalitarian revolution' (Boehm, 1999), which is suggested to have resulted in a transition from the hierarchical societies characteristic of chimpanzees to the egalitarian societies seen among human hunter-gatherers. Gavrilets et al. (2008) found support for Boehm's arguments and further suggested that the transition required a change in cognitive abilities. Gavrilets et al. (2008) assumed that decisions regarding whether to join a coalition were based on a simple heuristic rule that utilized the relative 'affinities' of a potential helper to the two individuals engaged in conflict. These 'affinities' reflected the history of past interactions and changed via a process akin to reinforcement learning: that is, they increased following a mutually beneficial interaction and decreased following an agonistic interaction. Affinities also continuously decayed to zero reflecting a loss of memory by the helpers and actors (or alternatively, the discounting of distant events in the past). Affinities thus represent a simple alternative to explicit fitness considerations. A particularly attractive feature of Gavrilets et al.'s (2008) model and similar approaches (e.g., Pacheco et al., 2008) is that they are scalable, i.e., they can easily be generalized to larger groups and multiple coalitions. Of course this would require individuals to be able to memorize a larger number of affinities. One serious limitation to this approach must also be emphasized, however: there is no guarantee that the heuristic rules used in this and similar models are evolutionarily stable. Consequently, the 'coalitionary psychology' postulated in these models is, potentially, biologically irrelevant. This is clearly an area on which empirical research can shed more light by testing which decision rules are used in coalitionary conflicts.

3.2.3. Evolution of behavioural rules and its consequences

Analysis of evolutionarily stable strategies has been an extremely important tool in theoretical studies of animal behaviour (Maynard Smith, 1982). There are, however, only a few models that explicitly study the emergence of evolutionarily stable behavioural rules in a coalitionary context (thus combining the two approaches outlined above). These models make specific assumptions with respect to possible coalitionary strategies, their costs and benefits, the information available to individuals, and the behavioural rules followed by individuals. Mesterton-Gibbons & Sherratt (2007), for example, consider competition among three individuals in a setup similar to that of Stamatopoulos et al. (2009) and Broom et al. (2009). A crucial novel feature of their model, however, is the assumption that individuals differ with respect to a genetically controlled trait ('alliance threshold') that determines whether an individual seeks coalitionary aid (if his strength falls below threshold) or goes it alone (if his strength exceeds threshold). Mesterton-Gibbons & Sherratt (2007) also allow for incomplete information about the strengths of other individuals, for dependence of fighting costs on the strengths of competitors, and for synergy/antergy between individual strengths in determining pooled strength. They investigated how evolutionarily stable alliance threshold values (which determine evolved 'coalitionary psychology') depend on various parameters of their model. In particular, they predicted that 2-versus-1 coalitions are more likely to occur when (a) the reliability of strength as a predictor of contest outcome is high, (b) there is high variation in fighting strengths, and counterintuitively (c) when the effective strength of a coalition is less than the sum of its individual strengths (see also Mesterton-Gibbons & Sherratt, 2009; Gavrilets, 2012). Using similar methods for identifying evolutionary stable behaviours in various coalitionary contexts would greatly inform the theory (but will likely be quite challenging mathematically).

4. Matching data to theory

When theoreticians build models to help answer specific biological questions, they start by identifying the biological processes they want to describe, and then decide upon appropriate mathematical descriptions of these processes (see Table 1 for examples of key model assumptions). In order to better inform theory, we selectively review the empirical literature on coalitions and alliances in the context of theoretical modelling, and discuss how the models' main assumptions compare to naturalistic observations. We also pinpoint important parameters that have been poorly quantified in the field, and stress those variables that are currently lacking in models, but suspected by empiricists to be critical to the dynamics of coalition formation.

4.1. Benefits of coalitions

Most models of coalition formation assume that individuals compete for a limited, tangible resource (food, mating opportunity), the value of which is fixed and the same for all players. The resource is claimed either by one coalition member or it can be divided equally or according to a certain rule (e.g., proportionally to the strength of the coalition members; Table 1).

4.1.1. Increasing access to mates

The benefits of coalitions can be directly quantified when two males join forces to take away an oestrous female from a higher-ranking competitor ('all-up, levelling', cf., van Schaik et al., 2006; e.g., Bercovitch, 1988; Noë, 1992; Thierry, 2007; Bissonnette et al., 2011; Young et al., 2014). This is probably the only context where coalitions can be classified unambiguously as successful or unsuccessful and one principal beneficiary can be identified (Noë, 1990). These outcome-levelling coalitions likely alter the distribution of payoffs (in terms of matings or paternities) among males and make it more egalitarian (cf., Pandit & van Schaik, 2003; e.g., Bissonnette et al., 2011). The benefits of outcome-levelling coalitions are best documented in savannah baboons and Barbary macaques, where mid-low ranking, post-prime males use this tactic to improve their access to mates (Kuester & Paul, 1992; Noë, 1992; Bissonnette et al., 2011). A recent survey, however, revealed that outcome-levelling coalitions are surprisingly rare across species in mixed-sex groups (A. Bissonnette, unpublished data). One possible reason is that the resulting mating opportunities are often unequally distributed among coalitions or alliances (Table 2). In what may be an extreme case in baboons, for instance, some alliance partners obtained no mating benefits despite having participated together in several winning coalitions over sexually receptive females (Noë, 1992). Noë (1992) concluded that it is unlikely that there is an appreciable compensation for the alliance partners who receive a low share of access to females, although he could not exclude the possibility that these males may derive some benefits in other types of coalitions (e.g., interference coalitions against higher-rankers). In this eventuality, one would run into the problem of having to add values that cannot be reduced to a common currency in a straightforward way (Noë, 1990).

Hierarchy-levelling coalitions occur when no resource is immediately at stake (van Schaik et al., 2006), as a way to equalize power between differently ranked individuals (cf., Boehm, 1999). This can occur, for example, if coalitions serve to undercut the intrinsic power of high-ranking males or intimidate them, thus leading high-rankers to show some restraint in mating competition, but without changing ranks. Although it is difficult to demonstrate the function of coalitions when no immediate effects are visible, there is evidence for hierarchy-levelling coalitions in Barbary macaques (Kuester & Paul, 1992; Paul et al., 1993; Bissonnette, 2009; Bissonnette et al., 2009a). In this species, older adult males often launch coalitionary attacks during the mating season but when no female is directly at stake, apparently as a means of driving away more dominant, younger competitors (Berghänel et al., 2010; Bissonnette et al., 2011). It has also been suggested that levelling may sometimes be at work in chimpanzees, when coalitions involving various combinations of lower-ranking males and targeting the top-ranking males are launched in the absence of any direct competition over females and without any effect on the ranks of the participants (van Schaik et al., 2006; e.g., Goodall, 1986).

Examples of coalitions by high-ranking males over access to females are scarce, probably because males occupying a high position in the dominance

Table 2.
Benefits of within-group coalitions over access to mates in empirical studies.

Study	Species	Sex of participants	Nature of benefits	Division of spoils
Noë (1990)	*Papio cynocephalus*	MM vs. M	Consortships	Skewed (100%) towards higher ranker within 3 alliances ($N = 17$ winning coalitions)
Collins (1981) (in Noë, 1990)	*Papio cynocephalus*	MM vs. M	Consortships	Skewed (87.5%) towards higher ranker within 1 alliance ($N = 8$ winning coalitions)
Bercovitch (1988)	*Papio anubis*	MM vs. M	Consortships	Equal (50% towards higher-ranker) in 36 winning coalitions[a]
Bissonnette (2009)	*Macaca sylvanus*	MM vs. M	Copulations/ consortships	Skewed (81.3%) towards higher-ranker in 16 winning coalitions[a]
Witt et al. (1981)	*Macaca sylvanus*	MM vs. M	Copulations	Skewed (100%) towards higher-ranker within one alliance
Watts (1998)	*Pan troglodytes*	MM vs. M	Copulations	Fairly equal in duos, slightly skewed towards higher-ranker in trios in 12 successful episodes of mate-guarding
Krützen et al. (2004)	*Tursius* spp.	MM vs. M	Paternities	Significantly skewed within 2 alliances
Kopps et al. (unpublished)	*Tursius* spp.	MM vs. M	Paternities	Not significantly skewed within 6 alliances
Wiszniewski et al. (2012)	*Tursiops aduncus*	MM vs. M	Paternities	Not significantly skewed within 5 alliances
Chagnon & Bugos (1979)	*Homo sapiens*	MM & MF vs. MM	Protection	–
Chagnon (1988)	*Homo sapiens*	MM & MF vs. MM	Paternities	Skewed (headmen > 2× reproductive success)
Chagnon et al. (1979)	[*Yanomamo*]	MM & MF vs. MM	Consortships	Skewed (headmen 50% more wives)
Flinn et al. (2012)	[*Bwa Mawego*]	MM vs. MM	Consortships	Not significantly skewed

[a] Calculated over all winning coalitions involving different duos or trios of males.

hierarchy can obtain mating access on their own. Apart from an early suggestion by Hall & DeVore (1965) on baboons, there is one report that describes 12 cases in chimpanzees in which pairs or trios of top-ranking males engaged in coalitionary mate-guarding to prevent oestrous females from mating with other males, but tolerated each other's mating activities (Watts, 1998). As a result, coalition members gained higher shares of copulations than they could have expected from solo mate guarding, and suffered lower per capita costs of guarding (as inferred from aggression rates; Watts, 1998). In Indo-Pacific bottlenose dolphins it was hypothesized that alliances may be formed by high-ranking males who choose their partners based on similar competitive abilities, resulting in paternities being relatively evenly distributed within most alliances (Wiszniewski et al., 2012).

High-ranking males may repay their lower-ranking allies by access to mates in a system of reciprocity. For example, in one well-studied chimpanzee community the alpha selectively tolerated matings by his allies and exchanged mating tolerance for support in conflict (Duffy et al., 2007). It is hypothesized that the ability to form these kinds of strategic coalitions may allow some male chimpanzees to maintain alpha status for a relatively longer period of time (Duffy et al., 2007). In another chimpanzee community consisting of three adult males, the alpha and the beta males competed for coalitionary support from the gamma male during a period of rank instability (Nishida, 1983; Muller & Mitani, 2005). Because the alliance with the most subordinate male was critical for the major competitors, the alpha and beta ceded matings to the gamma who mated most frequently during this period (see also de Waal, 1982; Noë, 1990).

4.1.2. Increasing access to food resources

Detailed accounts of coalitions over food resources are spotty (e.g., Janson, 1985; Mitchell et al., 1991; Perry, 1997; Hirsch, 2007; Vogel et al., 2007) and the empirical literature seems to be silent about their benefits or the division of rewards among the coalition members. This may reflect the fact that coalitions in a feeding context are rare, or researchers rarely report coalitions in this context. Yet, in some species an important proportion of conflicts over food are polyadic. For example, up to 22.8% of all resource-based conflicts in squirrel monkeys (*Saimiri sciureus*, Mitchell et al., 1991) are polyadic, and 25% of female–female coalitions against males in capuchin monkeys (*C. capucinus*) originate in the context of feeding competition between a male and a female (Perry, 1997; see also Vogel et al., 2007). Outside the primates, one study reported that coalitions failed to increase immediate access to food at carcasses in female hyenas (Smith et al., 2010). It was concluded that when food is present, dedicating time to feeding rather than forming coalitions is likely to be best way for females to maximize their energy gain (Smith et al., 2010).

A few researchers have investigated the possibility that coalitions may be repaid by access to food in a system of reciprocity. For example, Mitani & Watts (2001) found evidence that male chimpanzees primarily exchange meat for coalitionary support (see also Nishida et al., 1992). Similarly, Berman et al. (2007) found that higher ranking Tibetan macaque males allowed co-feeding specifically by lower-ranking males from whom they received coalitionary support.

4.1.3. Improving dominance rank

The most direct evidence for the role of coalitions in dominance competition comes from observations of rank changes temporally connected to joint aggression. All-up, rank-changing coalitions (cf., van Schaik et al., 2006) have been observed among males in the context of competition for alpha status in several species (langurs: Curtin, 1981; Japanese macaques: Kutsukake & Hasegawa, 2005; Tibetan macaques: Berman et al., 2007; rhesus macaques: Higham & Maestripieri, 2010; chimpanzees: Riss & Goodall, 1977; Nishida, 1983). For example, in a group of captive chimpanzees, rank reversals took place among the three highest-ranking males (de Waal, 1982). The beta and gamma males jointly attacked the alpha male, and both challengers enjoyed an increase in rank as a result. Another study using a Bayesian approach provided strong evidence that alpha male turnover would not have occurred in the absence of coalitions in three populations of chimpanzees (Hasegawa & Kutsukake, in press). Outside the primates, one study reported that the beta and gamma males exchanged coalitionary support in African wild dogs (de Villiers et al., 2003). It was inferred that this revolutionary alliance may have enabled the beta and gamma males to overthrow the alpha male. Rank-changing coalitions may also take place between females. In Hanuman langurs, for example, immature females sometimes form revolutionary coalitions with each other to raise to the top positions in the hierarchy (Borries et al., 1991). In three different populations of spotted hyenas, infrequent revolutionary coalitions from low-ranking matrilines resulting in the overthrow of higher-ranking matrilines had profound fitness consequences for the females involved (Mills, 1990; Holekamp et al., 1993; Hofer & East, 2003).

