

# Factors affecting individual participation in group-level aggression among non-human primates

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## Summary

Group members do not always act cohesively when facing extra-group rivals. When benefits such as group-defence are not monopolizable, it poses an economics problem: who should contribute to public goods and who should freeload? A collective action framework complements existing theoretical explanations for cooperation, and provides testable hypotheses about group-level behaviour based on individual costs and benefits. Using this approach, we review research on intergroup encounters in non-human primates published over the last 20 years, focusing on participation by different classes of individuals. While food- and mate-defence explain much between-sex variation in participation, rank and reproductive access frequently explain within-sex variation. In some species, individuals may use intergroup interactions to survey potential transfer locations and mating options, which might coincidentally intimidate rivals. Experimental evidence suggests that when intergroup dominance is based on relative number of fighters, individual participation still varies with sex, rank, companion behaviour and dependent offspring presence. Relatively few studies have examined how factors such as relationships within and between groups or individual temperament mediate aggression. Long-term studies of multiple habituated groups and methodological advances (e.g., playback experiments) will continue to improve our understanding of how complex group-level patterns are predictable when viewed from an individual perspective.

*Keywords:* intergroup encounters, competition, cooperation, collective action problems, primates.

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## Introduction

Although the phrase ‘intergroup aggression’ might conjure up an image of animals lined-up along their territory boundary, standing shoulder-to-shoulder with their group-mates against a common foe, this is rarely the case. Groups do not always, or even often, act as cohesive, cooperative units against extra-group animals, even when all members would benefit from excluding rivals.

How individuals respond when facing extra-group rivals can vary within a species and even among members of the same group. For example, when groups of black howler monkeys (*Alouatta pigra*) meet, the respective alpha males will often display, but whether they are joined by any or all of their group mates varies from group to group and from encounter to encounter (Kitchen, 2004). Conversely, all members are typically involved in aggressive interactions between groups of common marmosets (*Callithrix jacchus*), although strength of the response varies with sex and rank of the defender and sex of the intruder (Lazaro-Perea, 2001).

We are interested in the factors that promote participation by different classes of individuals in group-level contests. Group-defence provides a non-monopolizable, shared benefit to the entire group; consequently, some individuals will act as freeloaders, reaping the collective benefits without contributing (e.g., Nunn, 2000). Because members of a group do not share the same interests in thwarting competitors, nor do all individuals suffer the same costs if fighting erupts, group-level patterns are best understood using an individual-level cost-benefit analysis (reviewed in Nunn & Lewis, 2001). However, quantifying individual differences in participation, identifying the targets of aggression, and determining the outcome of a contest amid the chaos of an intergroup encounter is challenging and sometimes impossible. Two decades ago, Cheney (1987) reviewed the published literature on intergroup interactions in non-human primates. Although she summarized intersexual differences in participation in group-defence, intra-sexual data were only available from a few species. To rectify this, Cheney called for more research focusing on individual-level participation (or lack thereof) in extra-group conflicts. Our aim was to search the recent literature for studies that adopted this approach.

We begin with a brief review of theoretical cooperation models. Then we examine empirical data on the effects of resource distribution, rank, reproductive investment, relationships within and between groups, and the number

of rivals faced on individual participation in intergroup encounters. Although by no means an exhaustive list, Table 1 summarizes some of the major predictions and some of the best supporting examples found in the literature for each hypothesis discussed below.

The diverse forms of sociality represented and the number of long-term field studies makes the primate order ideal for a review on individual decision-making in a group context, whereas space constraints limit our coverage of other social animals. We include primate species not traditionally considered territorial (see Mitani & Rodman, 1979), and we use terms such as ‘extra-group animals’ or ‘intergroup encounters’ broadly to include single-males or coalitions of males attempting a ‘takeover’ along with interactions between reproductive units. Individuals are considered to participate in group-defence if they join in displays (e.g., loud calling, posturing), chases, or fights with rivals. Because methods such as staged contests and playback experiments overcome some logistic difficulties of studying multiple individuals simultaneously, we highlight such research.

### **A ‘collective action’ framework**

In the well-known children’s story, the Little Red Hen tries (in vain) to get help from the goose, the cat, and the pig to sow the seeds, reap the wheat, and make the bread. They offer her no assistance until it comes time to eat the bread. But, because the bread is monopolizable, the Little Red Hen is able to deny them any supper as punishment for their failure to participate earlier. In contrast with a loaf of bread, some advantages of living in a group (e.g., group-defence, predator avoidance, group hunting, cooperative breeding) are not monopolizable, and some individuals could reap these collective benefits without paying the costs of participating. If too many group members fail to chip in, the result is a ‘collective action problem’; in other words, extensive ‘free riding’ means collective goods are not optimised. This poses an old economics problem (e.g., Ostrom, 2001): which, if any, individuals will contribute to public goods and which will be free riders? This theoretical approach has recently been co-opted by behavioural ecologists to address individual decision-making in a group context (van Schaik, 1996; Nunn, 2000; Nunn & Lewis, 2001), and we used many of the ideas provided by these authors to frame our review.

**Table 1.** Self-serving reasons for individuals to participate in intergroup encounters and supporting examples in non-human primates.

| Factor                     | Hypothesis   | Predictions  | References                          |
|----------------------------|--|--|-------------------------------------|
| Sex                        | Males participate to defend mates  | <ul style="list-style-type: none"> <li>- Participate most when oestrous females present or female-to-male sex ratio high</li> <li>- Herd females away from rivals and target oestrous females</li> <li>- Direct intergroup aggression at same sex rivals (especially potential immigrants)</li> </ul>                  | 4, 5, 6, 11, 14, 19, 24, 42         |
|                            | Males participate to defend food resources for females                                   | <ul style="list-style-type: none"> <li>- Participate most when food and females defensible in time and space</li> <li>- Direct intergroup aggression at both sexes</li> <li>- Most likely in single-male, female transfer species</li> </ul>   | 5, 6, 10, 40                        |
|                            | Females participate to defend food resources   | <ul style="list-style-type: none"> <li>- Participate most when food valuable and defensible in time and space</li> <li>- Direct intergroup aggression at both sexes</li> <li>- Most likely in female philopatric, female-bonded species</li> <li>- Least likely in sexually dimorphic, infanticidal species</li> </ul> | 6, 16, 21, 35, 37, 42               |
| Rank & reproductive access | Participate based on rank and/or reproductive access                                     | <ul style="list-style-type: none"> <li>- Participate most when high-ranking</li> <li>- Participate most when reproductive access high</li> <li>- Participate most when an immigrant would directly impact own rank position</li> </ul>   | 4, 11, 14, 18, 19, 21, 24, 25, 42   |
| Mating opportunity         | Participate to assess other group before transferring or to gain extra-group copulations | <ul style="list-style-type: none"> <li>- Incursions made by potentially transferring animals</li> <li>- Potentially transferring animals affiliative to rival group</li> <li>- More likely when new group has improved reproductive opportunities</li> </ul>   | 11, 14, 16, 17, 18, 19, 22, 28, 42  |
| Reproductive investment    | Change behaviour based on potential infanticide  | <ul style="list-style-type: none"> <li>- Participate most when small, vulnerable offspring present</li> <li>- Females retreat when have dependent offspring</li> <li>- Males commit intergroup infanticide to recruit mates</li> </ul>   | 1, 6, 7, 12, 17, 23, 27, 36, 38, 39 |

Table 1. (Continued).

| Factor                     | Hypothesis  | Predictions   | References     |
|----------------------------|---|---|----------------|
| Intergroup dominance       | Participate based on chances of winning an encounter                      | – Participate most when in dominant group   | 2, 4, 12,      |
|                            |   | – Participate most when own group large   | 13, 14, 20,    |
|                            |   | – Participate least when own group outnumbered by rivals                                | 32, 33, 41     |
|                            |   | – Participate most when relative numbers even or own group outnumbered by rivals        |                |
| Intergroup relationships   | Participate based on experience with opposing group                       | – Participate least when relatedness to rival high                                      | 3, 8, 9, 26,   |
|                            |   | – Participate least when rival familiar   | 29, 36         |
| Intra-group relationships  | Participate based on behaviour of & relationship with other group members | – Participate most when companions assist   | 12, 15, 21,    |
|                            |   | – Participate most when related to companions   | 33             |
|                            |   | – Participate most when have strong bond or long association with companions            |                |
| Individual characteristics | Participate based on individual factors                                   | – Possibilities: age & experience; fighting ability; physiological state; 'personality' | 15, 18, 19, 30 |

