

A trait-based approach to understand the evolution of complex coalitions in male mammals

Lucretia E. Olson and Daniel T. Blumstein

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095-1606, USA

Coalitions occur when multiple individuals cooperate against a common opponent or for a common goal. Coalition formation is a complex behavior, typically described in highly social and cognitively complex species. Surprisingly, we know little about the social and environmental factors that may select for the evolution of coalitions. We studied the evolution of coalitionary behavior by first redefining it in a continuous way that acknowledges variation in the degree to which animals collaboratively work toward a common goal. We then examined the evolutionary association of coalition complexity with 3 social factors (estrous duration, group size, and presence of a dominance hierarchy) and 3 environmental factors (habitat type, diurnality, and diet type). We found that estrous duration, group size, and dominance hierarchy were significantly correlated with coalition complexity and thus conclude that social factors are relatively more important in the evolution of complex coalitions than are environmental factors. From these results, we infer that complex coalitions may be the product of social factors that reduce female monopolizability and encourage the aggregation of multiple males. *Key words:* coalitions, mammals, mutual tolerance, sociality. [*Behav Ecol* 20:624–632 (2009)]

Behavioral ecologists typically define coalitions as cooperation between 2 or more individuals against a third during an aggressive or competitive encounter (Harcourt 1992). Coalitions may also be formed for intergroup contests, where individuals of one group work together to defend a territory against outside males, as seen in cheetahs (*Acinonyx jubatus*), or to take over already established breeding groups, as seen in meerkats (*Suricata suricatta*) (Caro and Collins 1987; Doolan and Macdonald 1996). Although coalitions are formed by both males and females, the purpose of these coalitions usually differs. Female coalitions are generally formed to increase access to resources, as seen in coatis (*Nasua narica*), as well as more commonly in primates (Wrangham 1980; Gompper et al. 1997). Male groups may be formed for a variety of reasons. For instance, Cape ground squirrels (*Xerus inauris*) form all-male groups to increase their protection from predators (Waterman 1997), whereas coastal river otters (*Lutra canadensis*) form groups of mostly unrelated males to increase hunting success (Blundell et al. 2004). Because these types of cooperation are potentially explained by the mutualistic benefits of aggregation, we will restrict our focus here to coalitions formed to increase access to reproductive females. Reproductive coalition formation among males has been hypothesized by van Hooff and van Schaik (1992) to be difficult to explain because the main resource generally sought by males is successful fertilization, which is nondivisible; thus, it would appear to be most beneficial for a single male to attempt to monopolize as many females as possible and to be intolerant to the presence of competitor males. Therefore, the evolution of male coalitions is not readily explained (van Schaik 1996; Watts 1998). In this comparative review, we first propose a new metric to describe coalitionary behavior in a range of social species. Then, we use this metric in a com-

parative analysis to evaluate the extent to which specific social and environmental factors are responsible for the evolution of complex coalitions.

THE COALITIONARY TRAITS METRIC

As coalitions are now defined, their occurrence is largely limited to higher primates. An underlying assumption is that only primates are capable of assessing one another's competitive ability and, using this information, are thus able to select coalition partners (Harcourt 1992). This definition, however, forces us to view coalitionary behavior as a trait that has sprung into being fully formed, with no intermediate steps along the way to explain its evolution. Yet, recent research has shown that males of less social species are also capable of aiding, or at least tolerating, each other. Feral horses (*Equus caballus*) jointly defend their harems against rival male intruders (Feh 1999), whereas striped hyenas (*Hyaena hyaena*) will mutually tolerate up to 2 other males on the same territory to maximize their access to females (Wagner et al. 2008). As coalitions are now defined, these species would not be termed coalitionary. However, these species seem to possess attributes of coalitionary behavior, and thus, there may be utility in a broader definition that recognizes these attributes. Moreover, because coalitions, as currently defined, either occur in a highly developed form or are not said to occur at all, we possess a limited understanding of the factors that have led to their evolution. A definition that acknowledges the graded nature of coalitionary behavior will allow us to conduct formal comparative analyses and determine the correlation of environmental and social traits with increased coalition complexity.

We suggest that 3 key traits define complex coalitionary behavior: mutual tolerance, collaboration (against inter- or intragroup conspecifics), and preference for certain partners over others during intragroup competition. Generally, species such as baboons (*Papio* spp.) (Noë and Sluijter 1995) or bottlenose dolphins (*Tursiops truncatus*) (Connor et al. 1992) that possess all 3 traits are currently recognized as those that form coalitions. Species that have only a single trait can be viewed as

Address correspondence to L.E. Olson. E-mail: lucretia@ucla.edu.
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having rudimentary coalitional behavior. Although a temporal element may be associated with complex social interactions (e.g., reciprocal altruism requires actors to associate with each other over a period of time—Trivers 1971; Axelrod and Hamilton 1981), we did not include the temporal element on its own because it seems inherent to the other 3 traits. For instance, species with solely mutual tolerance usually interact for only a short amount of time, whereas those with more complex interactions tend to be longer term.

