1 **Coalitions in theory and reality: A review of pertinent variables and processes**

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24 Short title: Coalitions in theory and reality

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26 **Abstract**

27 Coalitions and alliances are ubiquitous in humans and many other mammals, being part of the fabric

28 of complex social systems. Field biologists and ethologists have accumulated a vast amount of data

29 on coalition and alliance formation, while theoretical biologists have developed modeling

30 approaches. With the accumulation of empirical data and sophisticated theory, we are now

31 potentially able to answer a host of questions about how coalitions emerge and are maintained in a

32 population over time, and how the psychology of this type of cooperation evolved. Progress can only

33 be achieved, however, by effectively bridging the communication gap that currently exists between

34 empiricists and theoreticians. In this paper, we aim to do so by asking three questions: (1) What are

35 the primary questions addressed by theoreticians interested in coalition formation, and what are the

36 main building blocks of their models? (2) Do empirical observations support the assumptions of

37 current models, and if not, how can we improve this situation? (3) Has theoretical work led to a

38 better understanding of coalition formation, and what are the most profitable lines of inquiry for the

39 future? Our overarching goal is to promote the integration of theoretical and field biology by

40 motivating empirical scientists to collect data on aspects of coalition formation that are currently

41 poorly quantified and to encourage theoreticians to develop a comprehensive theory of coalition

42 formation that is testable under real-world conditions.

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 behavioral 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 behavior 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 modeling. 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 modeling 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 behavior emerge from simple behavioral 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 (Mesterton-Gibbons et al., 2010). Here, we

70   attempt to forge an alliance between theoretical and empirical approaches as the first step toward

71   the long-term goal of achieving a more comprehensive theory of coalition formation.

72   We start by briefly describing patterns of coalition formation within and across species. We next

73   summarize the primary questions addressed by theoreticians, and identify the main building blocks

74   of their models. Then we selectively review the literature on coalition formation with the explicit aim

75   of contrasting empirical data with the assumptions made by theoretical models, pinpointing where

76   these might be overly simplistic, and identifying important parameters that have been poorly

77   quantified in the field. As the literature in this area remains heavily skewed toward the primates

78   (Smith et al., 2010), the empirical data presented here are derived mainly from this taxon. Finally, we

79   propose some profitable lines of inquiry for future theoretical and empirical research on coalition

80   formation.

81   **A Brief Primer on Coalition Formation**

82   The term "coalition" is used in various ways (e.g. an alliance between political parties, Mann, 1993)

83   but, in ethology and behavioral biology, the term typically refers to two (or more) individuals acting

84   together against a third party in an aggressive or competitive context (Harcourt & de Waal, 1992;

85   Figure 1). The term "alliance," on the other hand, generally refers to a long term relationship

86   characterized by repeated coalitions and high levels of association between the partners, which

87   means that when one partner is in trouble, his or her ally is often nearby and able to help ("alliance

88   behavior based on coalitions": cf. Feh, 1999; de Waal & Harcourt, 1992). Human coalitions and

89   alliances range from cooperation within a single family to acts of support between nation-states

90   (Chagnon, 1988b; Bowles, 2009; Apicella et al., 2012). On a smaller scale, coalitions and alliances are

91   common in our closest relatives, including for example the chimpanzee (*Pan troglodytes*, review in

92   Muller & Mitani, 2005), as well as a number of non-primate species (reviewed by Harcourt & de

93   Waal, 1992; Smith et al., 2010).

94   (Fig. 1 about here)

95   Animal coalitions and alliances are variable in duration and stability. Coalitions can occur

96   opportunistically on a case-by-case basis (e.g. Bissonnette, 2009; Smith et al., 2010), or they can be

97   observed frequently among the same partners as part of an enduring, long-term relationship (e.g. de

98   Waal, 1982; Packer & Pusey, 1982; Smuts, 1985; Goodall, 1986; Noë, 1986b; Caro & Collins, 1987;

99   Connor et al., 1992; Feh, 1999; Boesch & Boesch-Achermann, 2000; Connor et al., 2001; Boinski et

100   al., 2005; Schülke et al., 2010). One individual may establish year-long, stable alliances with one or a