References: <sup>1</sup>Hanuman langurs, Borries (1997); <sup>2</sup>Cheney (1987); <sup>3</sup>vervets, Cheney & Seyfarth (1983); <sup>4</sup>bonnet macaques, Cooper et al. (2004); <sup>5</sup>guereza colobus, Fashing (2001); <sup>6</sup>Fashing (2001); <sup>7</sup>capuchins, Fragaszy et al. (2004); <sup>8</sup>lion tamarin, French & Inglett (1989); <sup>9</sup>Wied's marmoset, French et al. (1995); <sup>10</sup>guereza colobus, Harris (2006); <sup>11</sup>chacma baboons, Henzi et al. (1998); <sup>12</sup>black howlers, Kitchen (2004); <sup>13</sup>Kitchen (2006); <sup>14</sup>chacma baboons, Kitchen et al. (2004a); <sup>15</sup>black howlers, Kitchen et al. (2004b); <sup>16</sup>black and white colobus, Korsjens et al. (2005); <sup>17</sup>olive colobus, Korsjens & Nde (2004); <sup>18</sup>common marmosets, Lazaro-Perea (2001); <sup>19</sup>Japanese macaques, Majolo et al. (2005); <sup>20</sup>chimpanzees, Mitani & Watts (2005); <sup>21</sup>ring-tailed lemur, Nunn & Deaner (2004); <sup>22</sup>gray-cheeked mangabey, Olupot & Waser (2005); <sup>23</sup>chacma baboon, Palombit et al. (2000); <sup>24</sup>blue monkey, Payne et al. (2003); <sup>25</sup>white-faced capuchin, Perry (1996); <sup>26</sup>white handed gibbon, Reichard & Sommer (1997); <sup>27</sup>Geoffroy's colobus, Saj & Sicotte (2005); <sup>28</sup>Wied's marmoset, Schaffner & French (1997); <sup>29</sup>capped langur, Stanford (1991); <sup>30</sup>Thomas langurs, Steenbeek (1999); <sup>31</sup>Steenbeek et al. (1999); <sup>32</sup>Japanese macaques, Sugura et al. (2000); <sup>33</sup>chimpanzees, Watts & Mitani (2001); <sup>34</sup>Watts et al. (2006); <sup>35</sup>mantled howlers, Whitehead (1989); <sup>36</sup>Thomas langurs, Wich et al. (2002a); <sup>37</sup>Wich et al. (2002b); <sup>38</sup>Wich et al. (2004); <sup>39</sup>Wich et al. (2003); <sup>40</sup>chimpanzees, Williams et al. (2004); <sup>41</sup>Wilson et al. (2001); <sup>42</sup>Tibetan macaques, Zhao (1997).

Public radio is often used as an example of a collective action problem (e.g., Nunn & Lewis, 2001). Public radio depends on membership dues from listeners, yet anyone can listen to a public radio station. There are no mechanisms to impugn those who do not pay membership dues. Still, if no one paid for public radio it would go off the air. Is it worth it for one or a few individuals to pay? If so, we would expect that these individuals would be either (1) those that benefit the most from having public radio available or (2) those for whom the costs of contributing are relatively low (Nunn, 2000).

Several explanations address why defectors might be tolerated in a group. First, freeloaders must be detected – an act which requires constant monitoring – and individuals must remember the previous behaviour of companions. This is confounded by the fact that cooperation is not an ‘all or nothing’ behaviour – a person could donate a few pennies to public radio and still be considered a donor. It might be difficult for animals (or human observers for that matter) to differentiate such ‘weak freeloaders’ (those not contributing at a level equivalent to benefits received: Nunn, 2000) from truly cooperative companions.

Second, even if animals can identify defectors in their midst, it might be impossible to oust or even punish them (e.g., Clutton-Brock & Parker, 1995). Whether dominant animals actually ‘police’ and coerce non-cooperators, or withhold future cooperation, has rarely been studied empirically (e.g., Flack et al., 2005). Among free-living lions (*Panthera leo*), Heinsohn & Packer (1995) demonstrated that females could identify but did not apparently punish freeloaders during encounters with simulated intruders. Perhaps this is because punishment itself is costly (e.g., retaliation). Taking this even further, because the benefits of enforcing cooperation cannot be monopolized, whether policing occurs is itself a collective action problem (reviewed in Nunn & Lewis, 2001).

Third, non-kin, defecting companions may be tolerated when animals have a stake in preserving their group’s size; for example, when large groups are necessary for predator avoidance (stakeholder altruism: Roberts, 2005). Finally, freeloaders in one situation might be cooperators in another (reviewed in Nunn & Deaner, 2004). For example, while non-breeding noisy miners (*Manorina melanocephala*) assist parents at the nest, they often specialize either in provisioning young or in attacking nest predators but rarely do both (Arnold et al., 2005).

By whatever means, collective action problems are sometimes overcome: public radio remains available and group-defence is, at least occasionally, provided. But, which individuals should be most likely to defend the group? To what extent will defenders participate? What factors influence individual strategies?

Theoretical models of cooperation are useful in building testable predictions, in quantifying fitness payoffs, and in identifying possible strategies used by animals in natural contests (Maynard Smith, 1982). At one end of the spectrum are traditional games (reviewed in Nunn & Lewis, 2001; Doebeli & Hauert, 2005), which, at their simplest, involve two equally-matched players making moves simultaneously, each choosing among a few discrete strategies. The three commonly used games (prisoner's dilemma, mutualism, and chicken/snowdrift/hawk-dove) differ only in their payoff matrices (set of rewards that are determined by what each contestant 'plays'). Overall these games have contributed a great deal to what we know about cooperation in dyadic contests. If all animals within a group had the same costs and benefits and always acted in a unified manner, we could also use simple two-player games to model group-level behaviour (e.g., Maynard Smith, 1982), but this is rarely the case.

Collective action is a useful framework for predicting individual behaviour in a group context, but as a quantitative modelling tool it is limited in that it does not explicitly define unique games; rather, it must build on existing models, inevitably adding complexity to increase realism. For example, models are more realistic if they permit contestants with asymmetric abilities (reviewed in Maynard Smith, 1982), multiple contestants (reviewed in Doebeli & Hauert, 2005), iterated play (e.g., Stephens et al., 1995), and sequential rather than simultaneous play (giving players the option to monitor their opponent; e.g., Kun et al., 2006). Other improvements include games that allow for continuous rather than discrete strategic options (e.g., Roberts & Sherratt, 1998; Killingback & Doebeli, 2002), mistakes (e.g., Boyd, 1989), variations that make additional cooperators more or less effective (e.g., Hauert et al., 2006), asymmetric costs and benefits among players within groups (e.g., Nunn & Lewis, 2001), an influence of past experience (e.g., Hsu & Wolf, 1999) or reputation (e.g., Panchanathan & Boyd, 2004), and additional benefits to cooperators via honest signalling of quality (e.g., Gintis et al., 2001). Simplicity is lost at this end of the spectrum, where a game may include several of these improvements.

In sum, traditional two-player games modelling cooperation and competition are simple to understand and apply, but have limited applications to group-level situations (e.g., Heinsohn and Packer, 1995). Other models more accurately represent the group-defence problem, but are so complicated as to be virtually impossible for empiricists to apply to natural systems. We, therefore, frame this review using a verbal collective action model, which is conceptually easy to work with, yet still allows us to form testable hypotheses (Table 1). For example, collective action theory predicts that if costs and benefits are distributed unevenly within a group, the 'privileged' members – who receive the greatest benefits or suffer the fewest costs – should provide the service, while others should attempt to freeload (Nunn, 2000; Nunn & Lewis, 2001).

We recognize that a collective action approach is not a replacement for other theoretical explanations of cooperative behaviour (kinship, by-product mutualism, or reciprocity: Dugatkin, 1997). Rather, it is complimentary and simply reminds us that complex and seemingly coordinated group-level patterns are probably nothing more than the result of individual decisions.

## **Review of empirical data**

### *Effect of sex and limiting resources*

Beginning with anisogamy, the differences between the sexes have important consequences on social systems. Whereas female fitness is limited by access to food resources, male fitness is limited by access to females (Trivers, 1972; Emlen & Oring, 1977). Males are, therefore, more likely to develop exaggerated, sexually dimorphic traits such as body size, weaponry, and aggressive tendencies with which they compete over access to females. Male participation in intergroup encounters has, therefore, been hypothesized to function as direct mate-defence, indirect mate-defence via protection of resources for females, or infant-defence in infanticidal species. None of these functions are necessarily mutually exclusive. Conversely, females should defend food resources or infants, but not mates.

An excellent recent review by Fashing (2001) summarizes the evidence in support of these different functions for intergroup aggression in primates, and points out how few long-term projects have systematically tested each hypothesis. Here we highlight those factors that influence variation among or within groups in intergroup aggressive behaviour.

### Male mate-defence hypothesis

If mate-defence can explain variation in male participation in intergroup aggression, then contests should escalate more often (1) when oestrous females are present, and (2) when the female–male sex ratio or overall number of females is high. Additionally, (3) males should herd their own females away from extra-group males, targeting oestrous females in particular.