We do not intend for these traits to be viewed as independent of one another, but rather as part of a continuum, with each trait building on those beneath it to define coalition complexity. Thus, species of low complexity will be characterized by mutual tolerance only; those of moderate complexity will have mutual tolerance and some form of collaboration; and coalitionarily complex species will possess mutual tolerance, collaboration, and within-group partner preference. The 3 traits will thus be viewed as a single continuous variable of coalition complexity.

Mutual tolerance can be said to occur whenever a social group contains 2 or more males; thus, all rudimentary coalitions are characterized by mutual tolerance. In such cases, males must tolerate each other to the point that neither is forced to leave the group. Mutual tolerance includes males that merely refrain from serious fighting, as seen in raccoons (*Procyon lotor*) that share territories and den together for short periods of time but do not appear to interact with each other in any other way (Gehrt and Fox 2004). It is also present when males maintain close physical proximity to each other, as seen in bottlenose dolphins (Connor et al. 1992) or African lions (*Panthera leo*), which appear to spend a majority of their time near to and interacting with other males in their social group (Packer and Pusey 1982; Packer et al. 1991). Species that lack male mutual tolerance are those where males associate with other conspecifics only during breeding and are solitary during the majority of the year, as seen in jaguars (*Panthera onca*) (Seymour 1989) or armadillos (*Oryzomys afer*) (Shoshani et al. 1988). Although the degree of mutual tolerance can vary between species, for purposes of comparative analysis, we consider a species that illustrates any form of this behavior to be a species that possesses mutual tolerance.

Collaboration is seen when 2 or more individuals work together to increase either participant's potential access to reproductive females. Collaboration can occur within a group, as in bonnet macaques (*Macaca radiata*) when individuals support each other against a group member to raise or maintain their position in a dominance hierarchy (Silk 1999), or against conspecifics in different social groups, as seen in the banded mongoose (*Mungos mungo*) when members of one group form coalitions to take over an existing group and oust the resident males (Waser et al. 1994).

Partner preference occurs when males have multiple individuals within a social group from which to choose a coalition partner and yet solicit aid from or come to the defense of certain males within a social group over that of others. Often this discrimination is based on known parameters such as fighting ability or dominance rank, as seen in some baboon species (*Papio cynocephalus cynocephalus* and *Papio cynocephalus anubis*) (Noë and Sluijter 1995), bonnet macaques (*M. radiata*) (Silk 1999), and chimpanzees (*Pan troglodytes*) (Mitani et al. 2000). By defining partner preference in this way, our definition of maximally complex coalitions (i.e., those with all 3 traits) matches the widely accepted definition of coalitions.

Using these 3 traits, we can define the coalitional complexity of a species. If no traits are present, the species cannot be said to form even a rudimentary coalition and thus falls at the beginning of the continuum, whereas species possessing all 3 traits form complex coalitions and make up the other end of

the continuum. We acknowledge that what we refer to as grades of coalitional behavior might be described by others as a type of social complexity (de Waal et al. 2003; Muller and Soligo 2005); however, if this is the case, our findings are then equally relevant to describe the evolution of social complexity as well.

EVOLUTION OF COALITION COMPLEXITY

The evolution of many complex behavioral traits may be influenced to differing degrees by social and environmental variables. For instance, reciprocal altruism, which has been reported in some mammals (Norway rats [*Rattus norvegicus*; Rutte and Taborsky 2008] and impala [*Aepyceros melampus*; Hart BL and Hart LA 1992]), is believed to largely depend on individual discrimination ability and repeated social interactions (Connor 1995; Trivers 1971). Alloparental care, in which an individual fosters another's young, is usually kin selected and may also be explained by group augmentation, where larger groups have increased survival and reproduction, and therefore, some individuals benefit by joining the group and forgoing reproduction in order to help (Kokko 2001). Alternatively, ecological factors, such as territory quality or availability, are hypothesized to be important for the evolution of cooperative breeding in birds (Emlen 1982; Arnold and Owens 1999).