When they are successful, revolutionary coalitions can translate into important long term or delayed benefits, as high dominance rank often determines access to mates for males (e.g., Cowlishaw & Dunbar, 1991; Kutsukake & Nunn, 2006) and food for females (e.g., Holekamp et al., 1996; Murray et al., 2006). As yet, the most direct evidence for the benefits of rank-changing coalitions was provided in two studies of Assamese macaque and chimpanzee males, where coalitionary aggression increased a male's chances of ascending in rank, which in turn was associated with increased reproductive success (Schülke et al., 2010; Gilby et al., 2013). Similarly, fight intervention was associated with an increase in rank early in the rut and accounted for increased mating success in male fallow deer (Jennings et al., 2011).

Overall, all-up, rank-changing coalitions seem to be rare in most well-studied primate species (A. Bissonnette, unpublished data; e.g., *M. mulatta*: Bernstein & Ehardt, 1985; *Barbary macaques*: Widdig et al., 2000; Bissonnette et al., 2011; *M. fuscata*: Kutsukake & Hasegawa, 2005; *M. radiata*: Silk, 1993; *P. cynocephalus*: Silk et al., 2004; *P. troglodytes*: Watts, 2002) and non-primate species (*C. crocuta*: Smith et al., 2010). One reason may be that they are not always successful and may entail high costs (see below). For example, Jones (1980, 2005) reported that in one group of mantled howler monkeys (*A. palliata*) the coalitionary attacks by the beta and gamma males were not intense enough to depose the alpha male. In the long run, attempts by the beta male to depose the alpha were unsuccessful, and the beta male was eventually expelled from the group by a coalition formed by the alpha and a young new immigrant. Another reason may be that certain demographic conditions necessary for the formation of successful revolutionary coalitions, such as the presence of competent partners, are not always met (Bissonnette et al., 2014).

4.1.4. Maintaining dominance rank

In many primate and non-primate species, a disproportionate number of coalitions involve targets that are subordinate to both coalition partners (e.g., *M. mulatta*: Bernstein & Erhardt, 1985; *M. radiata*: Silk, 1992, 1993; *M. sylvanus*, Widdig et al., 2000; *M. fuscata*: Chapais et al., 1991; *P. troglodytes*: Watts, 2002; *C. crocuta*: Smith et al., 2010; *L. pictus*: de Villiers et al., 2003). The most direct way of proving the conservative nature of these all-down coalitions is by analyzing the effect of the loss of an individual's presumed allies on its ability to maintain rank (Chapais et al., 1995). Experimental findings, for example, indicate that conservative alliances with both kin and non-kin play a determining role in a female's ability to maintain rank above any lower ranking female in Japanese macaques (Chapais et al., 1991, 1994). Conservative coalitions often seem to represent exploitation of low-cost opportunities to reinforce one's rank in situations where immediate retaliation by the target is unlikely (Watts, 2002). Preventing revolutionary coalitions is particularly important for the highest-ranking individuals if their positions allow them to secure large proportions of the resources within the group (Berman et al., 2007). As such, conservative coalitions may potentially bring important delayed benefits to their members (de Waal, 1982; Chapais, 1986, 1995; van Schaik et al., 2006).

Animals also engage in conservative coalitions after a successful dominance reversal. For example, after having deposed the alpha male by means of a revolutionary alliance, the new alpha and beta males supported each other against the new gamma male in a chimpanzee colony (de Waal, 1982). A few years later, when the beta male ceased to support the alpha male, the latter was defeated by the gamma male and suffered lethal injuries in the process (de Waal, 1986). This temporal connection between different coalition types is one important aspect that is often ignored in models of coalition formation.

4.1.5. Increasing inclusive fitness benefits

Even when an animal does not receive any direct benefits by participating in a coalition, he may receive indirect fitness benefits by helping close kin. There is considerable evidence of so-called nepotism in coalition formation among primates and other animals (Silk, 2002; Wahaj et al., 2004; Chapais, 2006; Smith et al., 2010; see below). One prominent example involves female Old World monkeys, such as baboons, vervets and macaques, where females intervene in disputes between their relatives and unrelated individuals, typically supporting the former against the latter (Silk et al., 2004). That kinship should play an integral role in influencing who forms coalitions with whom is not surprising, as kin selection provides a strong theoretical rationale for why related individuals should aid each other (Hamilton, 1964). A strong bias towards female philopatry (Smuts, 1987), however, limits the occurrence of male–male nepotistic coalitions in primates. As a result, increasing one's inclusive fitness is not expected to be a major benefit of coalitions among primate males (Chapais, 1995; van Schaik et al., 2006), with rare exceptions (Langergraber et al., 2007).

4.1.6. Benefits of coalitions: summary

1. The benefits of coalitions are manifold: they can be tangible or intangible, immediate or delayed, direct or indirect. This multifaceted nature of coalitions, often observed within a single species, seems to be the norm rather than the exception. This aspect is often forgotten in theoretical models of coalition formation for reasons of simplicity.

2. Coalitions over tangible resources are relatively rare in animals and when they do occur, the resulting benefits are not always distributed equally (Table 2). In many cases, the division of benefits should not pose a problem, because the coalition or alliance leads to the improvement or maintenance of status for all partners.

3. An important limitation of the empirical literature is that coalitions are often reported in the framework of studies on another topic and important details such as information on the outcome of coalitions (e.g., changing dominance rank or acquiring access to food or a receptive female) are often not reported. Moreover, scientists generally assume that coalitions have positive fitness consequences. However, despite much empirical work on the topic, very few studies have directly examined whether coalitions improve reproductive success. These are important gaps in current empirical research.

4.2. Costs of coalitions

The cost of participating in coalitions is usually partitioned in terms of time, energy and risk of injury confronted by the participants (Table 1). In modelling coalitions, costs may be absent (e.g., Stamatopoulos et al., 2009), constant, or dependent on the difference in the strengths of the opponents (so that equally matching opponents pay more costs; Mesterton-Gibbons & Sherratt, 2007; Gavrilets, 2010). They may differ for the winner and loser or be the same. They can be independent of the number of coalition members or be inversely proportional to the coalition size. Some models of group conflicts in economics allow for variation in costs between individuals (Konrad & Kovenock, 2009). Although empiricists usually assume that coalition participation is costly (e.g., Packer, 1977; Smuts, 1985; Noë, 1986a; Hruschka, 2010; Smith et al., 2010; Schneider & Krueger, 2012; Walker & Bailey, 2013), virtually no systematic attempt to measure the costs of coalitions has been attempted.

4.2.1. Risk of physical injury

Bercovitch (1988) is one of the few studies that quantified the rate of injury resulting from coalition formation. The risk of injury to males competing for mating access was found to be higher for those attempting solitary take-overs of consortships than those in coalitions. Indeed, 6% of solitary challenges yielded injuries (slash wounds) under such conditions, whereas only 2% of coalitions resulted in similar wounds. The risk of injury to individual participants in a coalition is even lower if considered on a 'per male', rather than a 'per event', basis. Bercovitch (1988) also notes that Smuts (1985) similarly reported that the worst injury seen in her study was sustained by a solitary challenger (see also Collins, 1981). Bercovitch (1988) viewed coalitions as a low-cost reproductive tactic, in which males act in their own interests to gain an immediate benefit. Bissonnette (2009) similarly reports only one incidence of 'mild injury' (a bloody nose) in 111 male–male coalitions (0.9%) during her study. Likewise, Kutsukake & Hasegawa (2005) noted that polyadic aggression never developed into physical aggression in their study of Japanese macaque males. These studies are silent about whether the rate of injury is the same for all coalition members or varies according to relative competitive ability.

One could argue that the risk of physical injury is more substantial than posited here. Reports of fatal fighting and coalitionary attacks, although sparse, are known from the literature (Perry, 1998a; Gros-Louis et al., 2003; Kaburu et al., 2013). Bissonnette et al. (2014) suggested that the rarity or complete absence of male coalitions in some despotic primate species may reflect extremely high costs based on the observation that, when there is an overthrow of the alpha male, the alpha and the challenger(s) usually are severely injured or killed (e.g., *C. nigritus*, Ramirez-Llorens et al., 2008; B. Tiddi and B. Wheeler, pers. comm.; *C. apella*, C. Janson, pers. comm.; see Perry, 2012 for a discussion). If the risk of injury is such that it makes coalition formation prohibitive, then we should expect coalitionary behaviour to reflect evolved strategies designed to optimize costs and benefits, with the result that only the lowest cost forms of such behaviour are now seen. Milner et al. (2011), for example, working on fiddler crabs, suggested that rates of coalition formation were low among territory-holding males (only 6.3% of fights against intruder males involves a coalition) precisely because potential intruders were sensitive to the risk of coalition formation between territory holders, and did not challenge those males likely to form an effective coalition. Whether primates or other mammals are similarly sensitive to such risks is not fully clear. The generally conservative nature of coalitions seen in many studies (e.g., Chapais et al., 1991; Silk, 1992, 1993; Widdig et al., 2000; Watts, 2002; Silk et al., 2004; Berman et al., 2007; Jennings et al., 2009; Ward et al., 2009; Smith et al., 2010), however, suggests that those forms of low-risk coalitions are probably the most widespread among the primates and other animals (Watts, 2002).

4.2.2. Time and energetic costs of fighting

In theory, the time and energy invested in coalition activity may also influence an animal's reproductive success adversely. Empirical data on the energy (e.g., estimated by the intensity of the behaviours involved) and time (e.g., estimated by the duration of the interaction) invested in coalitionary activity, however, is almost non-existent. In Bercovitch's (1988) study (see above), costs in terms of the time and energy invested in fighting were deemed too low to have an influence on male reproductive success. Coalitionary challenges were generally of short duration and involved a number of behaviours (e.g., presenting, mounting and threatening) that were unlikely to drain a male's energy resources. Similar observations were made in Barbary macaque males (A. Bissonnette, unpublished data). In contrast, in capuchin monkeys, female–female coalitions were not necessarily successful in driving away persistent males out of the group, apparently due to the high energetic costs involved in repeatedly chasing and wrestling with the males (Perry, 1997; Perry & Manson, 2008). Higham & Maestripieri (2010), in their study of revolutionary coalitions among male rhesus macaques on Cayo Santiago, noted that the coalitionary challenge was prolonged, taking place over the course of weeks, rather than hours or days. In coalitionary challenges of this nature, then, the time and energetic costs may be much higher, even though all participants may obtain a positive pay-off for their investment. Watts (2002) notes the same for chimpanzees, and further suggests that in these cases they also carry some potential for costly retaliation or punishment (de Waal, 1982; Nishida & Hosaka, 1996), especially if such bids ultimately prove unsuccessful.

4.2.3. Investment and opportunity costs

The empirical literature is almost silent about the potential investment and opportunity costs of coalitions. In terms of investment cost, one can think of all behavioural or physiological expenditures that facilitate the formation of coalitions. For example, research on primates and other mammals indicates that some individuals may establish enduring relationships with other conspecifics (so-called ‘friends’, Smuts, 1985; Seyfarth & Cheney, 2012) with whom they often form coalitions (e.g., Smuts, 1985; Silk, 1994; Mitani et al., 2002; Langergraber et al., 2007; Schülke et al., 2010). The establishment of such relationships may take considerable time, even though all participants may eventually obtain a positive pay-off for their investment. The question whether the time invested in alliance formation and its maintenance can influence an animal’s reproductive success adversely, however, remains unanswered, and the conditions favouring the establishment of alliances versus opportunistic coalitions are poorly understood (but see: Noë, 1989; Connor et al., 2001; Gavrilets et al., 2008). Furthermore, not all coalitions are based on long-term relationships (e.g., Bissonnette, 2009; Smith et al., 2010), suggesting that the investment cost, if any, may be variable.