These predictions have been supported in a number of primate species (e.g., Japanese macaques (*Macaca fuscata*), Majolo et al., 2005; bonnet macaques (*M. radiate*), Cooper et al., 2004; blue monkeys (*Cercopithecus mitis*), Payne et al., 2003; other species reviewed in Fashing, 2001). For example, in chacma baboons (*Papio ursinus*) males frequently produce loud call displays when two groups meet, and reports from three independent sites in southern Africa (Cowlshaw, 1995; Henzi et al., 1998; Kitchen et al., 2004a) suggest that displays function in mate-defence. Males frequently chase female members of their own group away from rival groups, targeting those in oestrus. Further, when oestrous females are absent, male loud call displays are shorter in duration, involve fewer participants, are less intense, and are more likely to result in peaceful mingling between groups.

The mate-defence hypothesis also predicts that aggression between groups should be largely intra-sexual. Support for this is particularly strong among the cooperatively breeding callitrichids (e.g., golden lion tamarins (*Leontopithecus rosalia*), Baker & Dietz, 1996; French & Inglett, 1989; Wied's black tufted-ear marmosets (*Callithrix kuhli*), Schaffner & French, 1997; common marmosets: Lazaro-Perea, 2001). However, in species with female transfer or frequent extra-group copulations, males might focus some of their attention on chasing extra-group females to gain additional mates. For example, although the majority of intergroup chases are between males in white-handed gibbons (*Hylobates lar*, Reichard & Sommer, 1997), a small fraction of males direct aggression at females from the opposing group, and it is possible that these are attempts to coerce females into mating.

Most species studied have demonstrated at least some evidence of male mate-defence (but see olive colobus (*Procolobus versus*), Korstjens & Noë, 2004). However, group-defence is not always optimized, particularly in large, multi-male groups. For example, male Tibetan macaques (*M. tibetana*, Zhao, 1997) do not increase their aggression toward other groups during the mating season, and although they herd females away from opposing groups, half of encounters still result in mating between groups. Such

examples could reflect collective action problems that, at least from the male standpoint, are not overcome. Because opportunities to freeloader increase with group size, it is not surprising that aggressive responses to extra-group animals diminish, particularly when male reproductive access (the collective benefit) is partially determined by scramble competition (reviewed in Nunn, 2000).

Rarely do males in multi-male groups act in unison when facing extra-group competitors. Thus, it is difficult to distinguish male mate-defence patterns that are 'intergroup' aggression (an action with collective benefit) from those that are simply male-male competition. For example, Fragaszy and colleagues (2004, p. 218) suggest that male-driven agonism in capuchins (*Cebus* spp.) is, "not so much between groups as between clumps of males". Additionally, in baboons, Kitchen and colleagues (2004a, p. 214) report that, "males treat extra-group and intra-group rivals similarly". However, even if intergroup male aggression functions solely as mate-defence, females could still receive a benefit if these displays, for example, thwart competitor attempts at accessing a contested resource. In such cases, when male mate-defence simultaneously drives away food competitors, males act as 'hired guns' for females (Rubenstein, 1986; Wrangham & Rubenstein, 1986). In other words, females can freeloader off the collective benefit provided by males (e.g., Nunn & Lewis, 2001; Cooper et al., 2004; Majolo et al., 2005). Even in species like gorillas (*Gorilla gorilla*), where female competition over food is low (but see Bermejo, 2004), mate-defence by males might coincidentally provide females with protection from potentially infanticidal outsiders (Watts, 1989). In this way, group-defence can be provided by the selfish behaviour of individuals.

#### Male resource-defence hypothesis

If male participation in intergroup encounters is due to defence of food resources that benefit females, then male responses should vary based on territory quality, resource distribution in space and time, and location within a home range. Additionally, males would be expected to chase both male and female rivals, and not necessarily herd their own females away from other groups.

The male resource-defence hypothesis has not received the same attention or support as the mate-defence hypothesis (e.g., Geoffroy's colobus (*Colobus*

*vellerosus*), Sicotte & Macintosh, 2004; black and white colobus (*C. polykomos*), Korstjens et al., 2005; others reviewed in Fashing, 2001). It may be that male primates rarely use resource attraction to increase their reproductive success. However, a review by Fashing (2001) suggests an alternative – namely, that more cases have not been uncovered because only a few long-term studies had been designed to systematically test this question. Fashing suggests that male resource-defence should occur when (1) food is limiting and defensible, (2) females transfer and are defensible (e.g., asynchronous breeders in small groups) and (3) groups contain one male (i.e., defender is guaranteed reproductive benefits). These conditions are met in guereza (*C. guereza*), and Fashing (2001) found evidence that male aggression toward extra-group rivals functions in resource-defence. Guereza males are significantly more likely to perform their most intense aggressive displays when the encounter occurs in a quadrant used with high frequency during monthly feeding analyses (see also Harris, 2006).

Williams and colleagues (2004) conclude that male chimpanzees also protect the food resources of their community's females. Using nearly 20 years of data on one community of chimpanzees (*Pan troglodytes*), they report that males attack extra-group individuals of both sexes, and that range expansion correlates with increased female reproductive success rather than with the number of females in the group. Additionally, in a meta-analysis of 42 ethnographic studies of human foraging societies, Manson and Wrangham (1991) found evidence that males defend resources (rather than females) when resources are monopolizable. The authors also suggest that resource-defence functions to attract women because of the correlation they found between wealth accumulation and polygyny in these systems, but not in female-defence systems. However, even if resource-defence explains some species-level variation in male aggression, it is unlikely to be the sole explanation for why some individual males participate more than others within the same species.

If males defend food resources to attract mates, it is possible that females 'pay back' contributing individuals in some manner. For example, female white-faced capuchins (*Cebus capucinus*) only excitedly greet returning resident males if they win an intergroup encounter (Perry, 1996). Similarly, female bonnet macaques in two separate populations preferentially mate with and groom the males that participate most in intergroup aggression (Cooper et al., 2004), although the authors point out that this pattern could also be

related to the high rank of participating males. Such a commodity exchange (Noë & Hammerstein, 1995) could be confirmed using playback experiments (e.g., Seyfarth & Cheney, 1984).

#### Female resource-defence hypothesis

Although females are often victims or bystanders who do not participate at all during intergroup encounters, they can be equally or more involved than males (e.g., blue monkeys, Payne et al., 2003; vervets (*Chlorocebus aethiops*), Cheney, 1992; Hanuman langurs (*Semnopithecus entellus*), Borries, 1993; ring-tailed lemurs (*Lemur catta*), Sauther et al., 1999; black and white colobus, Korstjens et al., 2005).

Given that nutrition limits female fitness (Trivers, 1972), female involvement in intergroup encounters with or without male accompaniment should occur more frequently when food resources are 'economically defensible' (Brown, 1964). Brown's classic model predicts that animals should defend a site or territory when population densities are intermediate, because active defence is not cost-effective when intrusion rates are too high or low. Similarly, it is more cost-effective to defend food that is valuable and clumped rather than low quality and uniformly distributed.

Closely following these predictions, Kinnaird (1992) reports a strong *seasonal* influence on responses of female Tana River mangabey (*Cercocebus galeritus*) to other groups. Groups are most likely to merge peacefully during seasons when patchy resources are rare and uniformly distributed resources are common, avoid each other in seasons when all food is low in abundance, and be highly aggressive when food is patchily distributed and, thus, defensible. Harris (2006) reports a site-dependent pattern in guereza colobus; both sexes are more aggressive in the core of their range, which has more abundant and higher quality resources compared to the periphery.

Resource distribution in time and space also explains behavioural variation in other studies (Whitehead, 1989; Zhao, 1997; Sauther et al., 1999; Wich et al., 2002b; Nunn & Deaner, 2004; Korstjens et al., 2005). However, female involvement in intergroup encounters is not universally explained by resource-defence (e.g., Cooper et al., 2004; see Fashing, 2001). Furthermore, resource-defence by males or females remains notoriously hard to recognize because of difficulties in (1) establishing resource phenology and assessing habitat quality, (2) identifying which resource most limits a species and (3) finding causal links between resources and intergroup aggression.

## Socioecology and female group-defence

Wrangham's (1980) classic paper suggested that when resources are limiting and patchy in distribution, a group of female primates could cooperatively defend a clump against another group. Because cooperation would most likely necessitate bonding among females, Wrangham predicted that group-defence would occur more often in primate species where philopatry allows females to form social bonds with kin. Many empirical studies support this hypothesis (Manson and Wrangham, 1991; Fashing, 2001). However, in some species with female philopatry, females rarely or never join males in overt aggression directed at other groups (e.g., moor macaques (*M. maurus*), Okamoto & Matsumura, 2002; baboons, Cowlshaw, 1995). Similarly, in the human foraging societies reviewed by Manson and Wrangham (1991), the occurrence of monopolizable resources never led to the formation of bonded groups of women defending themselves.