101   few partners and also participate in opportunistic coalitions with other group members in which

102   loyalties change regularly (Riss & Goodall, 1977; de Waal, 1982; Goodall, 1986; Noë, 1990; Uehara et

103   al., 1994; Connor et al., 2000; Sijtsema et al., 2009). For example, Nishida (1983) and de Waal (1984)

104   have argued that male chimpanzees intervene opportunistically in "political" conflicts and may turn

105   against former allies when it is beneficial to do so.

106   In group-living species, coalitions and alliances are important in both intergroup and intragroup

107   competition. Coalitions for competition against conspecifics from other groups (hereafter "group-

108   wide coalitions") occur when the opponents belong to different social groups (or family units, e.g.

109   Scheiber et al., 2005), whereas within-group coalitions occur when two or more members of the

110   same group compete against at least one other "in-group" member. Group-wide coalitions can be

111   offensive if individuals join forces to oust incumbent male(s) and take over a group (e.g. Pope, 1990;

112   Rood, 1990; Packer et al., 1991; Waser et al., 1994; Ostner & Kappeler, 2004; Wilson et al., 2014), or

113   to conduct a lethal attack on members of a neighbouring group (reviewed by Wrangham, 1999). They

114   can also be defensive, as when group members form a coalition to repel single challengers and/or an

115   out-group coalition (e.g. Feh, 1999). Group-wide coalitions can be very large (e.g. average size in

116   chimpanzees: 13, Watts & Mitani, 2001; hyenas: 14, Smith et al., 2010; human band and tribal level

117   raiding parties range from 10 - 100, Walker & Bailey, 2013; Mathew & Boyd, 2011), in contrast to

118   within-group coalitions, which often involve only two or three partners (reviewed by Smith et al.,

119   2010). It seems likely that group-wide coalition formation provides the only context in which the

120   opposing parties are not mutually dependent on each other (except in dolphins and especially

121   humans, where interdependence extends beyond the level of the group, e.g. Connor et al., 2001;

122   Walker et al., 2011): they usually occur in a clear and unambiguous competitive context and thus are

123   predictably hostile, in contrast to the interactions that occur within groups (Connor et al., 1992;

124   Harcourt, 1992; see below). Group-wide and within-group coalitions, however, are not mutually

125   exclusive phenomena: for example, the need for in-group members to cooperate during between-

126   group encounters is known to profoundly affect the social dynamics of groups, and hence the

127   formation of within-group coalitions (humans: Alexander, 1990; 2014; Flinn et al., 2005; Choi &

128   Bowles, 2007; Bowles, 2009; Rusch 2014; other animals: Watts & Mitani, 2001). Group-wide

129   coalitions have also been suggested as one possible evolutionary precursor of within-group coalitions

130   in animals (Harcourt, 1992), although a formal test of this hypothesis is lacking. Despite the likely

131   interdependence between intra- and inter-group coalition formation, the emphasis of this review is

132   on within-group coalitions, as these have received much more attention both theoretically and

133   empirically.

134   Research on within-group coalitions has historically focused on primates (Kawai, 1958; Kawamura,

135   1958; Hall & DeVore, 1965; Kummer, 1967; Packer, 1977; Riss & Goodall, 1977; de Waal, 1978b).

136   More recent empirical work, however, has revealed that a wide range of mammalian species and

137   some birds engage in coalitionary behaviour (reviewed by Smith et al., 2010), including several social

138   carnivores (e.g. hyenas, *Crocuta crocuta*: Zabel et al., 1992; Engh et al., 2002; Wahaj et al., 2004;

139   ring-tailed coatis, *Nasua nasua*: Romero & Aureli, 2008; African wild dog, *Lycaon pictus*: de Villiers et

140   al., 2003; Domestic dogs, *Canis lupus familiaris*: Ward et al., 2009), some artiodactyls (e.g. fallow

141   deer, *Dama dama*: Jennings et al., 2009; feral sheep, *Ovis aries*: Rowell & Rowell, 1993), some

142   perissodactyls (e.g. plain zebra, *Equus quagga*: Schilder, 1990), one proboscid (African elephant,

143   *Loxondonta africana*: Lee, 1987), and some birds (e.g. ravens, *Corvus frugilegus*: Seed et al., 2007;

144   *Corvus corax:* Fraser & Bugnyar, 2012).