To determine to what extent social and environmental factors played a role in the evolution of complex coalitions, we chose 3 social variables that, based on the literature, we believed would be most likely to influence the basic components of coalition formation. Our social factors included the length of estrous duration because a number of studies have shown that males base dispersal and territory choice decisions on the presence or availability of fertile females (Clutton-Brock 1989; Kappeler and van Schaik 2002). We included group size because small groups of females are more easily controlled by males, and thus, one would expect mutual tolerance of multiple males to be favored in large groups where males have incomplete control of reproduction (van Hooff and van Schaik 1994). The presence or absence of a dominance hierarchy because group members often use coalitions in order to manipulate their social standing and gain access to mates (de Villiers et al. 2003; Perry et al. 2004). Our environmental factors included habitat type, which was chosen because the relative openness of a species' habitat may influence visibility and ease of locomotion so that males in more open areas are able to exert more reproductive control over females (van Hooff and van Schaik 1994). Activity period (diurnality) was chosen because, in primates, it has been suggested that males have a more difficult time keeping a harem when active at night because mate guarding is more difficult when visibility is reduced; therefore, we may expect more multiple male groups in nocturnal species (Ostner and Kappeler 2004). Diet type was chosen because resources can be either patchy or evenly distributed, which may in turn influence a species' distribution: patchy food resources may encourage individuals to form groups (Wiens 1976). Our objective was to identify correlations between environmental and social factors and coalition complexity. We infer that factors highly correlated with coalition complexity may have been associated with the evolution of this behavior or possibly have evolved concurrently.

METHODS

Comparative data

Our comparative analysis used 37 mammals from 8 orders: 12 Primates, 1 Lagomorpha, 2 Rodentia, 1 Chiroptera, 16 Carnivora,

1 Perissodactyla, 3 Artiodactyla, and 1 Cetaceae. We selected our species using the ISI Web of Science and Google Scholar search engines with the search terms “coalition(s)” and “mammal(ian)” to find the most well-known coalition formers, such as dolphins and primates. We then used the terms “polyandry(drous)” and “multiple male group” to find the less complex species such as the red fox (*Vulpes vulpes*) and capybaras (*Hydrochoerus hydrochaeris*). We selected non-coalition-forming species by looking for solitary or family group living species among the close congeners of coalition formers.

We tabulated the number of traits present for each species. Non-coalition-forming species possessed none of our traits: they lacked multiple males per social group and most male-male interaction. Species with only a single trait were those that possessed some degree of mutual tolerance but little or no evidence of collaboration or partner preference. Species with 2 traits mutually tolerated each other and had evidence for basic or complex collaboration. Complex coalitions (those with 3 traits) were documented when individuals mutually tolerated each other, performed collaborative behaviors, and preferred certain coalition partners for within-group contests. We analyzed 8 species with 0 traits, 11 with 1, 17 with 2, and 8 with 3 traits (Table 1).

When possible, previously compiled summaries were used to obtain life-history and natural history variables; when this was unavailable, primary literature was consulted (sources in Table 1). We collected information on 3 social variables: duration of estrous cycle (the length of time, in days, in which a female was receptive toward the male), group size (the mean number of all individuals within a social group), and the presence or absence of a dominance hierarchy.

For nonprimates, the duration of the estrous cycle was measured as the length of time an animal was receptive to copulation. This varied widely between species, with some, such as Belding's ground squirrels (*Spermophilus beldingi*), only receptive for a few hours, leading to intense male scramble competition (Jenkins and Eshelman 1984), whereas other species had receptive periods that lasted days or weeks. Primates are not typically characterized by an estrous period but by ovarian cycles, during which they are sometimes more or less receptive to mating (Nowak and Paradiso 1983). For this analysis, we considered the length of estrous durations for primates to coincide with the follicular phase of the cycle and to end at ovulation, the time of peak fertility (Dixon 1998).

Group size was determined by counting adult males and females in the group because the variable of interest, coalition formation, is only performed by adult males to gain access to reproductive females. We did not include species that formed all-male, or “bachelor” groups, in our analysis, and so group sizes refer to mixed male and female groups or, when appropriate, the average number of males in a coalition combined with the average number of females they associate with, as in lions (Packer et al. 1991). Although it may be useful to look at female-only group size, this information was not available for many of the species in the analysis, and so to maximize sample size, we used a mixed sex group size measure. We believe that this is an equally relevant metric when considering variation in female availability because the composition of most social groups is determined by the distribution of females; thus, groups may have either a solitary male or a small group of males and one to many females (Clutton-Brock 1989).

A dominance hierarchy was considered present when at least one individual was recorded as being behaviorally dominant to one or more individuals in the group. In primates, the dominance hierarchies were often linear, whereas other species might have one dominant individual and the rest subordinates of roughly equal status, as in oribi (*Ourebia ourebi*), which have

a single dominant territory holder that tolerates several subordinate males (Arcese 1999).