Opportunity cost can be understood as the cost of an alternative that must be forgone in order to pursue a certain action (see http://www.investopedia.com/terms/o/opportunitycost.asp), or the benefits that must be given up to acquire an alternative resource or do something else. For example, Smith et al. (2010) noted that although coalitions are common in hyenas, they are rarely concerned with access to resources. The authors argue that although coalition formation might allow females to more effectively defend a carcass against within-group competitors, the feeding time lost due to the coordination of coalitionary behaviour, and the escalation in aggression that this would entail (reducing feeding efficiency and attracting additional competitors) appears to make such a tactic prohibitively costly (Smith et al., 2008, 2010; but see Vogel et al., 2007). The opportunity costs of engaging in a coalitionary conflict may also depend on age (e.g., Bissonnette, 2009), on the reproductive states of the individuals involved (e.g., Wasser & Starling, 1988; Barrett & Henzi, 2002), or on group composition and demography. For example, animals potentially may pay opportunity costs, in terms of failing to achieve high rank or mating access, because of a lack of suitable partners. In one chacma baboon population only two female–female coalitions against other females were observed over a 10-year period of study, and both were characterized by similar configurations of age and rank between mothers and daughters, suggesting that some of the rarity seen in coalition formation may reflect the corresponding rarity of circumstances that permit a positive pay-off for all participants (Henzi & Barrettt, 2007). Noë & Sluijter (1990) make an analogous point about partner availability in their study of male coalitions (see also Vogel et al., 2007; Bissonnette et al., 2014). Opportunity costs are, of course, inherently hard to demonstrate convincingly from an empirical perspective, since it involves trying to prove a negative. This is clearly an area where modelling can shed more light by testing intuitions about the manner in which such costs will influence the evolution, stability, and maintenance of coalitions.

4.2.4. Costs of coalitions: summary

1. Although model predictions depend crucially on the nature and extent of costs, empirical data are sparse. We are investigating a phenomenon on which selection has already acted, so perhaps only the lowest cost manifestations are now seen. Given the lack of formal quantification of costs in most studies, this statement remains speculative.

2. Modelling may be the most profitable means of initially examining the consequences of coalitionary costs, testing whether particular age–sex classes, populations and species are more vulnerable to such costs, and also identifying patterns that could be indicators that such costs are operating in a given population.

4.3. Victory odds and synergy

4.3.1. Coalition strength

Models of coalition formation make assumptions about the probability that individuals involved in a coalition will win a conflict (see Table 1). The most widely adopted rule is that the strength or 'resource holding potential' (RHP, sensu Parker, 1974) of the coalition is the sum of the strengths or RHP's of its members (Mesterton-Gibbons et al., 2011): the party with the highest RHP always wins (e.g., Pandit & van Schaik, 2003; van Schaik et al., 2004, 2006; Whitehead & Connor, 2005) or wins according to some probabilistic function (e.g., Stamatopoulos et al., 2009).

Empirical data show that coalitions are not always successful in defeating their target or reaching their apparent goal (e.g., access to food or mate), and sometimes end in a stalemate (Watts, 1997; Boesch & Boesch-Achermann, 2000; Kutsukake & Hasegawa, 2005; Bissonnette et al., 2009a; S. Perry and F. de Waal, pers. obs.). Thus, coalitions do not guarantee success, i.e., two always beat one (see e.g., Dugatkin, 1998). To empirically determine whether success depends on coalition strength is not trivial, as it requires that we estimate the strength (or RHP) of the players. For group-living animals, an individual RHP may be partially reflected in his place in a rank order based on dyadic dominance relationships (Noë, 1989). Indeed, several studies have shown that ordinal ranks (de Vries, 1998; de Vries & Appleby, 2000) and cardinal ranks (Boyd & Silk, 1983; Adams, 2005; Romero & Castellanos, 2010) correlate with some RHP components, such as body mass, body size, or age (e.g., Dittus, 1977; Packer, 1979; Jones, 1980; Clutton-Brock et al., 1982; Zucker & Clarke, 1998; Alberts et al., 2003; Setchell et al., 2006; Bissonnette et al., 2009b), but this is far from universal. For example, Fedigan (1992) reported that in wild capuchin monkeys, small, young and even incapacitated males have occupied alpha male positions, suggesting that social variables, instead of physical attributes of age and size, determine the dominance rankings of the males. Similarly, Perry has observed capuchin alpha males who are elderly or incapacitated (e.g., had a broken leg, a missing arm, or only one canine tooth) maintain alpha positions for long periods even when more physically formidable males are members of their groups (unpublished data). Similar observations have been made in chimpanzees (Goodall, 1986) and other species (e.g., Bernstein, 1981; Pusey & Packer, 1997; Chapais, 2006). Recently, Hasegawa & Kutsukake (in press) used a Bayesian approach to estimate the age-related RHP trajectories of wild male chimpanzees. They found that new alpha males had higher age-related RHP values than outranked males except when males achieved alpha status via coalition formation. In these cases, males were not stronger than outranked males but showed an increase in extrinsic dominance (and thus total RHP) due to support from coalition partners.

The few empirical investigations of the role of 'RHP' in coalition contests show that fighting ability is one key feature influencing coalition success. For example, Bissonnette et al. (2009a) used a cardinal measure of competitive ability in Barbary macaque males (Bissonnette et al., 2009b), based on normalized David's scores derived from dyadic winner–loser matrices, to test the assumption that a coalition is successful if the strength of the coalition members is greater than the strength of the target. They found that asymmetry in strength was a significant predictor of coalition success, and this factor alone could explain up to 78.6% of coalition outcomes in the study group. Their findings are in line with previous studies in baboons and macaques, according to which relative coalition strength (estimated from ordinal rank) is an important factor in coalition formation among primate males (Bercovitch, 1988; Silk, 1992; Noë, 1994). Findings in several species that high-ranking allies are more effective than low-ranking ones, as individuals are less likely to be defeated in coalitions when their allies outranked their opponents (e.g., Silk et al., 2004; Perry et al., 2008), also supports the asymmetry in strength assumption. Finally, a study using a computerized game has shown that even humans tend to choose coalition partners who are stronger, suggesting that human coalitionary decisions rest at least partially on perceptions of relative power (Benenson et al., 2009).

One important finding of empirical studies, however, is that fighting ability is unlikely to be the sole determinant of coalition success. For example, in Bissonnette et al.'s study (2009a), about 22% of all coalition outcomes could not be explained by asymmetry in strength. The authors proposed that other factors, such as synergy (see below) and motivation, also played a role. For example, they report how a target defeated two coalitions in a row, while the asymmetry in strength would have predicted the defeat of the target. Similarly, Goodall (1986) reports a coalition of five senior males unable to defeat the alpha male and a young male who won despite being attacked by an alliance of brothers, each heavier than himself. How to estimate motivation is an important empirical question for future work (Bissonnette et al., 2009a). Finally, it is possible that the role of 'RHP' in coalition contests may be less important among females, especially in animal societies with maternal rank inheritance (see references in Chapais, 1995, and below). Whether size, strength or other attributes predict coalition outcome in these societies, however, remains an empirical question.

4.3.2. Synergy and triadic awareness

Synergy allows the whole to exceed the sum of its parts. Some models allow for an effect of synergy (or antergy), whereby the strength of the coalition exceeds the sum of individual strengths. The corresponding coefficient measuring the extent of synergy (or antergy) can be constant (Mesterton-Gibbons & Sherratt, 2007) or depend on the number of coalition members (Gavrilets et al., 2008; see Table 1).

Although empiricists generally acknowledge that the role of synergy may be important in determining coalition success (e.g., Noë, 1994; Bissonnette et al., 2009a), to date there have been few attempts to quantify this parameter in the field. One important empirical problem is that it is not clear when and how a synergistic effect should be observed. In other words: does synergy kick in when the partners' actions are synchronized in time and space, or when they perform complementary actions towards the same target? Can we expect synergy when the partners are ‘friends’? For example, anecdotal reports suggest that two baboon males attacking in a very coordinated manner would be more effective than a coalition where one partner ‘does not pull his weight’ (Noë, 1994). Successful coalitionary challenges rely on tightly orchestrated, (synchronized) movements among allies (Smuts, 1985, page 145), although variation in the level of coordination and its effect on coalition success has not yet been quantified. One interesting question would be whether coordinated actions exert their effects on the target: it is possible that a coordinated pair presents a more intense and larger stimulus, hence increasing the chance of success of a coalition against a singleton. Perhaps the best documented example of one form of synergy (i.e., synchrony) comes from cetaceans. Male dolphins frequently perform synchronized displays where two individuals perform the same behaviour simultaneously (i.e., surfacing) in the presence of females with whom they are in consort (Connor et al., 2000). Dolphins have been documented to exhibit greater synchrony with alliance partners than with non-alliance partners, and the variation in synchrony between alliances is associated with a variation in male reproductive success (Connor et al., 2006). The degree to which synchrony is observed in the alliance behaviour of dolphins has been argued to be unique among mammals, with the exception of humans (cf., McNeill, 1995; Hagen & Bryant, 2003; Connor et al., 2006). Similar analyses, however, have not yet been applied to other species; they clearly would be a worthwhile endeavor.

Even in the absence of complete synchrony, other forms of coordinated action (e.g., for humans emotional sharing, Nummenmaa et al., 2012; and participation in music and dance, Kirschner & Tomasello, 2010; Phillips-Silver et al., 2010) have been speculated to aid dyads in achieving similar emotional states and prosocial attitudes towards the humans with whom they share these activities. While non-humans do not seem to exhibit joint displays as elaborate as those seen in humans, there may be some parallels. Capuchins, for example, engage in dyadic ‘dances’ involving rhythmic exchange of vocalizations while exhibiting stylized movements unique to this context (Gros-Louis et al., 2008). Although these vocalizations are not synchronous, their grunts are delivered in long sequences in which the partners alternate vocalizing. There is also variation in how precise the rhythm of their exchange is and how tightly coordinated their movements are in the dances (S. Perry, unpublished data). Moreover, in experiments capuchins prefer to interact with synchronizing human experimenters (Paukner et al., 2009). Male chimpanzees produce acoustically similar long-distance pant hoots when chorusing together (Mitani & Brandt, 1994) and chorusing behaviour is a good indicator of long- and short-term social bonds between specific pairs of males (Mitani & Gros-Louis, 1998; Fedurek et al., 2013). Smuts (2002), suggests, based on qualitative assessments of videotaped baboon greetings, that there is considerable variability in how well coordinated these greetings are, and that this variability seems to map on to the quality of the relationship.

One manifestation of synergy is the successful recruitment of partners and reinforcement of their commitment to joint purpose. Chimpanzees, for example, may hold out an open hand to another to solicit his or her support, embrace the other, or sit right behind an ally, hooting along with his vocal challenge of the common target (de Waal, 1982). De Waal & van Hooff (1981) provide a detailed analysis of side-directed behaviour in chimpanzees (see also Slocombe & Zuberbühler, 2007), but species-typical recruitment behaviour is also well-known of macaques (e.g., de Waal, 1976; Gouzoules & Gouzoules, 2000), baboons (e.g., Noë, 1990; Cheney et al., 2010), and capuchin monkeys, which encourage each other in a so-called ‘overlord’, with one coalition partner mounted on the shoulders of the other, while both threaten a common opponent (Perry et al., 2004; Figure 1). All of these behaviours may add to the degree of coordination within the coalition. Recruitment is moreover very dependent on the identities of the target and the potential supporter, suggesting a good understanding of the relationship network, dubbed ‘triadic awareness’ (cf., de Waal, 1982), i.e., knowledge of the affiliative and dominance relationships between individuals other than oneself (Perry et al., 2004; Slocombe & Zuberbühler, 2007; Wittig et al., 2014). The fact that many primates have evolved specialized signals for the recruitment of allies strongly suggests the importance of coalitionary synergy, but this idea remains to be tested empirically.

4.3.3. Winner–loser effect

A winner–loser effect is usually defined as a higher probability for a winner to win a subsequent encounter and for a loser to lose a subsequent encounter, respectively, regardless of the identity of the opponent (Chase et al., 1994; Hsu & Wolf, 1999; Dugatkin, 2004). There seems to be only two models that incorporate winner and loser effects into the likelihood of coalitionary encounters. One example is the model by Dugatkin and Johnstone (Dugatkin, 1998; Johnstone & Dugatkin, 2000; see also Hemelrijk & Puga-Gonzalez, 2012). The authors investigated the conditions under which focal individuals might be motivated to intervene in fights if, by helping one conspecific to win, this behaviour increases the chances of the loser subsequently losing against the focal (and the winner subsequently winning). Their models suggest that the predicted patterns of coalitions are strongly dependent on the way in which winner and loser effects change with contestant strength. Winner and loser effects have been demonstrated empirically for a wide range of animals in dyadic contests (Chase et al., 1994; Rutte et al., 2006). However, their role in coalitionary encounters remains largely unstudied. One notable exception is the study by Jennings et al. (2009) that suggests that a winner effect drives intervention behaviour in fallow deer fights.

4.3.4. Victory odds and synergy: summary

1. To determine whether and why a coalition is successful, or not, is relevant to coalition models and represents an important empirical issue that needs to be addressed.

2. Empirical data show that coalitions are not always successful in beating their target or reaching their goal. Fighting ability or ‘RHP’ is one key feature of coalition success, but it is not the sole factor involved.

3. Synergy may be an important additional factor influencing coalition success, and some ways to measure it will be to pay more attention to the synchrony of actions and the communication, such as recruitment behaviour, between coalition partners.

4.4. Rules of partner choice

Most models of coalition formation assume that an individual will form a coalition if it leads to an increase in fitness. These rules of partner choice are explicit in some models and implicit in others. Generally in these models, individuals base their decision to form a coalition on one another’s RHP or degree of affinity (Table 1). Empirical data, however, show that at least five factors can influence how animals choose their coalition partners. These factors are: dominance, kinship, sex, age and friendship.