Although the effects of food distribution, competition and female bonding are likely main factors in determining whether females will take part in group contests (e.g., van Schaik, 1989; Cheney, 1992; Sterck et al., 1997), sexual dimorphism may also act as a constraint on females in many species (Packer & Pusey, 1979; see also social carnivores: Boydston et al., 2001). Costs would be amplified for pregnant and lactating females due to increased energetic demands (e.g., Lazaro-Perea, 2001) and infanticide. Although a meta-analysis of 21 non-human primate species found no support for sexual dimorphism as an explanation of reduced female participation (Manson & Wrangham, 1991), this analysis included multiple species from the same genera (see Harvey & Pagel, 1991) and female-dispersing species in which no resource-defence is expected. Thus, it remains possible that females avoid physical confrontations with males in species where male–female size disparities make intersexual aggression especially risky. In fact, although female resource-defence predicts that females direct their aggression equally at competitors of both sexes (e.g., Japanese macaques: Saito et al., 1998), females in many species direct their aggression only at same-sex rivals (e.g., French & Inglett, 1989; Baker & Dietz, 1996; Schaffner & French, 1997; Lazaro-Perea, 2001; Korstjens et al., 2005).

Whether females dominate during intergroup aggression, join males, or have no response to intruders appears to be regulated by a number of factors. Participation by females is more likely (1) for female-philopatric species, (2)

when at least loose bonds exist among female group members, (3) in areas with defensible resources, high between-group competition and low within-group competition, (4) when facing female rather than male competitors (particularly in sexually dimorphic and infanticidal species) and (5) when there is no option to freeloader off male group-defence. These general trends, however, are more likely to explain group-level variation in responses. We now consider factors such as rank and mating opportunities that might better explain variation among females within a group.

#### *Effect of rank and resource access*

A strong rank effect on participation could eliminate the collective action problem of group-defence. High-ranking males and females have 'more to lose' in intergroup contests in that they typically have the best access to food or mates. Additionally, high-ranking individuals are probably in the best physical condition – they either occupy their position due to superior fighting ability or from their position they get the best access to food. These 'privileged groups', individuals that profit the most and suffer the fewest costs, should be the most likely to provide group-defence (Cheney, 1987; Nunn, 2000). Additionally, individuals of all ranks should act to thwart intruders if their own rank position or their immediate reproductive access is directly threatened (Nunn, 2000).

Indeed, rank explains behavioural variation in several species (capuchins, Frigaszy et al., 2004; Tibetan macaques, Zhao, 1997; blue monkeys, Payne et al., 2003; black howlers, Kitchen, 2004; ring-tailed lemurs, Nunn & Deaner, 2004; bonnet macaques, Cooper et al., 2004). For example, high-ranking male chacma baboons are more likely than low-ranking males to join intergroup loud call displays, produce more intense displays, and herd females away from the other group. Further, regardless of rank, male baboons in an exclusive consortship with an oestrous female are more likely to display at rival groups than males without immediate reproductive access (Kitchen et al., 2004a). Likewise, high-ranking but not low-ranking female Japanese macaques are aggressive to both sexes of extra-group rivals, and male rank is also linked to intergroup aggression during the mating season (Majolo et al., 2005).

Thus, collective action problems are solved in several species because the animals reaping the benefits are the ones providing the service. Although it

is likely an integral factor in individual participation in intergroup encounters, surprisingly few studies in the past 20 years have published results of participation by rank.

#### *Intergroup contact as mating opportunities*

There are incentives to interacting with members of other groups besides thwarting potential competitors from immigrating or from using resources. For example, individuals may participate in intergroup encounters merely to survey the mating opportunities in another group (e.g., brown jays (*Cyanocorax morio*), Hale et al., 2003). Evidence in some primate species suggests that animals make transfer decisions based on the composition of their future group (chacma baboons, Henzi et al., 1998; grey-cheeked mangabey (*Lophocebus albigena*), Olupot & Waser, 2005). Aggressive intrusions by potentially transferring males might also be a means to test the fighting ability of rivals and thereby assess the likelihood of climbing the dominance hierarchy should they transfer (e.g., chacma baboons: Kitchen et al., 2004a). Thus, visits to other groups could intimidate potential rivals and coincidentally benefit a male's current group, even though such forays are likely self-serving reconnaissance missions.

Another tactic for animals attempting transfers is to forge affiliative relationships with members of other groups. Under this strategy, we expect that the individuals most likely to transfer might be the least likely to provide group-defence for the current group. For example, affiliative interactions with the other group frequently involve low-ranking, subadult males (e.g., Japanese macaques, Majolo et al., 2005), or oestrous females in female transfer species (e.g., olive colobus, Korstjens & Noe, 2004; black and white colobus, Korstjens et al., 2005). Diminished aggression toward strangers might also function as a 'recruitment incentive' (Schaffner & French, 1997). In experiments on cooperatively breeding Wied's marmosets, where reproductive success is related to group size, breeders from small groups with few helpers are less likely to be aggressive to intruders than breeders in large groups.

An excellent example in common marmosets combines these ideas: Lazaro-Perea (2001) reports that the oldest among the non-breeding subordinates engage in both aggressive and sexual behaviour with members of other groups more than their younger group-mates. The author suggests this

is due to conflicting strategies – the oldest non-breeders are next in queue to become alpha (and, thus, have much to gain by defending the group), yet they also have a lot to lose compared to younger animals if they must delay their own reproduction another year. Therefore, their behaviour likely represents a trade-off and, although it might effectively defend the group, the tactic is self-serving.

#### *Protecting reproductive investments*

In non-seasonally breeding species with long lactation periods, infanticide is hypothesised to be an adaptive strategy to increase male reproductive opportunities (e.g., Hrdy, 1979), and can occur during takeover attempts or when two bisexual groups meet. Although only systematically examined in a few species, infant-defence explains some of the variation in male–male aggressive behaviour within and between groups (e.g., Hanuman langurs, Borries, 1997; chacma baboons, Palombit et al., 2000; Geoffroy's colobus, Saj & Sicotte, 2005). Likewise, lactating females in some species apparently change their behaviour based on infanticidal pressure, either retreating with (e.g., olive colobus, Korstjens & Noë, 2004) or defending their small offspring against extra-group threats (e.g., capuchins, Fragaszy et al., 2004; Thomas langurs, Steenbeek, 1999; but see black howlers, Kitchen, 2006). In some species, infanticidal attempts encourage female transfer and this might explain variation in male intrusion rates during intergroup encounters (e.g., black and white colobus, Korstjens et al., 2005; reviewed in Fashing, 2001).

Because these events are so rare, data on the impact of infanticidal threats on individual behaviour are slow to accumulate. Playback experiments offer a way to simulate takeover attempts and quantify male and female responses to potentially infanticidal intruders (e.g., Palombit et al., 1997). For example, the pioneering playback work on lions demonstrated that females were able to differentiate familiar from potentially infanticidal males and respond appropriately based on offspring presence (McComb et al., 1993). However, this experimental approach has only been used on a few primate species.

Like lions, intruding male black howlers may kill dependent infants following a successful group takeover. Following playbacks simulating unfamiliar males, Kitchen (2004) found that alpha male howlers had stronger responses when small infants were present in their group. In contrast, the presence of vulnerable infants had no effect on subordinate male howlers,

likely due to high male reproductive skew (Kitchen et al., 2004b). As predicted, protecting a reproductive investment seems to explain the willingness of individuals to defend the group, even when others do not assist.

Thomas langurs also face infanticide attempts from extra-group males (Steenbeek, 1999). Although female Thomas langurs are never aggressive during encounters with bisexual groups, they do defend their infants when attacked by an invading male, occasionally forming coalitions with other females. In playback experiments, following broadcast of unknown and potentially infanticidal males, females with small infants were less likely to approach the simulated calls and more likely to reduce mother-offspring distance than following playback of known males (Wich et al., 2002a). Furthermore, Wich and colleagues (2002a,b, 2003, 2004) report that resident male Thomas langurs exhibited stronger responses to playbacks simulating infanticidal intruders. Based on this and observational evidence (Steenbeek et al., 1999), researchers conclude that variation in male behaviour during intergroup encounters is at least partially a function of infanticide avoidance.

These data suggest collective group-defence benefits are often provided by individuals with a current reproductive investment, whose fitness would be most affected should a potentially infanticidal male join the group.

#### *Effect of intergroup dominance*

A group's overall ability to dominate another may influence the behaviour of its members. For example, Cooper and colleagues (2004) observed that in a subordinate group of bonnet macaques (consistently supplanted by neighbouring groups), females never joined displays and often fled. Yet, in a dominant group, females never fled and occasionally joined males in aggression directed at rival groups. Whether these observed differences in female macaque behaviour were the cause or effect of intergroup dominance remains unclear.

Although intergroup dominance has clear short-term benefits, long-term benefits are more difficult to quantify. However, in an extensive comparative habitat study across groups of guereza, Harris (2006) reports a strong correlation between the quality and quantity of food in a home range and the intergroup dominance rank of a group.