145   The pattern of within-group coalition formation most commonly reported in the literature is that of

146   one individual intervening in an on-going conflict and aligning itself with one of the original

147   opponents (variously referred as "agonistic intervention", "agonistic aid", "fight interference",

148   "support choice", de Waal & Harcourt, 1992). Individuals also sometimes join forces to

149   simultaneously attack the same target prior to the initiation of a conflict with that target (i.e.

150   instantaneous or parallel coalitions, cf. Noë, 1986c; e.g. de Waal, 1982; Bissonnette, 2009). For

151   example, most chimpanzee male coalitions at Ngogo formed spontaneously or when the males

152   jointly retaliated after another male displayed in the vicinity (Watts, 2002). The term coalition covers

153   both of these interaction patterns, but excludes cases where an intervening animal breaks up an

154   agonistic interaction between two others without siding or "acting together" with either putative

155   combatant (referred to as "pacifying", "neutral", "policing", "peaceful" or "impartial" interventions,

156   e.g. Bernstein, 1964; Boehm, 1994; Petit & Thierry, 1994; Roeder et al., 2002; Flack et al., 2006;

157   Rudolf von Rohr et al., 2012).

158   Three configurations of within-group coalitions formed by two partners against a single target have

159   been recognized (cf. Chapais, 1995; van Schaik et al., 2006; see Chapais 1995 for various examples in

160   primates):

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

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

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

164   Although some variation within- and across species has been reported (e.g. Harcourt, 1992; Boesch &

165   Boesch-Achermann, 2000; Young et al., 2014), all-down coalitions appear to be the most common

166   coalitionary pattern observed in animals when the beneficiary is not related to the supporter (e.g.

167   Harcourt & Stewart, 1989; Silk, 1993; Smith et al., 2010).

168   As we will see below, coalitions can serve different functions (van Schaik et al., 2006); they can be

169   observed among different sex and age classes (reviewed in Chapais, 1995); they can involve kin (e.g.

170   Riss & Goodall, 1977; Chagnon & Bugos, 1979b; Wahaj et al., 2004), non-kin (e.g. Vigilant et al.,

171   2001; Langergraber et al., 2007; Schuelke et al., 2010), and friends or acquaintances (Hruschka &

172   Henrich, 2006; Hruschka, 2010). As this brief review makes clear, coalitionary patterns are varied,

173   and understanding this diversity would be greatly enhanced by formal modeling that would allow us

174   to identify the general conditions under which coalition formation is expected to evolve, characterize

175   the degree of variability expected, and predict when coalitions should, and should not, occur. Below,

176   we summarize existing modeling approaches and highlight their main findings and predictions to

177   date.

178   **Modeling coalitions and alliances**

179   *General theoretical perspectives*

180   There exist four major mathematical theories that can provide insight into how coalitions and

181   alliances work (for more technical details see a recent review by Mesterton-Gibbons et al., 2011). Of

182   these, two have been most commonly applied to coalition formation. First, the *theory of endogenous*

183   *coalition formation* has been developed in the economics literature (Tullock, 1980; Skaperdas, 1996;

184   Skaperdas, 1998; Noh, 2002; Esteban & Sákovics, 2003; Garfinkel, 2004; Bloch et al., 2006; Sánchez-

185   Pagés, 2007; Konrad & Kovenock, 2009; Stamatopoulos et al., 2009; Tan & Wang, 2010). This theory

186   aims to predict coalitionary strategies that maximize individual fitness given a particular (ecological)

187   situation, the costs and benefits of different actions, and the information available to individuals.