We also collected information on 3 environmental variables: habitat type (divided into 3 categories: open, medium, and dense), diurnality (whether an animal was diurnal or not), and diet type (grouped into patchy or evenly distributed resources).

Habitat type is difficult to classify into the simplified categories necessary for this type of analysis. When determining categories, we decided to remain as simple as possible, so as to avoid complicated classification schemes. Habitats that have an unobstructed view most of the time, and where individuals can move about quickly and easily, were termed “open.” Open areas are places such as grasslands, deserts, or open woodland areas with limited undergrowth to obscure visibility. “Dense” habitats were those in which individuals might have a difficult time seeing around obstacles or are hampered in their movements by thick vegetation, such as dense rain forests. Habitats deemed “medium” fell in between the 2 extremes and encompass areas with limited visibility, such as tall brush or gallery forest.

Diet type was scored dichotomously because we expected that the most biologically relevant comparison was whether or not resources were clumped. This classification scheme accommodated many types of diet, including carnivores and frugivores (clumped: prey items or fruit distributed in either small groups, such as single pieces of fruit or a single carcass, or large groups such as fruit trees or ungulate herds; for either size, the resource can be viewed as a single unit, capable of being shared or monopolized [Johnson et al. 2002]), as well as omnivores and folivores (dispersed: food resources can be found in a greater variety of locations and may be less easily monopolized [Johnson et al. 2002]).

For activity period, we subsumed nocturnal, crepuscular (in which animals are active at dawn and dusk), and cathemeral (random bouts of activity) into one category. There were only 2 species in our analysis that were crepuscular and 3 that were cathemeral; so to maximize statistical power we grouped all nondiurnal species into one category and compared this with all diurnal species. Adult body mass (the mean adult male body mass in kilograms) was also collected for all species because body mass is sometimes correlated with other life-history traits as well as social complexity (Blumstein and Armitage 1998; Armitage and Blumstein 2002).

Data analysis

We conducted phylogenetically based analyses using independent contrasts. First, we compiled a single phylogeny consisting of our 37 species. The ordinal branches of the phylogeny were constructed using a molecular phylogeny (Murphy et al. 2001). Within each order, recent molecular phylogenies were used to resolve the tree down to the species level (see Figure 1 for the phylogeny). If molecular phylogenies were not available, the most well-supported morphological phylogeny was used. Equal branch lengths were assumed.

We used Phylogenetic Independence 2.0 (Reeve and Abouheif 2003) to determine whether the variables under study were affected by their phylogenetic history. We selected the test for serial independence for our continuous variables and the runs test for the discrete character state variables. Both types of tests were run with the 1000-simulation option. We found that 4 out of the 7 variables were significantly ($P < 0.05$) phylogenetically autocorrelated (body mass, habitat type, diet, and activity period) and thus were dependent on their phylogenetic history. To be conservative, we elected to use a phylogenetically based comparative method to analyze all data.

Table 1
Social and environmental variables for all 37 species in phylogenetic order