The size of a group – one possible determinant of intergroup dominance – may affect behaviour regardless of the number of rivals faced. For example,

feeding party size is the best predictor of whether a dangerous boundary patrol will form in chimpanzees (Mitani & Watts, 2005). In human children, Beneson and colleagues (2002) designed a study of behavioural responses to group size. Although relative team size was held constant during games (large groups were pitted against other large groups, small against small), kids in both winning and losing groups were more assertive if they were members of large rather than small groups. A similar phenomenon occurred when Tanner (2006) staged contests between two species of ants (*Formica* spp.). Despite significant size differences, single subjects from the smaller species were aggressive to the larger species, but only if the smaller subjects originated from a dense home cage population (in the wild, the smaller species often 'gang attack' the larger species). Thus, the experience of living in a group with some critical mass had at least a short-term effect on the smaller species when pitted one-on-one against the larger.

More than just the size of an individual's own group, relative group size should also influence behaviour in asymmetric encounters: because fighting is costly to both winners and losers, evolutionary game theory predicts that animals should assess their relative fighting ability and avoid contests they are likely to lose (e.g., Maynard Smith, 1982). Although some observational data in primates suggests larger groups displace smaller groups (e.g., Sugiura et al., 2000; reviewed by Cheney, 1987; but see Harris, 2006), it is often unclear whether retreating groups actually *assess* relative group size and avoid larger groups, or if they are simply physically forced to leave by their more numerous competitors. Additionally, natural observations are typically restricted to neighbouring groups, making it difficult to determine if individuals are influenced by previous experience with members of the opposing group rather than relative group size. Playback experiments allow researchers to control for such confounding effects, in cases where loud calls reliably indicate a rival group's size (choruses of multiple animals are impossible to fake by a single animal: McComb et al., 1994; Kitchen, 2004).

McComb and colleagues (1994) were the first to use playback trials to test the effect of 'numeric odds' (i.e., relative group size) by simultaneously varying the number of animals in a test group and the number of intruders broadcast from speakers. They found that numeric odds did indeed affect the behaviour of female lions – subjects were more likely to approach speakers if they greatly outnumbered simulated rivals. However, male lions in similar trials approached nearly all intruders regardless of the odds (Grinnell et

al., 1995). Because the value of maintaining residence in a group is so high (male reproductive tenure is short) and benefits are shared (males live with despotic male kin or share reproductive access to females in non-kin coalitions: Packer et al., 1991), male lions probably do not face collective action problems.

In a similar set of playback experiments testing the effects of numeric odds on black howler monkeys, responses to intruders were once again found to vary among different classes of group members. Subordinate male howlers were not affected by the numeric odds, but rather by their relationship with the alpha male (see below; Kitchen et al., 2004b). Conversely, alpha male howlers were strongly affected by the numeric odds, with the weakest response produced when their group was clearly outnumbered (Kitchen, 2004). In fact, when the odds were against them, alpha males only displayed at intruders if dependent offspring (vulnerable to infanticide) were present. Females sometimes participated in displays directed at other groups; however, while alpha males had an increasingly stronger response as numeric odds were more and more in their favour, females had the strongest response when the number of defending to intruding males was equal (Kitchen, 2006). Thus, females participated when their help would have been most effective in shifting contest outcome.

Relative group size and an individual's access to oestrous females appear to influence male chimpanzee participation in group-defence. Chimpanzees often conduct boundary patrols and deep incursions into the home range of opposing groups, with lethal consequences (e.g., Watts et al., 2006). The outcome of chimpanzee patrols probably provides a collective benefit to the entire group (Watts & Mitani, 2001; Wilson & Wrangham, 2003) by (1) eliminating dangerous outsiders, (2) weakening or even annihilating a neighbouring community, or (3) expanding their home range (Williams et al., 2004). In a playback study, Wilson and colleagues (2001) demonstrated that males were more willing to counter call and approach a simulated foreign male when their party greatly outnumbered the opponent. Given the fission-fusion social structure of chimpanzees, small groups or lone individuals from an otherwise large group can be attacked at low cost ('imbalance of power': Manson & Wrangham, 1991; see also spider monkeys (*Ateles geoffroyi*), Aureli et al., 2006). Still, incursions are relatively dangerous endeavours, and patrols consequently form at low rates, with variable participation among males. Watts & Mitani (2001) report that participation in patrols is predicted

by copulation rates with parous females rather than solely by male rank, and no strong rank-based pattern emerged to explain variation in male responses to playbacks of rivals (Wilson et al., 2001). Because alternative mating strategies means some low-ranking male chimpanzees have reproductive access (see Mitani et al., 2002), perhaps rank effects are less important than for other species.

Although more experimental data are needed across taxa, relative group size is probably a useful predictor of whether or not an intergroup interaction will escalate to displays and aggression. However, which individuals within a group participate and to what extent is more complex and likely influenced by sex, rank, reproductive investment and relationships among companions.

#### *Effect of intergroup relationships*

Collective action problems may exist when some group members are unwilling to join an escalating conflict against another group with whom they have previously associated. However, whether intergroup familiarity affects individual participation is difficult to test without long-term data on multiple habituated groups, combined with data on relatedness or dispersal patterns. Reichard & Sommer (1997) argue that by adopting such an approach with white-handed gibbons, they uncovered more variation in intergroup aggression than suggested by previous researchers. Although intergroup encounters can be lethal in gibbons (Palombit, 1993), many encounters are neutral or affiliative; in fact, adult males have even been reported to play with extra-group juveniles in this population. Some adjacent groups may contain close relatives due to extra-pair copulations and to dispersal patterns of offspring, and this may help explain the reduced aggression/competition observed between some neighbours. Intergroup relatedness or familiarity may account for patterns in other species as well (e.g., vervets: Cheney & Seyfarth, 1983; capuchins: reviewed in Fragaszy et al., 2004).

The 'dear enemy' hypothesis (Ydenberg et al., 1988) predicts that animals will also demonstrate diminished aggression when meeting a rival with whom they have previous agonistic experience. Although supported in experiments on a number of vertebrates, results from primate have been more mixed, with some species exhibiting no differences in response to neighbours vs. strangers (grey-cheeked mangabeys, spider monkeys and Mueller's gibbons, *H. muelleri*: reviewed in Wich et al., 2002a), and others responding

more aggressively to strangers (lion tamarin, French & Inglett, 1989; Wied's marmoset, French et al., 1995; Thomas langurs, Wich et al., 2002a).

Few studies have been able to examine whether familiarity or relatedness have an impact on the willingness of individuals to be hostile to members of another group. Playback experiments and staged contests in captive animals are promising methods for assessing this hypothesis in the future.

#### *Effect of intra-group relationships*

Why should subordinates cooperate in group-defence in any species, particularly in multi-male groups where only one male apparently breeds (e.g., mountain gorillas, Sicotte, 1993; olive colobus, Korstjens & Noë, 2004)? In addition to direct or inclusive fitness benefits, the benefits of living in a group (even with a despotic alpha) may surpass those of being solitary. For example, if evicted by a new male, subordinate males may lose (1) all chances of breeding, (2) experience gained by living in a group, (3) their position in a queue to takeover the group, or (4) their ability to use the relative safety of a multi-male group to assess future dispersal options during intergroup encounters. Subordinates may also help out because it affords them an opportunity to signal their value as a collaborator or mate, because they are coerced by the alpha, or because they are offered private incentives (e.g., grooming, food, Nunn & Lewis, 2001).

In capuchins, some of the variation in individual participation in intergroup encounters may be due to the strength of relationships among companions (reviewed in Perry, 1996; Fragaszy et al., 2004). For example, although the alpha male typically monopolizes all breeding in both brown (*C. apella*) and weeper capuchins (*C. olivaceus*), alpha male brown capuchins typically receive no assistance defending the group, while alpha male weeper capuchins often receive assistance from subordinate males. Perhaps future genetic tests will reveal that male weeper capuchins have higher intra-group relatedness than brown capuchins; in other words, kin selection would overcome collective action problems. In contrast, subordinate male white-fronted (*C. albifrons*) and white-faced capuchins have relatively high reproductive access. As predicted, subordinate males in both species frequently aid the alpha male in group-defence. Still, there appears to be variation in the willingness to cooperate among individual subordinate white-faced males (Perry, 1996). In a study of intra-group social behaviour, Jack

(2001) reported that white-faced males are more likely to invest in male–male relationships (by grooming and maintaining proximity) when they have been associated for long-periods of time. Although a link between male intra-group affiliation and cooperation during intergroup contests has not yet been firmly established in capuchins, relatedness correlates positively with rates of involvement in intergroup aggression among captive female ring-tailed lemurs (Nunn & Deaner, 2004).

Relationship formation and maintenance may be based on more than just genetic relatedness (e.g., Roberts, 2005). For example, kinship does not explain intra-group alliance formation patterns among male chimpanzees (reviewed in Mitani et al., 2002). Similarly, it is the quality of a social relationship that seems to influence male chimpanzee willingness to invest in dangerous patrols: Watts & Mitani (2001) report that males are more likely to join a boundary patrol if it contains males with whom they frequently groom and form intra-group alliances.