4.4.1. Dominance

In a coalitionary context it often makes sense to choose the strongest partner at hand, and indeed several studies suggest that primates choose coalition partners based on their competitive value (i.e., ability to help, usually equivalent to dominance or RHP, Chapais, 2006; e.g., Noë, 1994; Noë & Sluijter, 1995; Mitani et al., 2002; Langergraber et al., 2007; Bissonnette et al., 2009a; Higham & Maestripieri, 2010). Silk (1999), for example, showed that male bonnet macaques chose allies that outranked themselves and their opponents more often than expected by chance. Similarly, Perry et al. (2004) found that capuchin monkeys preferentially solicited coalition partners that were dominant to their opponent, though the simpler rule of soliciting the highest ranking individual present also fits the data. Schino et al. (2006) showed that macaques preferentially directed their recruitment attempts to individuals ranking higher than their opponent (and to individuals that were not the kin of their opponent). Furthermore, Range & Noë (2005) found that when sooty mangabeys intervened in a conflict, juveniles and adult females were significantly more likely to support the higher-ranking contestant and solicited help significantly more often from potential allies that outranked them and their target. Not all species seem to show such triadic awareness (Tomasello & Call, 1997), however, and cognitive shortcuts (i.e., evolved rules-of-thumb, cf., Gigerenzer et al., 1999) might also account for the patterns observed (e.g., Perry et al., 2004; Range & Noë, 2005).

4.4.2. Kinship

Empirical data suggest that kinship (the degree of relatedness between the coalition partners) also is an important variable that should be considered in models of coalition formation. Indeed, kinship often structures the availability of particular kinds of social partners in social groups, and inclusive fitness benefits can bias cooperation towards particular kinds of kin in particular kinds of contexts. Chapais (2006) points out, however, that even when kin are present, kin bias is not always predicted to exist. For example, when competitive ability strongly affects the outcome of conflicts and cooperating with a dominant partner would yield a higher benefit, this partner choice is expected to trump one based on kinship.

In humans, kinship is a fundamental building block of coalitions and alliances (Chagnon, 1979, 1982; Chagnon & Bugos, 1979; Walker et al., 2011). Many Old World monkey societies are organized around subsets of maternally related females, who remain in their natal groups for life (Kapsalis, 2004). Females who belong to the same matriline form strong friendly ties reflected in association and grooming behaviour. In these species, females intervene in disputes between their relatives and unrelated animals, typically supporting the former against the latter (Kurland, 1977; Silk et al., 2004). Extensive observational and experimental data show that coalitionary support from maternal kin plays a critical role in the acquisition and maintenance of female dominance rank (Chapais, 1992; Chapais et al., 1997, 2001; Langergraber, 2012; Lea et al., 2014). The same mechanism of rank inheritance has also been documented in female spotted hyenas (Engh et al., 2000; Smith et al., 2010). Observations of female white-faced capuchins, gorillas and white-nosed coatis also reveal that, like female Old World monkeys, individuals are more likely to aid their kin instead of non-kin in disputes (Watts, 1997; Perry & Manson, 2008). In studies of white-faced capuchins, Barbary macaques, bonnet macaques, chimpanzees and bottlenose dolphins, males sometimes form coalitions with their kin more often than with non-kin (Silk, 1992; Widdig et al., 2000; Langergraber et al., 2007; but see Vigilant et al., 2001). In some species mothers are known to provide aid to sons in conflicts with other males (Surbeck et al., 2011; see also Chapais, 1983; Kutsukake & Hasegawa, 2005). Although the role of paternal kinship has rarely been considered in studies of coalition formation, its influence is strongly suggested in adult female mountain gorillas (Watts, 1997), adult female rhesus macaques (Widdig et al., 2006), and spotted hyenas (Wahaj et al., 2004).

4.4.3. Sex differences

Substantial sex differences regarding the frequency and patterns of coalitions have been reported (e.g., Kaplan, 1977; Bernstein et al., 1983; Connor & Whitehead, 2005; Smith et al., 2010; Kulik et al., 2012). For example, the main sex difference in captive chimpanzees is that females have committed relationships, and intervene in agonistic conflicts in accordance with their affiliative preferences. They systematically support individuals they affiliate with (not only kin, but also close non-kin) against individuals with whom they affiliate less. Males, on the other hand, show a weaker tendency to prefer affiliative partners when choosing coalition partners (e.g., Hemelrijk & Ek, 1991). Particularly when males perform the control role (i.e., breaking up fights and pacifying interventions), they often deviate from their affiliative preferences while intervening, which lends their interventions an ‘impartial’ quality (de Waal, 1984; Boehm, 1994; Rudolf von Rohr et al., 2012). In white-faced capuchins (Perry et al., 2004), both males and females have a strong tendency to support the higher-ranking individual in a conflict. However, despite the fact that males are dominant to females, both males and females will support females over males in a conflict (thereby obscuring the relationship between rank and support if the data are not broken down by sex). In hyenas, females direct coalitionary aggression toward other females at higher rates than do any other age classes (Smith et al., 2010). For these reasons, coalitions are often studied separately for both sexes; for example, only for males (Ehardt & Bernstein, 1992; Silk, 1992; Noë & Sluijter, 1995; Duffy et al., 2007; Bissonnette et al., 2009a), whereas coalitions between the sexes, although prominent in some species (e.g., de Waal, 1982; Goodall, 1986; Boesch & Boesch-Achermann, 2000; Surbeck et al., 2011) are often excluded from empirical analyses.

4.4.4. Age

Age influences coalition formation in both primate and non-primate mammals. For example, in Barbary macaques and savannah baboons, old, post-prime males are generally lower ranking than young adult males. Prime, higher ranking males form all-up, levelling coalitions to increase their chances of mating (Bercovitch, 1988; Noë & Sluijter, 1990; Bissonnette et al., 2011). Observations of wild chimpanzees indicate that males who are similar in age form coalitions more often than males of different age cohorts (Mitani et al., 2002). Older male chimpanzees often end up in a key role, exploiting the rivalry among younger males by being fickle in their support (de Waal, 1982; Nishida, 1983). Age effects are not restricted to primates, but have also been documented in other mammals. For example, in a captive group of wild dogs, members of the same age cohort supported each other more than individuals of dissimilar ages (de Villiers et al., 2003). In addition to reinforcing the existing dominance hierarchy, male age-mates may have another important reason to form coalitions when they disperse together and attempt to establish their own breeding groups (de Villiers et al., 2003). An important consequence of this age-dependence of participation in coalitions is that the demographic structure of a group can act as an important constraint on behaviour (Chapais & Schulman, 1980; Barrett & Henzi, 2002; Mitani et al., 2002; Bissonnette, 2009).

4.4.5. Friendship

Finally, observations of non-human primates indicate that some individuals establish enduring relationships (e.g., apes: Gilby & Wrangham, 2008;

Mitani, 2009; Old World monkeys: Silk et al., 2006a, b; Schülke et al., 2010; New World monkeys: Boinski & Mitchell, 1994; Perry, 1998b), which have positive fitness consequences (e.g., Silk et al., 2003, 2006b; Silk, 2007; Schülke et al., 2010). Such pairs are typically referred to as 'friends' (Smuts, 1985; Seyfarth & Cheney, 2012). Research on primate and non-primate mammals suggests that friendship facilitates coalition formation, first analysed as 'familiarity dependent support' by de Waal (1978) in chimpanzees. Perry et al. (2004) found that capuchin monkeys preferentially recruit partners with whom they have closer social relationships than with their opponent, a preference that could not be explained via a simpler rule. Similarly, male bonnet and Assamese macaques preferentially support other males with whom they associate, groom, and interact affiliatively (Silk, 1994; Schülke et al., 2010). Male chimpanzees who frequently associate, groom, maintain proximity, share meat, and patrol their territory together form coalitions more frequently than other pairs (Mitani et al., 2002; Langergraber et al., 2007). Fewer cases of female primates forming coalitions with their friends have been described (but see e.g., de Waal, 1984). Female mountain gorillas, who frequently groom, play together, and maintain close proximity, form coalitions preferentially with each other (Watts, 1997), whereas female white-faced capuchins witnessing a fight support the opponent with whom they have the closest relationship (Perry et al., 2004). It has been suggested that animals may form differentiated affiliative bonds with others and as a special rule-of-thumb preferentially form coalitions with closely bonded partners instead of making cognitively demanding decisions every time they enter a polyadic conflict (e.g., Benenson et al., 2009; Berghänel et al., 2011).

4.4.6. Rules of partner choice: summary

1. Data show that animals choose coalition partners selectively, based on dominance, kinship, sex, age and/or friendship.

2. The degree to which these factors influence coalitions may ultimately be a function of the life-history traits of a species — e.g., migratory sex, birth cohort size and interbirth interval. Models explicitly accounting for the effects of kinship, sex, age and friendship, or life-history traits, are almost non-existent. This is an important gap in existing theory.

3. Unravelling which coalitionary rules apply and how these rules link to fitness maximization are important goals for future empirical research.

5. A look to the future

5.1. Types of data missing from empirical data sets

Clearly, many variables needed for successful mathematical modelling of cooperative competition — which is the essence of coalition formation — have thus far not been collected in any systematic fashion. There are many suggestions in the literature about the cost of coalitions, for example, but no studies at the level of detail and quantification needed for productive modelling. Data including the rate and type of injury (e.g., see Archie et al., 2014) resulting from coalitions (compared to dyadic conflicts), the behaviour observed during the interaction, and the nature of the partnership (short-term vs. long-term) would help to derive better estimates of the risk, energy and opportunity costs of this behaviour. Equally poorly studied are the chance of victory and the role of coalitionary synergy. These are no trivial issues: knowledge of costs and benefits is essential for any attempt to explain the evolution of coalitions and alliances.

Researchers interested in understanding why individuals form coalitions with certain partners but not others, or why coalitions occur only in certain contexts, need to know the options available at the time an aggressive encounter takes place. These options are not necessarily given by overall group composition. Obviously, an individual must be present on the scene at the time of a conflict to be a potential partner. Such critical information is rarely systematically recorded, however (notable exceptions are Perry et al., 2004; Smith et al., 2012). Groups with high levels of fission–fusion dynamics, for example, show tremendous variability in partner and opponent availability.

Finally, knowing more about the circumstances under which coalitions fail to occur may be as important as knowing when they do occur. Researchers need to feed information on the identity of all individuals present, the type of aggression, recruitment behaviour and the response to it, along with relevant environmental variables such as habitat type and the contested resources into a multi-level logistic model to predict the likelihood that coalitions will occur. This kind of data will help determine whether coalitions are rare or absent in certain species ‘by design’ as it were, or whether the conditions pertaining during their study made them simply unlikely.

5.2. The importance of cognitive mechanisms

Tinbergen’s (1963) suggestion to pay equal attention to multiple explanatory levels at once while studying behaviour, means that apart from ‘survival value', which has received much attention in recent modelling, we also need to know the development of a trait as well as the cognitive mechanisms involved. Insofar as mechanisms influence the costs and benefits of alliance formation, and hence their ultimate fitness consequences, lack of knowledge in these areas hampers our ability to calculate fitness. For example, the need for coordination among coalition partners is clearly pertinent to understanding what constitutes coalition strength and how synergy is manifested. If fitness depends on coalition strength, which in turn depends on synergy, such as the degree of coordination among individuals, then fitness-maximizing strategies can be modelled more effectively by including synergy-enhancing mechanisms. Some of these processes may have high cognitive demands, including the need to know when and how to recruit partners and which partners will be most effective against which opponents, although it is possible that cognitive shortcuts are at work. Studies of triadic awareness in the choice of coalition partners (e.g., Silk, 1999; Perry et al., 2004; Range & Noë, 2005), constraints on coalitions (i.e., developmental, social, ecological or cognitive; e.g., Bissonnette et al., 2014), and perhaps even post-conflict punishment of uncooperative coalition partners, are needed to elucidate the cognitive requirements for successful intervention in fights and recruitment of support.

More and better empirical data on potential decision rules could be put to the test theoretically. One might begin by specifying the simplest possible rules of thumb and test if these are sufficient to produce the observed pattern. If not, additional rules that specify more sophisticated cognitive assessments may be added to improve the fit between model and data. For example, Hemelrijk & Puga-Gonzalez (2012) have developed a computational model in which simple rules of aggression in pairs and spatial proximity of individuals can result in almost simultaneous aggression of two individuals against a single target. That is, coalitions are just an accidental by-product of exclusively dyadic behaviour. Of course, such theoretical rules do not necessarily identify the actual rules (whether complex or simple) followed by the animals themselves, but they will offer a better handle on the phenomenon, including cross-species comparisons. Ideally, computational models are developed on the basis of and in interaction with empirical testing so that models are fine-tuned to the actual actors' behaviour (e.g., Katz et al., 2011).