Species	Trait 1	Trait 2	Trait 3	Estrous duration (days)	Group Size (average)	Dominance hierarchy	Habitat type	Activity period	Food distribution	Male body mass (kg)	References
<i>Tursiops truncatus</i>	1	1	1	36	17.5	Yes	Open	Other	Patchy	260	1–4
<i>Ourebia ourebi</i>	1	1	0	6	5.5	Yes	Open	Other	Even	236	1,5–7
<i>Kobus ellipsiprymnus</i>	1	1	0	0.75	39	Yes	Open	Diurnal	Even	169.5	6,8
<i>Vicugna vicugna</i>	0	0	0	4.4	4.5	No	Open	Diurnal	Even	3.87	9–12
<i>Equus caballus</i>	1	1	0	6.5	3.5	Yes	Open	Diurnal	Even	350	13–15
<i>Puma yagouaroundi</i>	0	0	0	3.2	1.5	No	Open	Other	Patchy	0.04	16
<i>Acinonyx jubatus</i>	1	1	0	13.6	3.5	No	Open	Diurnal	Patchy	82.3	1,17–19
<i>Panthera onca</i>	0	0	0	10.15	1.5	No	Dense	Other	Patchy	275	1,20,21
<i>Panthera leo</i>	1	1	0	5.5	9.5	No	Open	Other	Patchy	49.7	1,22–24
<i>Hyaena hyaena</i>	1	1	0	1.5	3	No	Open	Other	Even	0.26	24,25
<i>Crocuta crocuta</i>	1	1	1	1	45	Yes	Open	Other	Patchy	47.75	1,26–28
<i>Herpestes auropunctatus</i>	1	0	0	3.5	4	No	Open	Diurnal	Even	13.3	24,29–31
<i>Suricata suricatta</i>	1	1	0	20	9.5	Yes	Open	Diurnal	Even	0.65	1,32,33
<i>Mungos mungo</i>	1	1	0	4.5	20	Yes	Open	Diurnal	Even	5.1	1,6,24
<i>Canis latrans</i>	0	0	0	3.5	1.5	No	Open	Other	Patchy	8.1	1,34
<i>Lycan pictus</i>	1	1	1	20	14.5	Yes	Open	Diurnal	Patchy	54.1	1,35–37
<i>Vulpes vulpes</i>	1	0	0	3.5	5	Yes	Medium	Other	Patchy	6.45	38,39
<i>Melursus ursinus</i>	1	0	0	4	1.5	Yes	Open	Other	Even	6.1	40,41
<i>Procyon lotor</i>	1	0	0	8.85	4	No	Medium	Other	Even	0.73	42–44
<i>Bassariscus astutus</i>	0	0	0	1.25	1.5	No	Medium	Other	Patchy	0.54	1,24,45
<i>Potos flavus</i>	1	1	0	17.6	3	No	Dense	Other	Patchy	16.2	1,24,46
<i>Artibeus jamaicensis</i>	1	1	0	22	11	No	Medium	Other	Patchy	14	24,47
<i>Hydrochoerus hydrochaeris</i>	1	1	0	0.63	10	Yes	Open	Diurnal	Even	21.8	48,49
<i>Spermophilus beldingi</i>	0	0	0	0.2	1.5	No	Open	Diurnal	Even	0.05	50
<i>Ochotona curzoniae</i>	1	0	0	1	3.5	No	Open	Diurnal	Even	160	1,51,52
<i>Eulemur fulvus rufus</i>	1	1	0	3.85	15.5	Yes	Dense	Other	Even	40.5	1,53,54
<i>Callithrix jacchus</i>	1	0	0	2.5	11.5	Yes	Dense	Diurnal	Patchy	50	1,53,55
<i>Cebus capucinus</i>	1	1	1	5	15	Yes	Dense	Diurnal	Patchy	1.62	1,53,56
<i>Aotus nigriceps</i>	0	0	0	6	3.5	No	Dense	Other	Patchy	2.71	53,57
<i>Gorilla gorilla</i>	0	0	0	2.5	4.5	No	Dense	Diurnal	Patchy	6.76	1,53
<i>Gorilla gorilla berengei</i>	1	1	0	2.5	12	Yes	Medium	Diurnal	Even	10.4	1,53,58
<i>Pan troglodytes</i>	1	1	1	6	50	Yes	Dense	Diurnal	Even	0.31	1,53,59
<i>Erythrocebus patas</i>	1	0	0	12.75	19.5	No	Medium	Diurnal	Even	2.28	1,6,53
<i>Papio anubis</i>	1	1	1	8	50	Yes	Medium	Diurnal	Even	21.5	53,60
<i>Macaca sylvanus</i>	1	1	1	6	24	Yes	Medium	Diurnal	Even	16.15	53,61
<i>Macaca radiata</i>	1	1	1	1.5	27.5	Yes	Dense	Diurnal	Even	7.13	53,62
<i>Macaca nigra</i>	1	0	0	8.5	15	Yes	Dense	Diurnal	Even	37.3	6,24,53,63