Whereas relying on observational data means confounding effects are not eliminated and sample sizes are kept low, playback experiments improve our ability to systematically test how intra-group cooperation impacts group-level competition. For example, in natural encounters, subordinate male black howler monkeys vary considerably in their willingness to join alpha males in group-defence – some subordinates participate in nearly all encounters, some never join, and some assist occasionally. Using playbacks, Kitchen and colleagues (2004b) found that the relationship between the alpha and the subordinate male helped explain some of this variation. Subordinate males in long-term associations with the alpha male (likely from the same natal group) had stronger responses to intruders than males in short-term associations with the alpha. Conversely, alpha male howler responses to playback trials were not affected by the duration of the alpha-subordinate association, but rather by the actual behaviour of subordinate males during an interaction (Kitchen, 2004). In other words, alpha males in multi-male groups receiving no help from other male group members were effectively alone and did not respond as strongly to multi-male intruders as alpha males with cooperative companions.

The few studies described here suggest that cooperative behaviour in a group-context might be fostered by intra-group relatedness, familiarity, and perhaps reciprocity. One major obstacle to testing additional populations is determining interindividual relationships, particularly in the dispersing sex.

Relationships among companions are well-established in some species, but these data come from long-term studies with known intra-group relatedness and clear, linear dominance hierarchies (e.g., female baboons: Silk et al., 2004). Without this information, it is difficult to determine whether similar patterns of dyadic cooperation emerge in within and between-group contexts.

#### *Individual characteristics*

Even when the factors discussed here statistically describe response patterns, some variation remains unexplained. In addition to stochastic effects, individuals might vary in their willingness to participate in intergroup aggression based on characteristics such as their age and experience (e.g., Lazaro-Perea, 2001; Kitchen et al., 2004b; Majolo et al., 2005), fighting ability (e.g., Steenbeek, 1999), changing state (e.g., lactating: Lazaro-Perea, 2001) and temperament. Heinsohn & Packer (1995) provide the classic example of how this latter factor might influence an individual's response. They used playback experiments to simulate female intruders to resident female lions. Despite approximately equal costs and benefits of group-defence and high relatedness among pride females, individual lions consistently used particular strategies – some always approached intruders, some never approached and some varied their responses from encounter to encounter (consistently behaving as either 'friends in need' or 'fair weather friends'). Such striking inter-individual variation (and little intra-individual variation), in the same or even in different contexts ('behavioural syndromes', Sih et al., 2004), may be analogous to human personality (Gosling, 2001). More than simple variation around some adaptive mean, 'personality' in non-human animals is at least partially heritable and lacks the plasticity of a 'strategy' (reviewed in Bell, 2007). Whether personality traits are adaptive is the topic of increasing interest for theoretical and empirical biologists (e.g., Dall et al., 2004). However, whether the existence of variable personalities in a population affects cooperation (e.g., McNamara et al., 2004) is in need of more explicit empirical study.

#### **Overcoming 'collective action problems'**

We structured this review in terms of how collective action problems are overcome in group-level contexts, a framework originally proposed elsewhere (van Schaik, 1996; Nunn, 2000; Nunn & Lewis, 2001). As predicted,

we found that the individuals most willing to provide group-defence, a non-monopolizable collective benefit, were those with the most to lose (or gain) in terms of lifetime reproductive fitness. Although the three traditional pathways to cooperation (kinship, mutualism and reciprocity; Dugatkin, 1997) explain most individual responses during intergroup encounters, applying a collective action framework reminds us that it is the combination of individual responses that results in the group-level phenomenon.

The experimental study of black howler monkeys discussed above is a good example of how understanding the nuances of individual behaviour can simplify seemingly complicated group-level patterns. To summarize, relative group size was useful in predicting whether a contest would escalate between two howler groups, as predicted by game theory. However, even when outnumbered by rivals, alpha male howlers were willing to defend the group when the stakes were high enough (when infanticide was a threat). Some subordinate males did not assist the alpha male, even when the numeric odds were in their favour; instead, subordinate male behaviour was based on their relationship with the alpha male. Consequently, subordinate male responses during each encounter altered the effective number of defenders in a group, which was found to further influence how much an alpha male invested in that encounter. Finally, females only joined displays when the numeric odds were even and their help would be most influential. This example highlights how predicting individual behaviour in a group context is not simply accomplished by identifying a single strategy, but rather by examining the interplay between individuals, and how strategies change within and between encounters.

### **Improved methods**

Two decades ago, Cheney (1987) urged researchers to adopt an individual-level analysis of group-level contests in wild primates. Although many studies have continued to use the group as the data point, increasingly researchers have opted for an individual focus to examine between-sex variation. However, only a few studies have examined within-sex variation based on age, rank and reproductive status (e.g., marmosets, Lazaro-Perea, 2001; macaques, Majolo et al., 2005).

Several other methodological improvements have followed directly from Cheney's suggestions. Long-term studies of multiple habituated groups have increased researchers' abilities to observe multiple encounters and assess re-

relationships within and between groups in some taxa (e.g., gibbons, Reichard & Sommer, 1997). Despite efforts, the difficulty of habituating and following multiple groups, especially simultaneously, continues to hinder such field studies.

Studies have increasingly attempted to quantify the costs and benefits of participating in contests. First, intensive ecological field techniques such as those used to measure resource distribution and quality in guereza colobus habitats (Harris, 2006) will improve what we know about food competition. Second, the advent of field methods for extracting hormones from faeces and urine will enable researchers to ask more specific questions about the causes and consequences of intergroup aggression; for example, elevated glucocorticoids in some individuals can indicate social stress resulting from between-group competition or infanticidal attacks (e.g., baboons, Beehner et al., 2005). Third, non-invasive means of extracting DNA from wild populations (e.g., chimpanzees, Vigilant et al., 2001) has the potential to provide paternity data with which we can quantify reproductive success, and to provide within- and between-group relatedness information so we can better understand the role of kinship in cooperation. Finally, captive studies such as Nunn and Deaner's work on ring-tailed lemurs (2004) can be used to more accurately measure the payoff for participating in intergroup conflicts.

Nevertheless, gaps remain in studies focusing on individuals in intergroup interactions. Some problems are unavoidable due to difficulties in quantifying behaviour and identifying individuals during the chaos of natural encounters, particularly in species interacting high in the canopy, and moving too quickly for observers to keep up. One option is to supplement observations with experimental studies. For example, safe and ethical staged contests can be conducted on captive primates (e.g., callitrichids, French et al., 1995; lemurs, Nunn & Deaner, 2004). In wild populations, playback studies such as those on langurs, howlers and chimpanzees will allow researchers to increase sample sizes, manipulate variables, and control for potentially confounding effects such as location, proximity, context, and familiarity. Studies like these will continue to improve our understanding of how complex group-level patterns are predictable when viewed from an individual perspective.

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### References

- Arnold, K.E., Owens, I.P.F. & Goldizen, A.W. (2005). Division of labour within cooperatively breeding groups. — *Behaviour* 142: 1577-1590.
- Aureli, F., Schaffner, C.M., Verpooten, J., Slater, K. & Ramos-Fernandez, G. (2006). Raiding parties of male spider monkeys: insights into human warfare? — *Am. J. Phys. Anthropol.* 131: 486-497.
- Baker, A.J. & Dietz, J.M. (1996). Immigration in wild groups of golden lion tamarins (*Leontopithecus rosalia*) — *Am. J. Primatol.* 38: 47-56.
- Beehner, J.C., Bergman, T.J., Cheney, D.L., Seyfarth, R.M. & Whitten, P.L. (2005). The effect of new alpha males on female stress in free-ranging baboons. — *Anim. Behav.* 69: 1211-1221.
- Bell, A.M. (2007). Future directions in behavioural syndromes research. — *Proc. Roy. Soc. Lond. B: Biol.* 274: 755-761.
- Benenson, J.F., Maiese, R., Dolensky, E., Dolensky, N., Sinclair, N. & Simpson, A. (2002). Group size regulates self-assertive versus self-deprecating responses to interpersonal competition. — *Child Dev.* 73: 1818-1829.
- Bermejo, M. (2004). Home-range and inter-group encounters in western gorillas (*Gorilla gorilla gorilla*) at Lossi Forest, North Congo. — *Am. J. Primatol.* 64: 223-232.
- Borries, C. (1993). Ecology of female social relationships: Hanuman langurs (*Presbytis entellus*) and the van Schaik model. — *Folia Primatol.* 61: 21-30.
- Borries, C. (1997). Infanticide in seasonally breeding multimale groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (South Nepal). — *Behav. Ecol. Sociobiol.* 41: 139-150.
- Boyd, R. (1989). Mistakes allow evolutionary stability in the repeated prisoner's dilemma game. — *J. Theor. Biol.* 136: 47-56.
- Boydston, E.E., Morelli, T.L. & Holekamp, K.E. (2001). Sex differences in territorial behavior exhibited by the spotted hyena (*Hyaenidae, Crocuta crocuta*). — *Ethology* 107: 69-85.
- Brown, J. (1964). The evolution of diversity in avian territorial systems. — *Wils. Bull.* 76: 160-169.
- Cheney, D.L. (1987). Interactions and relationships between groups. — In: *Primate societies* (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 267-281.
- Cheney, D.L. (1992). Intra-group cohesion and inter-group hostility: the relation between grooming distributions and inter-group competition among female primates. — *Behav. Ecol.* 3: 334-345.
- Cheney, D.L. & Seyfarth, R.M. (1983). Non-random dispersal in free-ranging vervet monkeys: social and genetic consequences. — *Am. Nat.* 122: 392-412.