5.3. Empirical patterns requiring theoretical explanations

Our analysis identifies areas that would greatly benefit from additional theoretical work. Why do within-group coalitions generally have the smallest possible size (i.e., two individuals)? Possible reasons include difficulties of coordination, the division of pay-offs or collective action problems (Olson, 1965; Willems et al., 2013; Gavrilets & Fortunato, 2014), and the presence of only a few 'friends' in a group (Young et al., 2014). Why are levelling coalitions so rare? Is it because of the high cost of attacking a dominant individual, or the fact that revolutionary alliances are discouraged by all-down coalitions or by separating interventions (where the dominants interfere in the affiliative rapprochement of potential challengers before it develops into an alliance; de Waal, 1982; Chapais et al., 1995; Nishida & Hosaka, 1996)? Can one use mathematical modelling to discriminate between coalitionary decisions based on immediate maximization of a particular fitness component and long-term friendships? How do animals lacking language 'negotiate' a particular division of tangible benefits? How are 'agreements' enforced? Also, as emphasized before, only a handful of modelling studies focuses on the evolution of behavioural rules of thumb in coalitionary decisions. Additional theoretical work in this direction is needed.

It is our hope that those who study coalition behaviour in the field or in naturalistic captive settings will begin collecting the specific information needed for modelling while the modellers themselves, rather than making theory-based assumptions about mechanisms and outcomes, will search the literature for information that will allow more realistic assumptions. This review is intended to aid the integration between theoretical and empirical work so as to produce predictive models of a behaviour that, as no other, makes complex social systems so fascinating.

Acknowledgements

This work was conducted as a part of the Coalitions and Alliances Working Group at the National Institute for Mathematical and Biological Synthesis (NIMBioS), sponsored by the National Science Foundation, the U.S. Department of Homeland Security, and the U.S. Department of Agriculture through NSF Award No. EF-0832858, with additional support from the University of Tennessee, Knoxville, TN. This work was also supported by the Alexander von Humboldt Foundation and the Fonds de recherche Société et culture of the province of Québec (FQRSC) to A.B. The authors thank Caitlin de Rango and three anonymous reviewers for commenting on an earlier version of the manuscript.

References

Adams, E.S. (2005). Bayesian analysis of linear dominance hierarchies. — Anim. Behav. 69: 1191-1201.

Akcay, E. & Roughgarden, J. (2007). Negotiation of mutualism: rhizobia and legumes. — Proc. Roy. Soc. Lond. B: Biol. Sci. 274: 25-32.

Aktipis, C.A. (2011). Is cooperation viable in mobile organisms? Simple Walk Away strategy favors the evolution of cooperation in groups. — Evol. Hum. Behav. 32: 263-276.

Alberts, S.C., Watts, H.E. & Altmann, J. (2003). Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. — Anim. Behav. 65: 821-840.

Alexander, R.D. (1990). How did humans evolve? Reflections on the uniquely unique species. — University of Michigan, Museum of Zoology (Special Publication), University of Michigan, Ann Arbor, MI.

Alexander, R.D. (2014). Darwin's challenges and the future of human society. — In: Predicting the future in science, economics, and politics (Williamson, P., Polachek, S. & Bueno de Mesquita, B., eds). Edward Elgar Press, Cheltenham, U.K.

Apicella, C.L., Marlowe, F.W., Fowler, J.H. & Christakis, N.A. (2012). Social networks and cooperation in hunter-gatherers. — Nature 481: 497-501.

Archie, E.A., Altmann, J. & Alberts, S.C. (2014). Costs of reproduction in a long-lived female primate: injury risk and wound healing. — Behav. Ecol. Sociobiol. 68: 1183-1193.

Barrett, L. & Henzi, S.P. (2002). Constraints on relationship formation among female primates. — Behaviour 139: 263-289.

Benenson, J.F., Markovits, H., Emery Thompson, M. & Wrangham, R.W. (2009). Strength determines coalitional strategies in humans. — Proc. Roy. Soc. Lond. B: Biol. Sci. 276: 2589-2595.

Bercovitch, F.B. (1988). Coalitions, cooperation and reproductive tactics among adult male baboons. — Anim. Behav. 36: 1198-1209.

Berghänel, A., Schülke, O. & Ostner, J. (2010). Coalition formation among Barbary macaque males: the influence of scramble competition. — Anim. Behav. 80: 675-682.

Berghänel, A., Ostner, J., Schroeder, U. & Schülke, O. (2011). Social bonds predict future cooperation in male Barbary macaques, *Macaca sylvanus*. — Anim. Behav. 81: 1109-1116.

Berman, C.M., Lonica, C. & Li, J. (2007). Supportive and tolerant relationships among male Tibetan macaques at Huangshan, China. — Behaviour 144: 631-661.

Bernstein, I., Williams, L. & Ramsay, M. (1983). The expression of aggression in old-world monkeys. — Int. J. Primatol. 4: 113-125.

Bernstein, I.S. (1964). Group social patterns as influenced by the removal and later reintroduction of the dominant male rhesus. — Psychol. Rep. 14: 3-10.

Bernstein, I.S. (1981). Dominance: the baby and the bathwater. — Behav. Brain Sci. 4: 419-429.

Bernstein, I.S. & Ehardt, C.L. (1985). Agonistic aiding — kinship, rank, age, and sex influences. — Am. J. Primatol. 8: 37-52.

Binmore, K. (2010). Bargaining in biology? — J. Evol. Biol. 23: 1351-1363.

Bissonnette, A. (2009). Testing a model on coalitions in Barbary macaque males (*Macaca sylvanus*). — PhD thesis, University of Zurich, Zurich.

Bissonnette, A., de Vries, H. & van Schaik, C.P. (2009a). Coalitions in Barbary macaque males, *Macaca sylvanus*: success, strength and rules of thumb. — Anim. Behav. 78: 329-335.

Bissonnette, A., Lange, E. & van Schaik, C.P. (2009b). A cardinal measure of competitive ability in Barbary macaque males (*Macaca sylvanus*). — Ethology 115: 671-681.

Bissonnette, A., Bischofberger, N. & van Schaik, C.P. (2011). Mating skew in Barbary macaque males: the role of cycle synchrony, female behavior and male coalitions. — Behav. Ecol. Sociobiol. 65: 167-182.

Bissonnette, A., Franz, M., Schülke, O. & Ostner, J. (2014). Socioecology, but not cognition, predicts male coalitions across primates. — Behav. Ecol. 25: 794-801.

Bloch, F., Sánchez-Pagés, S. & Soubeyran, R. (2006). When doesn't universal peace prevail? Secession and group formation in conflict. — Econ. Gov. 7: 3-29.

Boehm, C. (1994). Pacifying interventions at Arnhem Zoo and Gombe. — In: Chimpanzee cultures (Wrangham, R.W., McGrew, W.C., de Waal, F.B.M. & Heltne, P.G., eds). Harvard University Press, Cambridge, MA, p. 211-226.

Boehm, C. (1999). Hierarchy in the forest. The evolution of egalitarian behavior. — Harvard University Press, Cambridge, MA.

Boesch, C. & Boesch-Achermann, H. (2000). The chimpanzees of the Taï forest: behavioural ecology and evolution. — Oxford University Press, New York, NY.

Bohorquez, J.C., Gourley, S., Dixon, A.R., Spagat, M. & Johnson, N.F. (2009). Common ecology quantifies human insurgence. — Nature 462: 911-914.

Boinski, S. & Mitchell, C.L. (1994). Male residence and association patterns in Costa-Rican squirrel monkeys (*Saimiri oerstedi*). — Am. J. Primatol. 34: 157-169.

Boinski, S., Kauffman, L., Ehmke, E., Schet, S. & Vreedzaam, A. (2005). Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis* and *S. sciureus*): I. Divergent costs and benefits. — Behaviour 142: 525-632.

Borries, C., Sommer, V. & Srivastava, A. (1991). Dominance, age and reproductive sucess in free-ranging female Hanuman langurs (*Presbytis entellus*). — Int. J. Primatol. 12: 231-257.

Bowles, S. (2009). Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? — Science 324: 1293-1298.

Boyd, R. & Silk, J.B. (1983). A method for assigning cardinal dominance ranks. — Anim. Behav. 31: 45-58.

Broom, M., Koenig, A. & Borries, C. (2009). Variation in dominance hierarchies among group-living animals: modelling stability and the likelihood of coalitions. — Behav. Ecol. 20: 844-855.

Caro, T.M. & Collins, D.A. (1987). Male cheetah social-organization and territoriality. — Ethology 74: 52-64.

Chagnon, N.A. (1979). Is reproductive success equal in egalitarian societies? — In: Evolutionary biology and human social behavior: An anthropological perspective (Chagnon, N.A. & Irons, W., eds). Duxbury Press, North Scituate, MA, p. 374-401.

Chagnon, N.A. (1982). Socio-demographic attributes of nepotism in tribal populations: man the rule breaker. — In: Current problems in sociobiology (King's College Sociobiology Group, ed.). Cambridge University Press, Cambridge, p. 291-318.

Chagnon, N.A. (1988). Life histories, blood revenge, and warfare in a tribal population. — Science 239: 985-992.

Chagnon, N.A. & Bugos, P.E. (1979). Kin selection and conflict: an analysis of a Yanomamö ax fight. — In: Evolutionary biology and human social behavior: An anthropological perspective (Chagnon, N.A. & Irons, W., eds). Duxbury Press, North Scituate, MA, p. 213-238.

Chagnon, N.A., Flinn, M.V. & Melancon, T.F. (1979). Sex-ratio variation among the Yanomamö Indians. — In: Evolutionary biology and human social behavior: An anthropological perspective (Chagnon, N.A. & Irons, W., eds). Duxbury Press, North Scituate, MA, p. 290-320.

Chapais, B. (1983). Matriline membership and male rhesus reaching high ranks in the natal troops. — In: Primate social relationships: an integrated approach (Hinde, R.A., ed.). Sinauer Associates, Sunderland, MA, p. 171-175.

Chapais, B. (1986). Why do adult male and female rhesus monkeys affiliate during the birth season? — In: The Cayo Santiago macaques. History, behavior and biology (Rawlins, R.G. & Kessler, M.J., eds). State University of New York Press, Albany, NY, p. 173-200.

Chapais, B. (1992). The role of alliances in social inheritance of rank among female primates. — In: Coalitions and alliances in humans and other animals (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 29-59.

Chapais, B. (1995). Alliances as a means of competition in primates: evolutionary, developmental, and cognitive aspects. — Am. J. Phys. Anthropol. 38: 115-136.

Chapais, B. (2006). Kinship, competence and cooperation in primates. — In: Cooperation in primates and humans: mechanisms and evolution (Kappeler, P.M. & van Schaik, C.P., eds). Springer, New York, NY, p. 47-64.

Chapais, B., Girard, M. & Primi, G. (1991). Nonkin alliances, and the stability of matrilineal relations in Japanese macaques. — Anim. Behav. 41: 481-491.

Chapais, B., Prud'Homme, J. & Teijeiro, S. (1994). Dominance competition among siblings in Japanese macaques: constraints on nepotism. — Anim. Behav. 48: 1335-1347.

Chapais, B., Gauthier, C. & Prud'homme, J. (1995). Dominance competition through affiliation and support in Japanese macaques: an experimental study. — Int. J. Primatol. 16: 521-536.

Chapais, B., Gauthier, C., Prud'Homme, J. & Vasey, P. (1997). Relatedness threshold for nepotism in Japanese macaques. — Anim. Behav. 53: 1089-1101.

Chapais, B., Savard, L. & Gauthier, C. (2001). Kin selection and the distribution of altruism in relation to degree of kinship in Japanese macaques (*Macaca fuscata*). — Behav. Ecol. Sociobiol. 49: 493-502.

Chapais, B. & Schulman, S.R. (1980). Evolutionary model of female dominance relations in primates. — J. Theor. Biol. 82: 47-89.

Chase, I.D., Bartolomeo, C. & Dugatkin, L.A. (1994). Aggressive interactions and intercontest interval: how long do winners keep winning. — Anim. Behav. 48: 393-400.

Cheney, D.L., Moscovice, L.R., Heesen, M., Mundry, R. & Seyfarth, R.M. (2010). Contingent cooperation between wild female baboons. — Proc. Natl. Acad. Sci. USA 107: 9562-9566.

Choi, J.K. & Bowles, S. (2007). The coevolution of parochial altruism and war. — Science 318: 636-640.

Clutton-Brock, T.H., Guiness, F.E. & Albon, S.D. (1982). Red deer: behavior and ecology of two sexes. — University of Chicago Press, Chicago, IL.

Cohen, J. (1972). Markov population processes as models of primate social and population dynamics. — J. Theor. Biol. 3: 19-134.

Collins, D.A. (1981). Social behaviour and patterns of mating among adult yellowbaboons (*Papio c. cynocephalus* L. 1766). — PhD thesis, University of Edinburgh, Edinburgh.