188   Most existing models of coalition formation in animals belong to this general framework, which

189   overlaps with evolutionary game theory (Noë, 1990; 1992; 1994; Pandit & van Schaik, 2003; van

190   Schaik et al., 2004; 2006; Connor & Whitehead, 2005; Whitehead & Connor, 2005; Mesterton-

191   Gibbons & Sherratt, 2007; Broom et al., 2009; Okasha, 2009). We will discuss a number of these

192   models in more detail below.

193   Second, the *theory of cooperative games* models situations where players that have pooled their

194   resources attempt to come to an agreement on how to divide the spoils (von Newmann &

195   Morgenstern, 1947; Kahan & Rapoport, 1984; Myerson, 1991; Ray, 2007; Gilles, 2010). Coalitionary

196   theory using this perspective on cooperation predicts which coalitions can form and how the benefits

197   are distributed. Cooperative game theory proved to be useful in the study of human behavior, but

198   has rarely been applied to coalitions in non-human animals. This is at least partly because it remains

199   unclear how animals could negotiate without language and how any agreement could be enforced

200   (McNamara et al., 2006; Akcay & Roughgarden, 2007; Binmore, 2010). One notable exception is Noë

201   (1990), who used a veto game from cooperative game theory to explain patterns of coalition

202   formation among adult males in a group of wild baboons. In the veto game, there is a single "strong"

203   player who is able to claim (i.e., without negotiating) most of the spoils by playing other individuals

204   against each other. The power of a veto player may also be based on a unique skill, or possession of a

205   unique resource. A key player playing off two partners against each other is a situation that has been

206   described for both captive and wild chimpanzees (de Waal, 1982; Nishida, 1983; Muller & Mitani,

207   2005), and primate negotiation without language is discussed by de Waal (1996) and Melis et al.

208   (2009).

209   Third, the *theory of dynamic linking and network formation* focuses on dyadic or polyadic games

210   played by individuals in which the outcomes of previous interactions determine who interacts with

211   whom in the future (Skyrms & Pemantle, 2000; Pemantle & Skyrms, 2004a; 2004b; Hruschka &

212   Henrich, 2006; Santos et al., 2006; Pacheco et al., 2006; 2008; Gavrilets et al., 2008; Aktipis, 2011).

213   We discuss one application of this theory below.

214   Fourth, *coagulation-fragmentation theory* studies the dynamics of the population structure given

215   some simple rules concerning the mechanisms by which individuals join and leave groups (which in

216   our context can be thought of as representing coalitions). Its origins go back to a 1917 study of

217   polymers by Smoluchowski (Wattis, 2006), and have only recently found a way into the social

218   sciences (Euguíluz & Zimmermann, 2000; Bohorquez et al., 2009; but see: Cohen, 1972). This

219   promising approach will not be discussed further in this paper because it has not yet been applied to

220   coalitionary behavior in animals.

221   *Specific goals of theoretical models*

222   From a biological perspective, there are three major sets of questions that modelers aim to answer.

223   First, which strategies maximize individual fitness? Second, which coalitionary patterns are expected

224   to emerge, and how do they affect individual fitness and behavior? Third, how do the behavioral

225   rules used by individuals evolve and what are the individual and group level consequences of such

226   evolution? To illustrate how theoreticians address these questions, we discuss several recent models

227   in more detail and present their central assumptions in Table 1.

228   Fitness maximization

229   An overwhelming majority of coalitionary models focuses on determining which of a possible set of

230   coalitionary strategies maximizes individual fitness, given specific assumptions about the costs and

231   benefits to individuals, as well as the group composition and the information available to individuals.