The presence or absence of mutual tolerance (trait 1), collaboration (trait 2), and partner preference (trait 3) is shown for each species, followed by estrous duration (in days), average group size, whether or not a dominance hierarchy is present, habitat type (open, medium, dense), whether a species is diurnal or not, whether food resources are clumped or not, and male body mass (in kilograms). References are as follows: 1, Hayssen et al. 1993; 2, Reynolds et al. 2000; 3, Leatherwood and Reeves 1983; 4, Robeck et al. 2005; 5, Arcese 1999; 6, Nowak and Paradiso 1983; 7, T. Brashares (personal communication); 8, Spinage 1982; 9, Miragaya et al. 2004; 10, Vila and Roig 1992; 11, Bravo and Fowler 2001; 12, Perez-Barberia and Gordon 2000; 13, Feh 1999; 14, Bennett and Hoffmann 1999; 15, Owen-Smith 1988; 16, de Oliveira 1998; 17, Gittleman and Harvey 1982; 18, Caro and Collins 1987; 19, Brown et al. 1996; 20, Seymour 1989; 21, Schaller and Crawshaw 1980; 22, Christiansen 1999; 23, Packer et al. 1991; 24, Silva and Downing 1995; 25, Rieger 1981; 26, Gittleman 1985; 27, Holekamp et al. 1997; 28, Holekamp and Smale 1998; 29, Hays and Conant 2003; 30, Nellis 1989; 31, Rood 1986; 32, van Staaden 1994; 33, Moss et al. 2001; 34, Bekoff 1977; 35, Creel S and Creel NM 2002; 36, Creel et al. 1997; 37, Gittleman and Harvey 1982; 38, Larivière and Pasitschniak-Arts 1996; 39, Baker et al. 2004; 40, Joshi et al. 1999; 41, Spady et al. 2007; 42, Gehrt and Fox 2004; 43, Herrera and Macdonald 1993; 44, Morris 1975; 45, Poglajen-Neuwall and Towell 1988; 46, Kays et al. 2000; 47, Ortega et al. 2003; 48, Herrera and Macdonald 1993; 49, de Barros Ferraz et al. 2005; 50, Jenkins and Eshelman 1984; 51, Dobson et al. 1998; 52, Smith and Gao 1991; 53, Rowe 1996; 54, Ostner and Kappeler 2004; 55, Hubrecht 1984; 56, Carnegie et al. 2005; 57, Baer et al. 1994; 58, Robbins 1999; 59, Jones et al. 1996; 60, Shaikh et al. 1982; 61, Küster and Paul 1984; 62, Parkin and Hendrickx 1975; 63, Bernstein et al. 1982.

To determine whether the 3 coalitionary traits are evolutionarily independent, that is, that the evolution of partner preference follows the evolution of collaboration and the evolution of collaboration follows the evolution of mutual tolerance, we used a concentrated changes test. This test determines the likelihood that evolutionary gains of a given trait were concentrated on areas of the phylogeny where another trait was already present (Maddison 1990). We tested the likelihood of collaboration (trait 2) being concentrated on areas of the tree where tolerance (trait 1) occurred, as well as the likelihood of partner preference (trait 3), given the presence of collaboration (trait 2). The test was performed in MacClade

Version 3; ambiguities in character states traced onto the phylogeny were resolved using the “Deltran” option, which delays transformations from one character state to the next until as near to the branches as possible (Maddison WP and Maddison DR 1992). To be conservative, we selected either character state as the ancestral state and counted only gains of the dependent trait concentrated on the independent trait. We used the 10 000-simulation option and tested the likelihood that as many or more gains occurred as could be expected in the phylogeny by chance.

We calculated independent contrasts for each variable. We used a simple linear regression where contrasts from coalition