Connor, R. & Whitehead, H. (2005). Alliances II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission–fussion societies. — Anim. Behav. 69: 127-132.

Connor, R.C., Smolker, R.A. & Richards, A.F. (1992). Dolphin alliances and coalitions. — In: Coalitions and alliances in humans and other animals (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 233-257.

Connor, R.C., Wells, R.S., Mann, J. & Read, A.J. (2000). The bottlenose dolphin: social relationships in a fission–fusion society. — In: Cetacean societies: field studies of whales and dolphins (Mann, J., Connor, R., Tyack, P. & Whitehead, H., eds). University of Chicago Press, Chicago, IL, p. 91-126.

Connor, R.C., Heithaus, M.R. & Barre, L.M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. — Proc. Roy. Soc. Lond. B: Biol. Sci. 268: 263-267.

Connor, R.C., Smolker, R. & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. — Anim. Behav. 72: 1371-1378.

Cowlishaw, G. & Dunbar, R.I.M. (1991). Dominance rank and mating success in male primates. — Anim. Behav. 41: 1045-1056.

Curtin, R.A. (1981). Strategy and tactics in male gray langur competition. — J. Hum. Evol. 10: 245-253.

de Villiers, M.S., Richardson, P.R.K. & van Jaarsveld, A.S. (2003). Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (*Lycaon pictus*). — J. Zool. 260: 377-389.

de Vries, H. (1998). Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. — Anim. Behav. 55: 827-843.

de Vries, H. & Appleby, M.C. (2000). Finding an appropriate order for a hierarchy: a comparison of the I&SI and the BBS methods. — Anim. Behav. 59: 239-245.

de Waal, F.B.M. (1976). Straight aggression and appeal aggression in *Macaca fascicularis*. — Experientia (Basel) 32: 1268-1270.

de Waal, F.B.M. (1978). Exploitative and familiarity-dependent support strategies in a colony of semi-free-living chimpanzees. — Behaviour 66: 268-312.

de Waal, F.B.M. (1982). Chimpanzee politics: power and sex among apes. — Jonathan Cape, London.

de Waal, F.B.M. (1984). Sex-differences in the formation of coalitions among chimpanzees. — Ethol. Sociobiol. 5: 239-255.

de Waal, F.B.M. (1986). The brutal elimination of a rival among captive male chimpanzees. — Ethol. Sociobiol. 7: 237-251.

de Waal, F.B.M. (1996). Conflict as negotiation. — In: Great ape societies (McGrew, W.C., Marchant, L.F. & Nishida, T., eds). Cambridge University Press, Cambridge, p. 159-172.

de Waal, F.B.M. & Harcourt, A.H. (1992). Coalitions and alliances: a history of ethological research. — In: Coalitions and alliances in humans and other animals (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 1-19.

de Waal, F.B.M. & van Hooff, J.A.R.A.M. (1981). Side directed communication and agonistic interactions in chimpanzees. — Behaviour 77: 164-196.

Dittus, W.P.J. (1977). The social regulation of population density and age–sex distribution in the toque monkey. — Behaviour 63: 281-322.

Duffy, K.G., Wrangham, R.W. & Silk, J.B. (2007). Male chimpanzees exchange political support for mating opportunities. — Curr. Biol. 17: R586-R587.

Dugatkin, L.A. (1998). A model of coalition formation in animals. — Proc. Roy. Soc. Lond. B: Biol. Sci. 265: 2121-2125.

Dugatkin, L.A. (2004). Principles of animal behavior. — WW Norton, New York, NY.

Ehardt, C.L. & Bernstein, I.S. (1992). Conflict intervention behaviour by adult male macaques: structural and functional aspects. — In: Coalitions and alliances in humans and other animals (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 83-111.

Engh, A.L., Esch, K., Smale, L. & Holekamp, K.E. (2000). Mechanisms of maternal rank ‘inheritance’ in the spotted hyaena, *Crocuta crocuta*. — Anim. Behav. 60: 323-332.

Engh, A.L., Funk, S.M., Van Horn, R.C., Scribner, K.T., Bruford, M.W., Libants, S., Szykman, M., Smale, L. & Holekamp, K.E. (2002). Reproductive skew among males in a female-dominated mammalian society. — Behav. Ecol. 13: 193-200.

Esteban, J. & Sákovics, J. (2003). Olson vs. Coase: coalition worth in conflict. — Theor. Decis. 55: 339-357.

Euguíluz, V.M. & Zimmermann, M.G. (2000). Transmission of information and herd behavior: an application to financial markets. — Phys. Rev. Lett. 85: 5659-5662.

Fedigan, L.M. (1992). Primate paradigms. — University of Chicago Press, Chicago, IL.

Fedurek, P., Machanda, Z.P., Schel, A.M. & Slocombe, K.E. (2013). Pant hoot chorusing and social bonds in male chimpanzees. — Anim. Behav. 86: 189-196.

Feh, C. (1999). Alliances and reproductive success in Camargue stallions. — Anim. Behav. 57: 705-713.

Flack, J.C., Girvan, M., de Waal, F.B.M. & Krakauer, D.C. (2006). Policing stabilizes construction of social niches in primates. — Nature 439: 426-429.

Flinn, M.V., Geary, D.C. & Ward, C.V. (2005). Ecological dominance, social competition, and coalitionary arms races: why humans evolved extraordinary intelligence. — Evol. Hum. Behav. 26: 10-46.

Flinn, M.V., Ponzi, D. & Muehlenbein, M.P. (2012). Hormonal mechanisms for regulation of aggression in human coalitions. — Hum. Nat. 22: 68-88.

Fraser, O.N. & Bugnyar, T. (2012). Reciprocity of agonistic support in ravens. — Anim. Behav. 83: 171-177.

Garfinkel, M.R. (2004). Stable alliance formation in distributional conflict. — Eur. J. Politic. Econ. 20: 829-852.

Gavrilets, S. (2010). Rapid transition towards the division of labor via evolution of developmental plasticity. — PLOS Comp. Biol. 6: e1000805.

Gavrilets, S. (2012). On the evolutionary origins of the egalitarian syndrome. — Proc. Natl. Acad. Sci. USA 109: 14069-14074.

Gavrilets, S. & Fortunato, L. (2014). Evolution of social instincts in between-group conflict with within-group inequality. — Nature Commun. 5: 3526.

Gavrilets, S., Duenez-Guzman, E.A. & Vose, M.D. (2008). Dynamics of coalition formation and the egalitarian revolution. — PLoS ONE 3: e3293.

Gigerenzer, G., Todd, P.M. & Group, A.R. (1999). Simple heuristics that make us smart. — Oxford University Press, New York.

Gilby, I.C., Brent, L.J.N., Wroblewski, E.E., Rudicell, R.S., Hahn, B.H., Goodall, J. & Pusey, A.E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. — Behav. Ecol. Sociobiol. 67: 373-381.

Gilby, I.C. & Wrangham, R.W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. — Behav. Ecol. Sociobiol. 62: 1831-1842.

Gilles, R.P. (2010). The cooperative game theory of networks and hierarchies. — Springer, Heidelberg.

Goodall, J. (1986). The chimpanzees of Gombe: patterns of behavior. — Harvard University Press, Cambridge, MA.

Gouzoules, H. & Gouzoules, S. (2000). Agonistic screams differ among four species of macaques: the significance of motivation-structural rules. — Anim. Behav. 59: 501-512.

Gros-Louis, J., Perry, S., Fichtel, C., Wikberg, E., Gilkenson, H., Wofsy, S. & Fuentes, A. (2008). Vocal repertoire of white-faced capuchin monkeys (*Cebus capucinus*): acoustic structure, context and usage. — Int. J. Primatol. 29: 641-670.

Gros-Louis, J., Perry, S. & Manson, J.H. (2003). Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). — Primates 44: 341-346.

Hagen, E.H. & Bryant, G.A. (2003). Music and dance as a coalition signaling system. — Hum. Nat. 14: 21-51.

Hall, K.R.L. & DeVore, I. (1965). Baboon social behavior. — In: Primate behavior. Field studies of monkeys and apes (DeVore, I., ed.). Holt, Rinehart & Winston, New York, NY, p. 53-110.

Hamilton, W.D. (1964). Genetical evolution of social behaviour; I and II. — J. Theor. Biol. 7: 1-52.

Harcourt, A.H. (1992). Coalitions and alliances: are primates more complex than non-primates? — In: Coalitions and alliances in humans and other animals (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 445-471.

Harcourt, A.H. & de Waal, F.B.M. (1992). Coalitions and alliances in humans and other animals. — Oxford University Press, Oxford.

Harcourt, A.H. & Stewart, K.J. (1989). Function of alliances in contests within wild gorilla groups. — Behaviour 109: 176-190.

Hasegawa, M. & Kutsukake, N. (in press). Bayesian competitiveness estimation predicts dominance turnover among wild male chimpanzees. — Behav. Ecol. Sociobiol.

Hemelrijk, C.K. & Ek, A. (1991). Reciprocity and interchange of grooming and ‘support’ in captive chimpanzees. — Anim. Behav. 41: 923-935.

Hemelrijk, C.K. & Puga-Gonzalez, I. (2012). An individual-oriented model on the emergence of support in fights, its reciprocation and exchange. — Plos ONE 7: e0037271.

Henzi, S.P. & Barrettt, L. (2007). Coexistence in female-bonded primate groups. — Adv. Stud. Behav. 37: 43-81.

Higham, J.P. & Maestripieri, D. (2010). Revolutionary coalitions in male rhesus macaques. — Behaviour 147: 1889-1908.

Hirsch, B.T. (2007). Spoiled brats: is extreme juvenile agonism in ring-tailed coatis (*Nasua nasua*) dominance or tolerated aggression? — Ethology 113: 446-456.

Hofer, H. & East, M.L. (2003). Behavioral processes and costs of co-existence in female spotted hyenas: a life history perspective. — Evol. Ecol. 17: 315-331.

Holekamp, K.E., Ogutu, J.O., Dublin, H.T., Frank, L.G. & Smale, L. (1993). Fission of a spotted hyena clan: consequences of prolonged female absenteeism and causes of female emigration. — Ethology 93: 285-299.

Holekamp, K.E., Smale, L. & Szykman, M. (1996). Rank and reproduction in the female spotted hyaena. — J. Reprod. Fertil. 108: 229-237.

Hruschka, D.J. (2010). Friendship: development, ecology, and evolution of a relationship. — University of California Press, Berkeley, CA.

Hruschka, D.J. & Henrich, J. (2006). Friendship, cliqueness, and the emergence of cooperation. — J. Theor. Biol. 239: 1-15.

Hsu, Y.Y. & Wolf, L.L. (1999). The winner and loser effect: integrating multiple experiences. — Anim. Behav. 57: 903-910.

Janson, C. (1985). Aggressive competition and individual food comsumption in wild brown capuchin monkeys (*Cebus apella*). — Behav. Ecol. Sociobiol. 18: 125-138.

Jennings, D.J., Carlin, C.M. & Gammell, M.P. (2009). A winner effect supports third-party intervention behaviour during fallow deer, *Dama dama*, fights. — Anim. Behav. 77: 343-348.

Jennings, D.J., Carlin, C.M., Hayden, T.J. & Gammell, M.P. (2011). Third-party intervention behaviour during fallow deer fights: the role of dominance, age, fighting and body size. — Anim. Behav. 81: 1217-1222.

Johnstone, R.A. & Dugatkin, L.A. (2000). Coalition formation in animals and the nature of winner and loser effects. — Proc. Roy. Soc. Lond. B: Biol. Sci. 267: 17-21.

Jones, B.M. (1980). The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: intraspecific competition for group membership in a folivorous neotropical primate. — Primates 21: 389-405.

Jones, C. (2005). A preliminary test of the van Schaik model of male coalitions for Costa Rican mantled howler monkeys (*Alouatta palliata*). — Lab. Prim. Newslett. 44: 3-4.

Kaburu, S.S.K., Inoue, S. & Newton-Fisher, N.E. (2013). Death of the Apha: within-community lethal violence among chimpanzees of the Mahale Mountains National Park. — Am. J. Primatol. 75: 789-797.

Kahan, J.P. & Rapoport, A. (1984). The theory of coalition formation. — Lawrence Erlbaum Associates, Hillsdale, New Jersey.

Kaplan, J.R. (1977). Patterns of fight interference in free-ranging rhesus monkeys. — Am. J. Phys. Anthropol. 47: 279-288.

Kapsalis, E. (2004). Matrilineal kinship and primate behavior. — In: Kinship and behavior in primates (Chapais, B. & Berman, C.M., eds). Oxford University Press, Oxford, p. 153-176.

Katz, Y., Tunstrøm, K., Ioannou, C.C., Huepe, C. & Couzin, I.D. (2011). Inferring the structure and dynamics of interactions in schooling fish. — Proc. Natl. Acad. Sci. USA 108: 18720-18725.

Kawai, M. (1958). On the system of social ranks in a natural troop of Japanese monkey (I) — basic rank and dependent rank. — Primates 1: 111-130.