232   Typically these models involve only three individuals. One of the oldest models is the one of

233   "minimally winning coalitions" of Riker (1962), i.e. rational players form coalitions in which the

234   pooled resources are as small as possible yet sufficient to win. In a more detailed analysis,

235   Stamatopoulos et al. (2009) investigated how differences in strength between three individuals

236   competing for a unit of divisible resource affect whether coalitions of two against one will emerge

237   and which individuals will form them. In their model, they assumed that: (a) the strength of a

238   coalition is given by the sum of the strengths of its participants, (b) the probability of winning a fight

239   (and thus obtaining the resource) is given by a logistic function of the difference in strengths, (c) a

240   winning coalition divides the reward in proportion to the strengths of the individuals in the coalition,

241   and (d) the costs of fighting are absent. Using additional assumptions about how the reward is

242   divided if no coalition is formed, Stamatopoulos et al. (2009) showed that if the strongest individual

243   is sufficiently strong relative to the weakest members, the latter should form an all-up coalition

244 against the former. If the strengths of the two strongest members are relatively close to that of the

245 weakest member, they should form an all-down coalition. In all other cases, the strongest and the

246 weakest players should form a bridging coalition against the medium-strength player. Consistent

247 with one of the model's prediction, Benenson et al. (2009) found that human subjects are

248 increasingly willing to form coalitions as their own level of perceived strength diminishes.

249 Broom et al. (2009) studied the effects of coalitionary support by kin on the stability of dominance

250 hierarchies in group-living animals. Their model considers a conflict between a high-ranking

251 individual and a challenger seeking to replace it in the hierarchy. The conflict is observed by a third

252 individual who can decide to help one of the two parties. Helpers derive only indirect fitness benefits

253 as a consequence of their relatedness to the main actors. Specifying the costs and benefits of

254 different actions, Broom et al.'s (2009) model predicts who should attack whom under which

255 circumstances. An interesting prediction is that increased variance in relatedness within a group, but

256 not the mean relatedness, makes formation of coalitions more plausible (i.e. if variance in

257 relatedness is low, regardless of the mean degree of relatedness among all individuals, coalitions will

258 not occur).

259   Using a similar approach, van Schaik and colleagues (Pandit & van Schaik, 2003; van Schaik et al.,

260 2004; 2006) aimed to predict the type of coalitions formed (i.e. all-up, bridging, or all-down; rank-

261 changing or leveling) in a group of males competing for fertilization opportunities. They considered

262 primate males living in groups of an arbitrary size, where individuals ranked in a linear hierarchy

263 compete over increases in ranks. van Schaik et al. (2004; 2006) assumed: (a) that the relationship

264 between the rank and fitness pay-off is exponential, (b) that coalitions are formed only against a

265 single target, (c) that coalition strength is given by a sum of the strengths of its participants, and (d)

266 that the stronger party always wins. Using an idealized cost parameter, van Schaik et al. (2004; 2006)

267 identified regions of parameter space where coalitions were both feasible (i.e., are stronger than the

268 target) and profitable. Building on these results, van Schaik et al. (2004; 2006) made a number of

269 testable predictions. For example, they predicted that all-up rank-changing coalitions should (a) arise

270   only in groups with a medium degree of despotism, (b) be a small coalition (two or three members),

271   (c) target the top individual, and (d) involve individuals ranking just below the target. Recent

272   empirical tests have provided support for some predictions of the Pandit/van Schaik model in

273   primate males (Jones, 2005; Bissonnette, 2009; Higham & Maestripieri, 2010; but see Kulik et al.,

274   2012), although important limitations of the approach have also been discussed (Bissonnette, 2009;

275   Berghänel et al., 2010; Young et al., 2014).

276   There is a general criticism of the optimization approach embodied in fitness maximization

277   models. Specifically, the applicability of this approach hinges on the assumption that the optimal

278   strategies identified in the mathematical models are (or closely approximate) the strategies used by

279   real individuals. How can animals know what the best strategies are? One common answer is that

280   natural selection is able to find the best strategy so that organisms have evolved to develop an

281   optimum "coalitionary psychology". Given the multiplicity and interdependence of possible

282   behaviors and the complexity of resulting evolutionary dynamics in a coalitionary context, this

283   answer is not entirely satisfactory (McNamara & Houston, 2009). Also, it is possible that the

284   optimization problem has multiple alternative solutions, which means that the most relevant

285   solution is not always obvious.