- Clutton-Brock, T.H. & Parker, G.A. (1995). Punishment in animal societies. — *Nature* 373: 58-60.
- Cooper, M.A., Aureli, F. & Singh, M. (2004). Between-group encounters among bonnet macaques (*Macaca radiata*). — *Behav. Ecol. Sociobiol.* 56: 217-227.
- Cowlshaw, G. (1995). Behavioural patterns in baboon group encounters: the role of resource competition and male reproductive strategies. — *Behaviour* 132: 75-86.
- Dall, S.R.X., Houston, A.I. & McNamara, J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. — *Ecol. Lett.* 7: 734-739.
- Doebeli, M. & Hauert, C. (2005). Models of cooperation based on the prisoner's dilemma and the snowdrift game. — *Ecol. Lett.* 8: 748-766.
- Dugatkin, L.A. (1997). Cooperation among animals: an evolutionary perspective. — Oxford University Press, Oxford.
- Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. — *Science* 197: 215-223.
- Fashing, P.J. (2001). Male and female strategies during inter-group encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates. — *Behav. Ecol. Sociobiol.* 50: 219-230.
- Flack, J.C., de Waal, F.B.M. & Krakauer, D.C. (2005). Social structure, robustness, and policing cost in a cognitively sophisticated species. — *Am. Nat.* 165: E126-E139.
- French, J.A. & Inglett, B.J. (1989). Female-female aggression and male indifference in response to unfamiliar intruders in lion tamarins. — *Anim. Behav.* 27: 487-497.
- French, J.A., Schaffner, C.M., Shepherd, R.E. & Miller, M.E. (1995). Familiarity with intruders modulates agonism towards outgroup conspecifics in Wied's black-tufted-ear marmoset (*Callithrix kuhli*: Primates, Callitrichidae). — *Ethology* 99: 24-38.
- Fragaszy, D.M., Visalberghi, E. & Fedigan, L.M. (2004). The complete capuchin: the biology of the genus *Cebus*. — Cambridge University Press, Cambridge.
- Gintis, H., Smith, E.A. & Bowles, S. (2001). Costly signaling and cooperation. — *J. Theor. Biol.* 213: 103-119.
- Gosling, S.D. (2001). From mice to men: what can we learn about personality from animal research? — *Psychol. Bull.* 127: 45-86.
- Grinnell, J., Packer, C. & Pusey, A.E. (1995). Cooperation in male lions: kinship, reciprocity, or mutualism? — *Anim. Behav.* 49: 95-105.
- Hale, A.M., Williams, D.A. & Rabenold, K.N. (2003). Territoriality and neighbor assessment in brown jays (*Cyanocorax morio*) in Costa Rica. — *Auk* 120: 446-456.
- Harris, T.R. (2006). Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). — *Behav. Ecol. Sociobiol.* 61: 317-329.
- Hauert, C., Michor, F., Nowak, M.A. & Doebeli, M. (2006). Synergy and discounting of cooperation in social dilemmas. — *J. Theor. Biol.* 239: 195-202.
- Harvey, P.H. & Pagel, M.D. (1991). The comparative method in evolutionary biology. Oxford series in ecology and evolution, vol. 1. — Oxford University Press, Oxford.
- Heinsohn, R. & Packer, C. (1995). Complex cooperative strategies in group-territorial African lions. — *Science* 269: 1260-1262.
- Henzi, S.P., Lycett, J.E. & Weingrill, T. (1998). Mate guarding and risk assessment by male mountain baboons during inter-troop encounters. — *Anim. Behav.* 55: 1421-1428.

- Hrdy, S.B. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. — *Ethol. Sociobiol.* 1: 13-40.
- Hsu, Y. & Wolf, L.L. (1999). The winner and loser effect: integrating multiple experiences. — *Anim. Behav.* 57: 903-910.
- Jack, K.M. (2001). Explaining variation in affiliative relationships among male white-faced capuchins (*Cebus capucinus*). — *Folia Primatol.* 74: 1-16.
- Killingback, T. & Doebeli, M. (2002). The continuous prisoner's dilemma and the evolution of cooperation through reciprocal altruism with variable investment. — *Am. Nat.* 160: 421-438.
- Kinnaird, M.F. (1992). Variable resource defense by the Tana River crested mangabey. — *Behav. Ecol. Sociobiol.* 31: 115-122.
- Kitchen, D.M. (2004). Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour, and reproductive investment. — *Anim. Behav.* 67: 125-139.
- Kitchen, D.M. (2006). Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: effects of numeric odds, vulnerable offspring and companion behavior. — *Am. J. Phys. Anthropol.* 131: 73-83.
- Kitchen, D.M., Cheney, D.L. & Seyfarth, R.M. (2004a). Factors mediating inter-group encounters in chacma baboons (*Papio cynocephalus ursinus*). — *Behaviour* 141: 197-218.
- Kitchen, D.M., Horwich, R.H. & James, R.A. (2004b). Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: experimental evidence for the effects of intra-group male relationships and age. — *Behaviour* 141: 703-723.
- Korstjens, A.H., Nijssen, E.C. & Nöe, R. (2005). Inter-group relationships in western black-and-white colobus, *Colobus polykomos polykomos*. — *Int. J. Primatol.* 26: 1267-1289.
- Korstjens, A.H. & Nöe, R. (2004). The mating system of an exceptional primate, the olive colobus (*Procolobus verus*). — *Am. J. Primatol.* 62: 261-273.
- Kun, A., Boza, G. & Scheuring, I. (2006). Asynchronous snowdrift game with synergistic effect as a model of cooperation. — *Behav. Ecol.* 17: 633-641.
- Lazaro-Perea, C. (2001). Inter-group interactions in wild common marmosets, *Callithrix jacchus*: territorial defense and assessment of neighbours. — *Anim. Behav.* 62: 11-21.
- Majolo, B., Ventura, R. & Koyama, N.F. (2005). Sex, rank and age differences in the Japanese macaque (*Macaca fuscata yakui*) participation in inter-group encounters. — *Ethology* 111: 455-468.
- Manson, J.H. & Wrangham, R.W. (1991). Inter-group aggression in chimpanzees and humans. — *Curr. Anthropol.* 32: 396-390.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. — Cambridge University Press, Cambridge.
- McComb, K., Packer, C. & Pusey, A. (1994). Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. — *Anim. Behav.* 47: 379-387.
- McComb, K., Pusey, A., Packer, C. & Grinnell, J. (1993). Female lions can identify potentially infanticidal males from their roars. — *Proc. Roy. Soc. Lond. B: Biol.* 252: 59-64.
- McNamara, J.M., Barta, Z. & Houston, A.I. (2004). Variation promotes cooperation in the Prisoner's Dilemma game. — *Nature* 428: 745-747.
- Mitani, J.C. & Rodman, P.S. (1979). Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. — *Behav. Ecol. Sociobiol.* 5: 241-251.