Kawamura, S. (1958). Matriarchal social ranks in the Minoo-B troop: a study of the rank system of Japanese monkeys. — Primates 1: 149-156.

Kirschner, S. & Tomasello, M. (2010). Joint music making promotes prosocial behavior in 4-year-old children. — Evol. Hum. Behav. 31: 354-364.

Konrad, K.A. & Kovenock, D. (2009). The alliance formation puzzle and capacity constraints. — Econ. Lett. 103: 84-86.

Krützen, M., Barre, L.M., Connor, R.C., Mann, J. & Sherwin, W.B. (2004). 'O father: where art thou?' — paternity assessment in an open fission–fusion society of wild bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. — Mol. Ecol. 13: 1975-1990.

Kuester, J. & Paul, A. (1992). Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). — Behaviour 120: 192-217.

Kulik, L., Muniz, L., Mundry, R. & Widdig, A. (2012). Patterns of interventions and the effect of coalitions and sociality on male fitness. — Mol. Ecol. 21: 699-714.

Kummer, H. (1967). Tripartite relations in hamadryas baboons. — In: Social communication among primates (Altmann, S.A., ed.). University of Chicago Press, Chicago, IL, p. 63-71.

Kurland, J. (1977). Kin selection in the Japanese monkey. — Contr. Primatol. 12: 1-145.

Kutsukake, N. & Hasegawa, T. (2005). Dominance turnover between an alpha and a beta male and dynamics of social relationships in Japanese macaques. — Int. J. Primatol. 26: 775-800.

Kutsukake, N. & Nunn, C.L. (2006). Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control. — Behav. Ecol. Sociobiol. 60: 695-706.

Langergraber, K.A. (2012). Cooperation among kin. — In: The evolution of primate societies (Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A. & Silk, J.B., eds). The University of Chicago Press, London, p. 491-513.

Langergraber, K.E., Mitani, J.C. & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. — Proc. Natl. Acad. Sci. USA 104: 7786-7790.

Lea, A.J., Learn, N.H., Theus, M.J., Altmann, J. & Alberts, S.C. (2014). Complex sources of variance in female dominance rank in a nepotistic society. — Anim. Behav. 94: 87-99.

Lee, P.C. (1987). Allomothering among African elephants. — Anim. Behav. 35: 278-291.

Leimar, O. & Hammerstein, P. (2006). Facing the facts. — J. Evol. Biol. 19: 1403-1405.

Mann, M. (1993). The sources of social power: the rise of classes and nation states. — Cambridge University Press, Cambridge.

Mathew, S. & Boyd, R. (2011). Punishment sustains large-scale cooperation in pre-state warfare. — Proc. Natl. Acad. Sci. USA 108: 11375-11380.

Maynard Smith, J. (1982). Evolution and the theory of games. — Cambridge University Press, Cambridge.

McNamara, J.M. & Houston, A.I. (2009). Integrating function and mechanism. — Trends Ecol. Evol. 24: 670-675.

McNamara, J.M., Binmore, K. & Houston, A.I. (2006). Cooperation should not be assumed. — Trends Ecol. Evol. 21: 476-478.

McNeill, W.H. (1995). Keeping together in time: dance and drill in human history. — Harvard University Press, Cambridge, MA.

Melis, A., Hare, B. & Tomasello, M. (2009). Chimpanzees negotiate in a bargaining game. — Evol. Hum. Behav. 30: 381-392.

Mesterton-Gibbons, M., Gavrilets, S., Gravner, J. & Akcay, E. (2011). Models of coalition or alliance formation. — J. Theor. Biol. 274: 187-204.

Mesterton-Gibbons, M. & Sherratt, T.N. (2007). Coalition formation: a game-theoretic analysis. — Behav. Ecol. 18: 277-286.

Mesterton-Gibbons, M. & Sherratt, T.N. (2009). Neighbor intervention: a game-theoretic model. — J. Theor. Biol. 256: 263-275.

Mills, M.G.L. (1990). Kalahari hyaenas: comparative behavioural ecology of two species. — Blackburn Press, Caldwell, NJ.

Milner, R.N.C., Jennions, M.D. & Backwell, P.R.Y. (2011). Know thine enemy's neighbor: neighbor size affects floaters' choice of whom to fight. — Behav. Ecol. 22: 947-950.

Mitani, J.C. (2009). Male chimpanzees form enduring and equitable social bonds. — Anim. Behav. 77: 633-640.

Mitani, J.C. & Brandt, K.L. (1994). Social factors influence the acoustic variability in the long-distance calls of male chimpanzees. — Ethology 96: 233-252.

Mitani, J.C. & Gros-Louis, J. (1998). Chorusing and call convergence in chimpanzees: tests of three hypotheses. — Behaviour 135: 1041-1064.

Mitani, J.C. & Watts, D. (2001). Why do chimpanzees hunt and share meat? — Anim. Behav. 61: 915-924.

Mitani, J.C., Merriwether, D.A. & Zhang, C.B. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. — Anim. Behav. 59: 885-893.

Mitani, J., Watts, D., Pepper, J. & Merriwether, D.A. (2002). Demographic and social constraints on male chimpanzee behavior. — Anim. Behav. 63: 727-737.

Mitchell, C.L., Boinski, S. & van Schaik, C.P. (1991). Competitive regimes and female bonding in 2 species of squirell monkeys (*Saimiri oerstedi* and *S. sciureus*). — Behav. Ecol. Sociobiol. 28: 55-60.

Muller, M.N. & Mitani, J.C. (2005). Conflict and cooperation in wild chimpanzees. — Adv. Stud. Behav. 35: 275-331.

Murray, C.M., Eberly, L.E. & Pusey, A.E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). — Behav. Ecol. 17: 1020-1028.

Myerson, R.B. (1991). Game theory. Analysis of conflict. — Harvard University Press, Cambridge, MA.

Nishida, T. (1983). Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). — Primates 24: 318-336.

Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y. & Uehara, S. (1992). Meat-sharing as a coalition strategy by an alpha male chimpanzee? — In: Topics in primatology, Vol. 1: human origins (Nishida, T., McGrew, W.C. & Marler, P., eds). University of Tokyo Press, Tokyo, p. 159-174.

Nishida, T. & Hosaka, K. (1996). Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. — In: The great ape societies (McGrew, W.C., Marchant, L.F. & Nishida, T., eds). Cambridge University Press, Cambridge, p. 114-134.

Noë, R. (1986a). Asymmetry in alliances of baboons. — Prim. Rep. 14: 108.

Noë, R. (1986b). Lasting alliances among adult male savannah baboons. — In: Primate ontogeny, cognition and social behaviour (Else, J.M. & Lee, P.H., eds). Cambridge University Press, New York, NY, p. 381-392.

Noë, R. (1989). Coalition formation among male baboons. — PhD thesis, University of Utrecht, Utrecht.

Noë, R. (1990). A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. — Anim. Behav. 39: 78-90.

Noë, R. (1992). Alliance formation among male baboons: shopping for profitable partners. — In: Coalitions and alliances in humans and other animals (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 233-257.

Noë, R. (1994). A model of coalition formation among male baboons with fighting ability as the crucial parameter. — Anim. Behav. 47: 211-213.

Noë, R. & Sluijter, A.A. (1990). Reproductive tactics of male savanna baboons. — Behaviour 113: 117-170.

Noë, R. & Sluijter, A.A. (1995). Which adult male savanna baboons form coalitions. — Int. J. Primatol. 16: 77-105.

Noh, S.J. (2002). Sequential distribution and stable alliances with endogenous sharing rule. — Eur. J. Politic. Econ. 18: 129-151.

Nummenmaa, L., Glerean, E., Viinikainen, M., Jääskeläinen, L.P., Hari, R. & Sams, M. (2012). Emotions promote social interaction by synchronizing brain activity across individuals. — Proc. Natl. Acad. Sci. USA 109: 9599-9604.

Okasha, S. (2009). Evolution and the levels of selection. — Oxford University Press, Oxford.

Olson, M. (1965). Logic of collective action: public goods and the theory of groups. — Harvard University Press, Cambridge, MA.

Ostner, J. & Kappeler, P.M. (2004). Male life history and the unusual adult sex ratios of redfronted lemur, *Eulemur fulvus rufus*, groups. — Anim. Behav. 67: 249-259.

Pacheco, J.M., Traulsen, A. & Nowak, M.A. (2006). Active linking in evolutionary games. — J. Theor. Biol. 243: 437-443.

Pacheco, J.M., Traulsen, A., Ohtsuki, J. & Nowak, M.A. (2008). Repeated games and direct reciprocity under active linking. — J. Theor. Biol. 250: 723-731.

Packer, C. (1977). Recirpocal altruism in *Papio anubis*. — Nature 265: 441-443.

Packer, C. (1979). Male dominance and reproductive activity in *Papio anubis*. — Anim. Behav. 27: 37-45.

Packer, C. & Pusey, A.E. (1982). Cooperation and competition within coalitions of male lions: kin selection or game theory? — Nature 296: 740-742.

Packer, C., Gilbert, D.A., Pusey, A.E. & O'Brien, S.J. (1991). A molecular genetic analysis of kinship and cooperation in African lions. — Nature 351: 562-565.

Pandit, S.A. & van Schaik, C.P. (2003). A model of levelling coalitions among primate males: towards a theory of egalitarianism. — Behav. Ecol. Sociobiol. 55: 161-168.

Parker, G.A. (1974). Assessment strategy and evolution of fighting behavior. — J. Theor. Biol. 47: 223-243.

Paukner, A., Suomi, S.J., Visalberghi, E. & Ferrari, P.F. (2009). Capuchin monkeys display affiliation toward humans who imitate them. — Science 325: 880-883.

Paul, A., Kuester, J., Timme, A. & Arnemann, J. (1993). The association between rank, mating effort, and reproductive success in male Barbary macaques (*Macaca sylvanus*). — Primates 34: 491-502.

Pemantle, R. & Skyrms, B. (2004a). Network formation by reinforcement learning: the long and medium runs. — Math. Soc. Sci. 48: 315-327.

Pemantle, R. & Skyrms, B. (2004b). Time to absorption in discounted reinforcement models. — Stoch. Proc. Appl. 109: 1-12.

Perry, S. (1997). Male–female social relationships in wild white-faced capuchins (*Cebus capucinus*). — Behaviour 134: 477-510.

Perry, S. (1998a). A case report of a male rank reversal in a group of wild white-faced capuchins (*Cebus capucinus*). — Primates 39: 51-70.

Perry, S. (1998b). Male–male social relationships in wild white-faced capuchins, *Cebus capucinus*. — Behaviour 135: 139-172.

Perry, S. (2012). The behavior of wild white-faced capuchins: demography, life history, social relationships, and communication. — Adv. Stud. Behav. 44: 135-181.

Perry, S. & Manson, J.H. (2008). Manipulative monkeys: the capuchins of Lomas Barbudal. — Harvard University Press, Cambridge, MA.

Perry, S., Barrett, H.C. & Manson, J.H. (2004). White-faced capuchin monkeys show triadic awareness in their choice of allies. — Anim. Behav. 67: 165-170.

Perry, S., Manson, J.H., Muniz, L., Gros-Louis, J. & Vigilant, L. (2008). Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capucinus*. — Anim. Behav. 76: 187-199.

Petit, O. & Thierry, B. (1994). Aggressive and peaceful interventions in conflicts in Tonkean macaques. — Anim. Behav. 48: 1427-1436.

Phillips-Silver, J., Aktipis, C.A. & Bryant, G.A. (2010). The ecology of entrainment: foundations of coordinated rhythmic movement. — Music Perception 28: 3-14.

Pope, T.R. (1990). The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multimale and single-male troops using genetic markers. — Behav. Ecol. Sociobiol. 27: 439-446.

Pusey, A.E. & Packer, C. (1997). The ecology of relationships. — In: Behavioral ecology. An evolutionary approach (Krebs, J.R. & Davies, N.B., eds). Blackwell, Oxford, p. 254-283.

Ramirez-Llorens, P., Di Bitetti, M.S., Baldovino, M.C. & Janson, C.H. (2008). Infanticide in black capuchin monkeys (*Cebus apella nigritus*) in Iguazu National Park, Argentina. — Am. J. Primatol. 70: 473-484.

Range, F. & Noë, R. (2005). Can simple rules account for the pattern of triadic interactions in juvenile and adult female sooty mangabeys? — Anim. Behav. 69: 445-452.

Ray, D. (2007). A game-theoretic perspective on coalition formation. — Oxford University Press, Oxford.

Riker, W.H. (1962). The theory of political coalitions. — Yale University Press, New Haven, CT.

Riss, D. & Goodall, J. (1977). Recent rise to alpha-rank in a population of free-living chimpanzees. — Folia Primatol. 27: 134-151.

Roeder, J.J., Duval, L. & Gosset, D. (2002). Aggressive and neutral interventions in conflicts in captive groups of brown lemurs (*Eulemur fulvus fulvus*). — Am. J. Phys. Anthropol. 118: 253-258.