286   From behavioral rules to coalitionary patterns

287   An alternative approach is to predict group level coalitionary patterns and their effects on individual

288   fitness and behavior, given the assumptions listed above, as well as some additional assumptions

289   about how individuals interact in dyadic and polyadic conflicts. For example, using the theory of

290   dynamic linking, Gavrilets et al. (2008) examine the theoretical plausibility of an argument about the

291   role of coalitions in the "egalitarian revolution" (Boehm, 1999), which is suggested to have resulted

292   in a transition from the hierarchical societies characteristic of chimpanzees to the egalitarian

293   societies seen among human hunter-gatherers. Gavrilets et al. (2008) found support for Boehm's

294   arguments and further suggested that the transition required a change in cognitive abilities. Gavrilets

295   et al. (2008) assumed that decisions regarding whether to join a coalition were based on a simple

296   heuristic rule that utilized the relative "affinities" of a potential helper to the two individuals engaged

297   in conflict. These "affinities" reflected the history of past interactions and changed via a process akin

298   to reinforcement learning: that is, they increased following a mutually beneficial interaction and

299   decreased following an agonistic interaction. Affinities also continuously decayed to zero reflecting a

300   loss of memory by the helpers and actors (or alternatively, the discounting of distant events in the

301   past). Affinities thus represent a simple alternative to explicit fitness considerations. A particularly

302   attractive feature of Gavrilets *et al.*'s (2008) model and similar approaches (e.g. Pacheco et al., 2008)

303   is that they are scalable, i.e. they can easily be generalized to larger groups and multiple coalitions.

304   Of course this would require individuals to be able to memorize a larger number of affinities**.** One

305   serious limitation to this approach must also be emphasized, however: there is no guarantee that the

306   heuristic rules used in this and similar models are evolutionarily stable. Consequently, the

307   "coalitionary psychology" postulated in these models is, potentially, biologically irrelevant. This is

308   clearly an area on which empirical research can shed more light by testing which decision rules are

309   used in coalitionary conflicts.

310   Evolution of behavioral rules and its consequences

311   Analysis of evolutionarily stable strategies has been an extremely important tool in theoretical

312   studies of animal behavior (Maynard Smith, 1982). There are, however, only a few models that

313   explicitly study the emergence of evolutionarily stable behavioral rules in a coalitionary context (thus

314   combining the two approaches outlined above). These models make specific assumptions with

315   respect to possible coalitionary strategies, their costs and benefits, the information available to

316   individuals, and the behavioral rules followed by individuals**.** Mesterton-Gibbons and Sherratt

317   (2007), for example, consider competition among three individuals in a setup similar to that of

318   Stamatopoulos et al. (2009) and Broom et al. (2009). A crucial novel feature of their model, however,

319   is the assumption that individuals differ with respect to a genetically controlled trait ("alliance

320   threshold") that determines whether an individual seeks coalitionary aid (if his strength falls below

321   threshold) or goes it alone (if his strength exceeds threshold). Mesterton-Gibbons and Sherratt

322   (2007) also allow for incomplete information about the strengths of other individuals, for

323   dependence of fighting costs on the strengths of competitors, and for synergy/antergy between

324   individual strengths in determining pooled strength. They investigated how evolutionarily stable

325   alliance threshold values (which determine evolved "coalitionary psychology") depend on various

326   parameters of their model. In particular, they predicted that 2-versus-1 coalitions are more likely to

327   occur when (a) the reliability of strength as a predictor of contest outcome is high, (b) there is high

328   variation in fighting strengths, and counterintuitively (c) when the effective strength of a coalition is

329   less than the sum of its individual strengths (see also Mesterton-Gibbons & Sherratt, 2009; Gavrilets,

330   2012). Using similar methods for identifying evolutionary stable behaviors in various coalitionary

331   contexts would greatly inform the theory (but will likely be quite challenging mathematically).