- Mitani, J.C., Watts, D.P. & Muller, M.N. (2002). Recent developments in the study of wild chimpanzee behavior. — *Evol. Anthropol.* 11: 9-25.
- Mitani, J.C. & Watts, D.P. (2005). Correlates of territorial boundary patrol behaviour in wild chimpanzees. — *Anim. Behav.* 70: 1079-1086.
- Noë, R. & Hammerstein, P. (1995). Biological markets. — *Trends Ecol. Evol.* 10: 336-339.
- Nunn, C.L. (2000). Collective benefits, free-riders, and male extra-group conflict. — In: *Primate males: causes and consequences of variation in group composition* (Kappeler, P., ed.). Cambridge University Press, Cambridge, p. 192-204.
- Nunn, C.L. & Deaner, R.O. (2004). Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*). — *Behav. Ecol. Sociobiol.* 57: 50-61.
- Nunn, C.L. & Lewis, R.J. (2001). Cooperation and collective action in animal behaviour. — In: *Economics in nature: social dilemmas, mate choice and biological markets* (Noë, R., van Hooff, J.A.R.A.M. & Hammerstein, P., eds). Cambridge University Press, Cambridge, p. 42-66.
- Okamoto, K. & Matsumura, S. (2002). Inter-group encounters in wild moor macaques (*Macaca maurus*). — *Primates* 43: 119-125.
- Olupot, W. & Waser, P.M. (2005). Patterns of male residence and inter-group transfer in gray-cheeked mangabeys (*Lophocebus albigena*). — *Am. J. Primatol.* 66: 331-349.
- Ostrom, E. (2001). Social dilemmas and human behaviour. — In: *Economics in nature: social dilemmas, mate choice and biological markets* (Noë, R., van Hooff, J.A.R.A.M. & Hammerstein, P., eds). Cambridge University Press, Cambridge, p. 23-41.
- 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.
- Packer, C. & Pusey, A.E. (1979). Female aggression and male membership in troops of Japanese macaques and live baboons. — *Folia Primatol.* 31: 212-218.
- Palombit, R.A. (1993). Lethal territorial aggression in a white-handed gibbon. — *Am. J. Primatol.* 31: 311-318.
- Palombit, R.A., Cheney, D.L., Fisher, J., Johnson, S., Rendall, D., Seyfarth, R. & Silk, J. (2000). Male infanticide and defense of infants in chacma baboons. — In: *Infanticide by males and its implications* (van Schaik, C.P. & Janson, C.H., eds). Cambridge University Press, Cambridge, p. 123-152.
- Palombit, R.A., Seyfarth, R.M. & Cheney, D.L. (1997). The adaptive value of "friendships" to female baboons: experimental and observational evidence. — *Anim. Behav.* 54 (1997): 599-614.
- Panchanathan, K. & Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. — *Nature* 432: 499-502.
- Payne, H.F.P., Lawes, M.J. & Henzi, S.P. (2003). Competition and the exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). — *Behaviour* 140: 453-471.
- Perry, S. (1996). Inter-group encounters in wild white-faced capuchins (*Cebus capucinus*). — *Int. J. Primatol.* 17: 309-330.
- Reichard, U. & Sommer, V. (1997). Group encounters in wild gibbons (*Hylobates lar*): agonism, affiliation, and the concept of infanticide. — *Behaviour* 134: 1135-1174.
- Roberts, G. (2005). Cooperation through interdependence. — *Anim. Behav.* 70: 901-908.
- Roberts, G. & Sherratt, T.N. (1998). Development of cooperative relationship through increasing investment. — *Nature* 394: 175-179.

- Rubenstein, D.I. (1986). Ecology and sociality in horses and zebras. — In: Ecological determinants of social evolution (Rubenstein, D.I. & Wrangham, R.W., eds). Princeton University Press, Princeton, NJ, p. 282-302.
- Saito, C., Sato, S., Suzuki, S., Sugiura, H., Agetsuma, N., Takahata, Y., Sasaki, C., Takahashi, H., Tanaka, T. & Yamagiwa, J. (1998). Aggressive inter-group encounters in two populations of Japanese macaques (*Macaca fuscata*). — *Primates* 29: 303-312.
- Saj, T.L. & Sicotte, P. (2005). Male takeover in *Colobus vellerosus* at Boabeng-Fiema Monkey Sanctuary, central Ghana. — *Primates* 46: 211-214.
- Sauther, M.L., Sussman, R.W. & Gould, L. (1999). The socioecology of the ringtailed lemur: thirty-five years of research. — *Evol. Anthropol.* 120-132.
- Schaffner, C.M. & French, J.A. (1997). Group size and aggression: 'recruitment incentives' in a cooperatively breeding primate. — *Anim. Behav.* 54: 171-180.
- van Schaik, C.P. (1989). The ecology of social relationships amongst female primates. — In: Comparative socioecology: the behavioural ecology of humans and other mammals (Standen, V. & Foley, R.A., eds). Blackwell Scientific Publications, Oxford, p. 195-218.
- van Schaik, C.P. (1996). Social evolution in primates: the role of ecological factors and male behaviour. — *Proc. Br. Acad.* 88: 9-31.
- Seyfarth, R.M. & Cheney, D.L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. — *Nature* 308: 541-543.
- Sicotte, P. (1993). Inter-group encounters and female transfer in mountain gorillas: influence of group composition on male behavior. — *Am. J. Primatol.* 30: 21-36.
- Sicotte, P. & MacIntosh, A.J. (2004). Inter-group encounters and male incursions in *Colobus vellerosus* in Central Ghana. — *Behaviour* 141: 533-553.
- Sih, A., Bell, A.M., Johnson, J.C. & Ziemba, R.E. (2004b). Behavioral syndromes: an integrative overview. — *Q. Rev. Biol.* 79: 241-277.
- 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.
- Stanford, C.B. (1991). Social dynamics of inter-group encounters in the capped langur (*Presbytis pileata*). — *Am. J. Primatol.* 25: 35-47.
- Steenbeek, R. (1999). Tenure related changes in wild Thomas's langurs I: between-group interactions. — *Behaviour* 136: 595-625.
- Steenbeek, R., Piek, R.C., van Buul, M. & van Hoof, J.A.R.A.M. (1999). Vigilance in wild Thomas's langurs (*Presbytis thomasi*): the importance of infanticide risk. — *Behav. Ecol. Sociobiol.* 45: 137-150.
- Stephens, D.W., Nishimura, K. & Toyer, K.B. (1995). Error and discounting in the iterated prisoner's dilemma. — *J. Theor. Biol.* 176: 457-469.
- Sterck, E.H.M., Watts, D.P. & van Schaik, C.P. (1997). The evolution of female social relationships in nonhuman primates. — *Behav. Ecol. Sociobiol.* 41: 291-309.
- Sugiura, H., Saito, C., Sato, S., Agetsuma, N., Takahashi, H., Tanaka, T., Furuichi, T. & Takahata, Y. (2000). Variation in inter-group encounters in two populations of Japanese macaques. — *Int. J. Primatol.* 21: 519-535.
- Tanner, C.J. (2006). Numerical assessment affects aggression and competitive ability: a team-fighting strategy for the ant *Formica xerophila*. — *Proc. Roy. Soc. Lond. B: Biol.* 273: 2737-2742.
- Trivers, R.L. (1972). Parental investment and sexual selection. — In: Sexual selection and the descent of man (Campbell, B., ed.). Aldine, Chicago, IL, p. 136-179.

- Vigilant, L., Hofreiter, M., Siedel, H. & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. — *Proc. Natl. Acad. Sci. USA* 98: 12890-12895.
- Watts, D.P. (1989). Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. — *Ethology* 81: 1-18.
- Watts, D.P. & Mitani, J.C. (2001). Boundary patrols and inter-group encounters in wild chimpanzees. — *Behaviour* 138: 299-327.
- Watts, D.P., Muller, M., Amsler, S.J., Mbabazi, G. & Mitani, J.C. (2006). Lethal inter-group aggression by chimpanzees in Kibale National Park, Uganda. — *Am. J. Primatol.* 68: 161-180.
- Whitehead, J.M. (1989). The effect of the location of a simulated intruder on responses to long-distance vocalisations of mantled howling monkeys, *Alouatta palliata palliata*. — *Behaviour* 108: 73-103.
- Wich, S.A., Assink, P.R., Becher, F. & Sterck, E.H.M. (2002a). Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of familiarity. — *Behaviour* 139: 79-87.
- Wich, S.A., Assink, P.R., Becher, F. & Sterck, E.H.M. (2002b). Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): the effect of location. — *Behaviour* 139: 65-78.
- Wich, S.A., Assink, P.R. & Sterck, E.H.M. (2004). Thomas langurs (*Presbytis thomasi*) discriminate between calls of young solitary versus older group-living males: a factor in avoiding infanticide? — *Behaviour* 141: 41-51.
- Wich, S.A., van der Post, D.J., Heistermann, M., Möhle, U., van Hooff, J.A.R.M. & Sterck, E.H.M. (2003). Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. — *Int. J. Primatol.* 24: 1251-1265.
- Williams, J.M., Oehlert, G.W., Carlis, J.V. & Pusey, A.E. (2004). Why do male chimpanzees defend a group range? — *Anim. Behav.* 68: 523-532.
- Wilson, M.L., Hauser, M.D. & Wrangham, R.W. (2001). Does participation in inter-group conflict depend on numerical assessment, range location, or rank for wild chimpanzees? — *Anim. Behav.* 61: 1203-1216.
- Wilson, M.L. & Wrangham, R.W. (2003). Inter-group relations in chimpanzees. — *Annu. Rev. Anthropol.* 32: 363-392.
- Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. — *Behaviour* 75: 262-300.
- Wrangham, R.W. & Rubenstein, D.I. (1986). Social evolution in birds and mammals. — In: *Ecological determinants of social evolution* (Rubenstein, D.I. & Wrangham, R.W., eds). Princeton University Press, Princeton, NJ, p. 452-470.
- Ydenberg, R.C., Giraldeau, L.A. & Falls, J.B. (1988). Neighbours, strangers, and the asymmetric war of attrition. — *Anim. Behav.* 36: 343-347.
- Zhao, Q. (1997). Inter-group interactions in Tibetan macaques at Mt. Emei, China. — *Am. J. Phys. Anthropol.* 104: 459-470.
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