Romero, T. & Aureli, F. (2008). Reciprocity of support in coatis (*Nasua nasua*). — J. Comp. Psychol. 122: 19-25.

Romero, T. & Castellanos, M.A. (2010). Dominance relationships among male hamadryas baboons (*Papio hamadryas*). — J. Ethol. 28: 113-121.

Rood, J.P. (1990). Group size, survival, reproduction, and routes to breeding in dwarf mongooses. — Anim. Behav. 39: 566-572.

Rowell, T.E. & Rowell, C.A. (1993). The social organization of feral *Ovis aries* Ram groups in the pre-rut period. — Ethology 95: 213-232.

Rudolf von Rohr, C., Koski, S.E., Burkart, J.M., Caws, C., Fraser, O.N., Ziltener, A. & van Schaik, C.P. (2012). Impartial third-party interventions in captive chimpanzees: a reflection of community concern. — PLoS ONE 7: e32494.

Rusch, H. (2014). The evolutionary interplay of intergroup conflict and altruism in humans: a review of parochial altruism theory and prospects for its extension. — Proc. Roy. Soc. Lond. B: Biol. Sci. 281: 20141539.

Rutte, C., Taborsky, M. & Brinkhof, M.W.G. (2006). What sets the odds of winning and losing? — Trends Ecol. Evol. 21: 16-21.

Sánchez-Pagés, S. (2007). Endogenous coalition formation in contests. — Rev. Econ. Design 11: 139-163.

Santos, F.C., Pacheco, J.M. & Lenaerts, T. (2006). Cooperation prevails when individuals adjust their social ties. — PLOS Comp. Biol. 2: 1284-1291.

Scheiber, I.B.R., Weiss, B.M., Frigerio, D. & Kotrschal, K. (2005). Active and passive social support in families of greylag geese (*Anser anser*). — Behaviour 142: 1535-1557.

Schilder, M.B.H. (1990). Interventions in a herd of semicaptive plains zebras. — Behaviour 112: 53-83.

Schino, G., Tiddi, B., Polizzi, E. & Si Sorrentino, P. (2006). Simultaneous classification by rank and kinship in Japanese macaques. — Anim. Behav. 71: 1069-1074.

Schneider, G. & Krueger, K. (2012). Third-party interventions keep social partners from exchanging affiliative interactions with others. — Anim. Behav. 83: 377-387.

Schülke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. — Curr. Biol. 20: 2207-2210.

Seed, A.M., Clayton, N.S. & Emery, N.J. (2007). Postconflict third-party affiliation in rooks, *Corvus frugilegus*. — Curr. Biol. 17: 152-158.

Setchell, J.M., Wickings, E.J. & Knapp, L.A. (2006). Life history in male mandrills (*Mandrillus sphinx*): physical development, dominance rank, and group association. — Am. J. Phys. Anthropol. 131: 498-510.

Seyfarth, R.M. & Cheney, D.L. (2012). The evolutionary origins of friendship. — Annu. Rev. Psychol. 63: 153-177.

Sijtsema, J.J., Ojanen, T., Veenstra, R., Lindenberg, S., Hawley, P.H. & Little, T.D. (2010). Forms and functions of aggression in adolescent friendship selection and influence: a longitudinal social network analysis. — Soc. Dev. 19: 1-20.

Silk, J.B. (1992). The patterning of intervention among male bonnet macaques: reciprocity, revenge and loyalty. — Curr. Anthropol. 33: 318-325.

Silk, J.B. (1993). Does participation in coalitions influence dominance relationships among male bonnet macaques? — Behaviour 126: 171-189.

Silk, J.B. (1994). Social relationships of male bonnet macaques: male bonding in a matrilineal society. — Behaviour 130: 271-291.

Silk, J.B. (1999). Male bonnet macaques use information about third-party rank relationships to recruit allies. — Anim. Behav. 58: 45-51.

Silk, J.B. (2002). Kin selection in primate groups. — Int. J. Primatol. 23: 849-875.

Silk, J.B. (2007). Social components of fitness in primate groups. — Science 317: 1347-1351.

Silk, J.B., Alberts, S.C. & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. — Science 302: 1231-1234.

Silk, J.B., Alberts, S.C. & Altmann, J. (2004). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. — Anim. Behav. 67: 573-582.

Silk, J.B., Alberts, S.C. & Altmann, J. (2006a). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. — Behav. Ecol. Sociobiol. 61: 197-204.

Silk, J.B., Altmann, J. & Alberts, S.C. (2006b). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. — Behav. Ecol. Sociobiol. 61: 183-195.

Skaperdas, S. (1996). Contest success functions. — Econ. Theor. 7: 283-290.

Skaperdas, S. (1998). On the formation of alliances in conflict and contests. — Public Choice 96: 25-42.

Skyrms, B. & Pemantle, R. (2000). A dynamic model of social network formation. — Proc. Natl. Acad. Sci. USA 97: 9340-9346.

Slocombe, K.E. & Zuberbühler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. — Proc. Natl. Acad. Sci. USA 104: 17228-17233.

Smith, J.E., Kolowski, J.M., Graham, K.E., Dawes, S.E. & Holekamp, K.E. (2008). Social and ecological determinants of fission–fusion dynamics in the spotted hyaena. — Anim. Behav. 76: 619-636.

Smith, J.E., Van Horn, R.C., Powning, K.S., Cole, A.R., Graham, K.E., Memenis, S.K. & Holekamp, K.E. (2010). Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. — Behav. Ecol. 21: 284-303.

Smuts, B.B. (1985). Sex and frienship in baboons. — Aldine, New York, NY.

Smuts, B. (1987). Sexual competition and mate choice. — In: Primate societies (Smuts, B., Cheney, D.L., Seyfarth, R.M., Wrangham, R. & Struhsaker, T.T., eds). The University of Chicago Press, Chicago, IL, p. 385-399.

Smuts, B. (2002). Gestural communication in olive baboons and domestic dogs. — In: The cognitive animal: empirical and theoretical perspectives on animal cognition (Bekoff, M., Allen, C. & Burghardt, G.M., eds). MIT Press, Cambridge, MA, p. 301-306.

Stamatopoulos, G., Sengupta, A., Vogel, E. & Janson, C. (2009). A game-theoretic model of coalition among primates. — J. Bioeconom. 11: 165-183.

Surbeck, M., Mundry, R. & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). — Proc. Roy. Soc. Lond. B: Biol. Sci. 278: 590-598.

Tan, G. & Wang, R. (2010). Coalition formation in the presence of continuing conflict. — Int. J. Game Theor. 39: 273-299.

Thierry, B. (2007). The macaques: a double-layered social organization. — In: Primates in perspective (Campbell, C., Fuentes, A., MacKinnon, K.C., Panger, M. & Bearder, S., eds). Oxford University Press, New York, NY, p. 224-239.

Tinbergen, N. (1963). On aims and methods of ethology. — Z. Tierpsychol. 20: 410-433.

Tomasello, M. & Call, J. (1997). Primate cognition. — Oxford University Press, New York, NY.

Tullock, G. (1980). Efficient rent seeking. — In: Toward a theory of the rent-seeking society. Texas A & M University, College Station, TX, p. 97-112.

Uehara, S., Hiraiwahasegawa, M., Hosaka, K. & Hamai, M. (1994). The fate of defeated alpha male chimpanzees in relation to their social networks. — Primates 35: 49-55.

van Schaik, C.P., Pandit, S.A. & Vogel, E.R. (2004). A model for within-group coalitionary aggression among males. — Behav. Ecol. Sociobiol. 57: 101-109.

van Schaik, C.P., Pandit, S.A. & Vogel, E.R. (2006). Toward a general model for male–male coalitions in primate groups. — In: Cooperation in primates and humans (Kappeler, P.M. & van Schaik, C.P., eds). Springer, Berlin, p. 143-163.

Vigilant, L., Hofreiter, M., Siedel, H. & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. — Proc. Natl. Acad. Sci. USA 98: 12890-12895.

Vogel, E.R., Munch, S.B. & Janson, C.H. (2007). Understanding escalated aggression over food resources in white-faced capuchin monkeys. — Anim. Behav. 74: 71-80.

von Newmann, J. & Morgenstern, O. (1947). Theory of games and economic behavior. — Princeton University Press, Princeton, NJ.

Wahaj, S.A., Van Horn, R.C., Van Horn, T.L., Dreyer, R., Hilgris, R., Schwarz, J. & Holekamp, K.E. (2004). Kin discrimination in the spotted hyena (*Crocuta crocuta*): nepotism among siblings. — Behav. Ecol. Sociobiol. 56: 237-247.

Walker, R.S. & Bailey, D.H. (2013). Body counts in lowland South American violence. — Evol. Hum. Behav. 34: 29-34.

Walker, R.S., Hill, K.R., Flinn, M.V. & Ellsworth, R.M. (2011). Evolutionary history of hunter–gatherer marriage practices. — PLoS ONE 6: e19066.

Ward, C., Trisko, R. & Smuts, B.B. (2009). Third-party interventions in dyadic play between littermates of domestic dogs, *Canis lupus familiaris*. — Anim. Behav. 78: 1153-1160.

Waser, P.M., Keane, B., Creel, S.R., Elliott, L.F. & Minchella, D.J. (1994). Possible male coalitions in a solitary mongoose. — Anim. Behav. 47: 289-294.

Wasser, S.K. & Starling, A.K. (1988). Proximate and ultimate causes of reproductive suppression among female yellow baboons at Mikumi National Park, Tanzania. — Am. J. Primatol. 16: 97-121.

Wattis, J.A.D. (2006). An introduction to mathematical models of coagulation-fragmentation processes: a discrete deterministic mean-field approach. — Physica D 222: 1-20.

Watts, D.P. (1997). Agonistic interventions in wild mountain gorilla groups. — Behaviour 134: 23-57.

Watts, D.P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. — Behav. Ecol. Sociobiol. 44: 43-55.

Watts, D.P. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. — Behaviour 139: 343-370.

Watts, D.P. & Mitani, J.C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. — Behaviour 138: 299-327.

Whitehead, H. & Connor, R. (2005). Alliances I. How large should alliance be? — Anim. Behav. 69: 117-126.

Widdig, A., Streich, W.J. & Tembrock, G. (2000). Coalition formation among male Barbary macaques (*Macaca sylvanus*). — Am. J. Primatol. 50: 37-51.

Widdig, A., Streich, W.J., Nuernberg, P., Croucher, P.J.P., Bercovitch, F.B. & Krawczak, M. (2006). Paternal kin bias in the agonistic interventions of adult female rhesus macaques (*Macaca mulatta*). — Behav. Ecol. Sociobiol. 61: 205-214.

Willems, E., Hellriegel, B. & van Schaik, C.P. (2013). The collective action problem in primate territory conflicts. — Proc. Roy. Soc. Lond. B: Biol. Sci. 280: 20130081.

Wilson, M.L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I.C., Hashimoto, C., Hobaiter, C.L., Hohmann, G., Itoh, N., Koops, K., Lloyd, J.N., Matsuzawa, T., Mitani, J.C., Mjungu, D.C., Morgan, D., Muller, M.N., Mundry, R., Nakamura, M., Pruetz, J., Pusey, A.E., Riedel, J., Sanz, C., Schel, A.M., Simmons, N., Waller, M., Watts, D.P., White, F., Wittig, R.M., Zuberbühler, K. & Wrangham, R.W. (2014). Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. — Nature 513: 414-417.

Wiszniewski, J., Corrigan, S., Beheregaray, L.B. & Moeller, L.M. (2012). Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). — J. Anim. Ecol. 81: 423-431.

Witt, R., Schmidt, C. & Schmitt, J. (1981). Social rank and darwinian fitness in a multi-male group of Barbary macaques (*Macaca sylvana* L. 1758). Dominance reversals and male reproductive success. — Folia Primatol. 36: 201-211.

Wittig, R.M., Crockford, C., Langergraber, K.E. & Zuberbühler, K. (2014). Triadic social interactions operate across time: a field experiment with wild chimpanzees. — Proc. Roy. Soc. Lond. B: Biol. Sci. 281: 20133155.

Wrangham, R.W. (1999). Evolution of coalitionary killing. — Yb. Phys. Anthropol. 42: 1-30.

Young, C., Schülke, O. & Ostner, J. (2014). How males form coalitions against group rivals and the Pandit/van Schaik coalition model. — Behaviour 151: 907-934.

Zabel, C.J., Glickman, S.E., Frank, L.G., Woodmansee, K.B. & Keppel, G. (1992). Coalition formation in a colony of prepubertal spotted hyenas. — In: Coalitions and alliances in humans and other animals (Harcourt, A.H. & de Waal, F.B.M., eds). Oxford University Press, Oxford, p. 233-257.

Zucker, E.L. & Clarke, M.R. (1998). Agonistic and affiliative relationships of adult female howlers (*Alouatta palliata*) in Costa Rica over a 4-year period. — Int. J. Primatol. 19: 433-449.