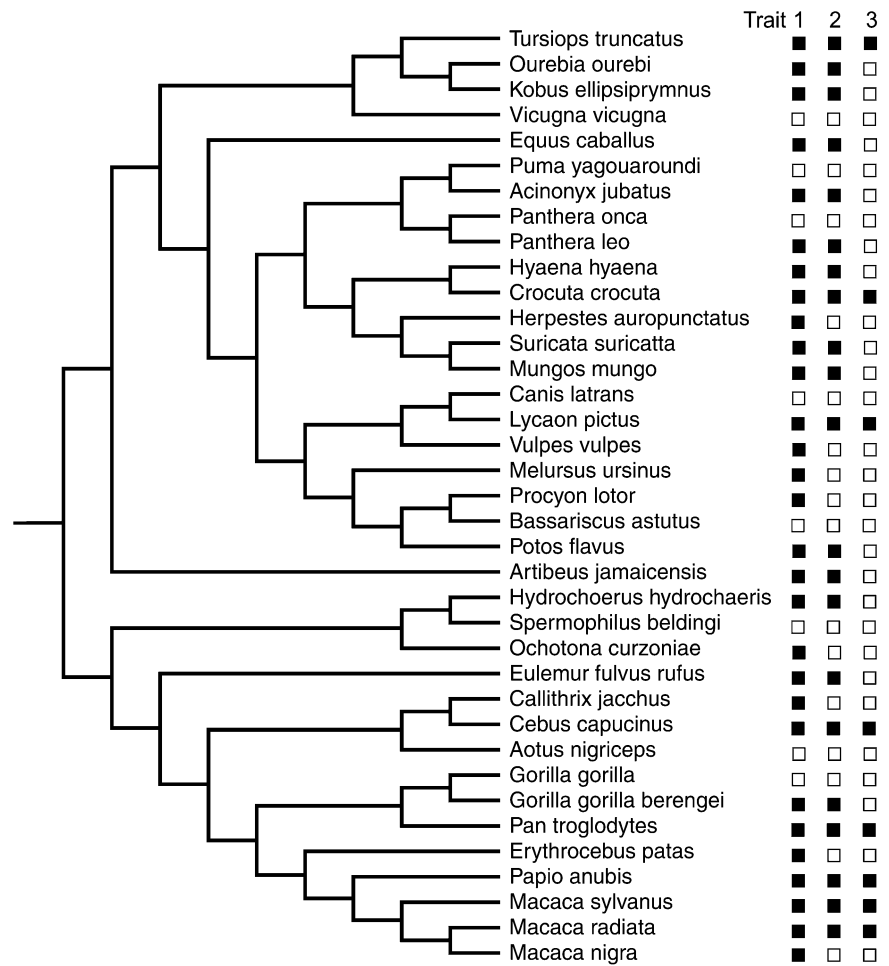


Figure 1

Complete phylogeny for all 37 species used in the analysis; equal branch lengths are assumed. The state of each character trait is indicated by the boxes to the right: mutual tolerance is trait 1, collaboration trait 2, and partner preference trait 3. Boxes are black if trait is present and white if trait is absent. Compiled from Purvis 1995; Gatesy et al. 1999; Murphy et al. 2001; Veron et al. 2004; Flynn et al. 2005; Lindblad-Toh et al. 2005; Johnson et al. 2006; Koepfli et al. 2007.

complexity index were the dependent variables and contrasts from all 6 social and environmental variables were the independent variables, along with body mass. With the exception of contrasts of group size and the presence or absence of a dominance hierarchy ($R = 0.52$), other independent variables were weakly correlated with each other ($R < 0.35$). The regression model fitted to the independent contrasts had no intercept, as is required when analyzing phylogenetically independent contrasts (Garland et al. 1992). Three of the variables were dichotomous: dominance hierarchy, activity period, and diet type. Contrasts for each variable were calculated using Compare 4.6b (Martins 2004). All analyses were performed with SPSS Version 10, and results were considered significant if $P < 0.05$.

RESULTS

The full regression model containing all 7 independent variables was significant ($R^2 = 0.638$, $F_{7,36} = 7.306$, $P < 0.0001$), but we were concerned that we overfit the model given only 37 cases (Green 1991). Thus, we removed body mass from the analysis and noted that its removal had no effect on the overall significance of the model or on the individual effects of the other 6 variables; therefore, we left it out of the final model. The 6-variable multiple regression was significant ($R^2 = 0.635$, $F_{6,36} = 8.71$, $P < 0.0001$) and explained 63.5% of the variation in coalition complexity. Social variables explained more of the variation in coalition complexity than did environmental variables. Estrous duration was positively correlated with

coalition complexity: as the number of days that females are sexually receptive increased, so did the species' likelihood to form a complex coalition. Dominance hierarchy was also positively correlated with coalition complexity, with species in which a hierarchy is present more likely to form complex coalitions. Group size also had a positive correlation: species with larger group sizes were more likely to form more complex coalitions (Table 2). None of the environmental variables were significantly correlated with coalition complexity.

The concentrated changes test suggested that it was unlikely that collaboration was evolutionarily independent of the

Table 2

Estrous duration, group size, and the presence of a dominance hierarchy are significantly positively correlated with an increase in coalition complexity

Variable	β Coefficient	P value	Partial η^2
Estrous duration	0.059	0.0023	0.520
Group size	0.033	0.0116	0.441
Dominance hierarchy	0.944	0.0066	0.471
Habitat type	-0.234	0.3393	-0.175
Activity period	0.123	0.7159	0.067
Food distribution	-0.206	0.5763	-0.103

Beta coefficients, P values, and partial η^2 (a measure of effect size) are shown from a simple linear regression with coalition complexity as the dependent variable. Significant ($P < 0.05$) values are indicated in bold.

evolution of mutual tolerance ($P < 0.001$) and that it was unlikely that partner preference was evolutionarily independent of collaboration ($P < 0.001$).

DISCUSSION

Many models of social evolution focus on environmental constraints, yet the evolution of coalitions, which is arguably one of the most complex types of social behavior, is more strongly correlated with social rather than environmental factors. We found that social factors explain more variation in coalition complexity than environmental factors. All 3 social variables (estrous duration, group size, and dominance hierarchy) were significantly correlated with coalition complexity, whereas none of the environmental variables (habitat type, diurnality, or diet type) were.

Existing hypotheses for the formation of multiple male groups and mutual tolerance stress the importance of female availability and social interactions among males (Altmann 1990). Tolerance and cooperation, which are both necessary factors in coalition formation, have been hypothesized to be favored among primate males when there is a limited ability to monopolize females in a social group (van Hooff and van Schaik 1994). If females are not monopolizable, the value of an individual female is lessened, so that males are more likely to share access to many reproductive females than to compete for access to one female (Strier et al. 2002). Our results for estrous duration and group size are consistent with these expectations. Long estrous duration (i.e., long receptive periods) may allow females to solicit multiple copulations, potentially from multiple males, and thus will decrease a single male's opportunity for monopolization (Eberle and Kappeler 2002; Ostner and Kappeler 2004). In species with cryptic female fertility, females may exhibit behavioral estrus, whereby they allow males to mate or actively solicit copulations for longer than their actual fertile period (Dixson 1998). Thus, one male cannot monopolize a female during the time she is most likely to conceive, and multiple males will be forced to share reproductive access. In saddle-backed tamarins (*Saguinus fuscicollis*), for example, females appear to have no overt signs of estrus and will copulate with males at any time in the ovarian cycle, thereby confusing paternity and making it more likely that multiple males will remain in the group and contribute to offspring care (Terborgh and Goldizen 1985).

Large group sizes will also limit male monopolization of females through simple male-to-female availability ratios. If large groups have more females per male, this might mitigate intense male-male competition because competition for females will be reduced (Altmann 1990; Janson 1992). A previous comparative study by Mitani et al. (1996) found a positive relationship between the number of males and females in groups, with large groups of females more likely to have multiple males. When single males are unable to monopolize all the females in a group, less effort should go into male-male competition, and mutual tolerance may be more likely to occur (van Hooff and van Schaik 1994).

A significant effect of dominance hierarchies also highlights the importance of male competition. In species with a dominance hierarchy, subordinate individuals often obtain little reproductive success (Dixson et al. 1993; Ellis 1995). The formation of coalitions, however, may enable lower ranked individuals to gain reproductive opportunities. African wild dogs (*Lycaon pictus*) have been shown to use coalitionary support to successfully increase their dominance rank (de Villiers et al. 2003), and savannah baboons (*P. cynocephalus*) will form coalitions in which one of the members will distract a female-guarding male while the other member will begin guarding the displaced male's receptive female (Alberts et al. 2003).

Decreases in group competition may favor mutual male tolerance, and once males have aggregated, other socioecological factors may play a role in maintaining multiple male groups and even encourage increased levels of cooperation and coalition formation. There are several potential benefits to males to remain mutually tolerant, including increased protection from predators, increased opportunity for inclusive fitness benefits, and potential coalition support by group members against intruders (Ostner and Kappeler 2004). Even with the necessity of sharing copulations, an individual's lifetime reproductive success can be increased through coalition formation (Packer et al. 1991; Clutton-Brock and Isvaran 2006).

The lack of a correlation between coalition complexity and any of our environmental variables is puzzling. Environmental correlates of social organization have been found in a diverse array of species. Gregariousness in various mongoose species (Herpestidae) has been shown to be correlated with diurnality and an insectivorous diet (Rood 1986). In populations of olive (*Papio anubis*) and hamadryas baboons (*Papio hamadryas*), female philopatry and affiliation, as well as the tendency to form female-female coalitions, are greater in populations with clumped food resources and potentially higher levels of predation (Barton et al. 1996). The lack of a significant relationship with any of the environmental correlates is, however, consistent with the hypothesis that female distribution and behavior is largely influenced by the distribution of resources, whereas male behavior is often influenced by the distribution or behavior of females (Wrangham 1980; Altmann 1990; Mitani et al. 1996).

The results of our concentrated changes test indicate that evolutionary gains of collaboration occur more often than expected by chance on those branches of the tree that also show mutual tolerance, and the occurrence of partner preference occurs more often on those branches that have collaboration. This supports our idea that each trait may build on the last in a progression of increasing complexity.

In summary, we found that our coalitionary trait metric generates new insights into the evolution of complex coalitions. By dividing complex coalitionary behavior into a set of component parts, we create a continuous view of coalitionary behavior. Our comparative analysis suggests that the evolution of reproductive coalitions among male mammals was influenced more by a species' social characteristics than its environmental qualities and that more complex coalitions are more likely to evolve in species where males have limited abilities to monopolize females. Of course, we must always interpret results from comparative analyses with a certain amount of caution because results are always correlative in nature and do not necessarily reflect causality. Ultimately, however, we believe that a trait-based approach to studying coalitionary behavior will allow us to identify rudimentary coalitionary behavior in other taxa and will thus increase our understanding of the evolution of complex social behavior.

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