

Variation in dominance hierarchies among group-living animals: modeling stability and the likelihood of coalitions

Mark Broom,^a Andreas Koenig,^b and Carola Borries^b

^aDepartment of Mathematics, University of Sussex, Brighton BN1 9RF, UK and ^bDepartment of Anthropology, Stony Brook University, Stony Brook, NY 11794–4364, USA

Dominance hierarchies based on resource holding potential (RHP) or age are central to the social structure of many group-living animals. Nonhuman primate females and some other mammals are unusual because ranks can depend on kin support or follow an inverse age-graded pattern independent of kin. Whereas the former hierarchies are mediated by frequent coalitions leading to long-term stability, the latter are unstable due to individualistic contests and occasional revolutionary coalitions. We use mathematical modeling to investigate this variation, based on the interaction of triads, subgroups of the group consisting of 3 individuals. This produces 4 key situations, namely that relationships can be either stable or unstable, and involving coalitional support or not. Varying the parameter values of our model and applying it to real-world examples, we conclude that the emergence of different dominance hierarchies depends on 6 major factors. In addition to RHP, reproductive skew and demography often suggested previously, we stress the importance of 1) the variance in relatedness; 2) the costs and likelihood of interventions; and 3) the value of resources and rank in different life stages, which might be tightly linked to the life history of a species. *Key words*: age-inversed hierarchies, ESS, evolutionary games, matrilineal hierarchies, triads. [*Behav Ecol* 20:844–855 (2009)]

Agonistic interactions on an individual basis are part of everyday life for most animals (Huntingford and Turner 1987). In group-living animals, these interactions may result in complex hierarchical structures (Pusey and Packer 1997). The formation and parameters of these dominance hierarchies have been the subject of an enormous research effort since early observations of Schjelderup-Ebbe (1922) of agonistic behavior in birds (overview in, e.g., Drews 1993). At its simplest, rank may be determined by differences in resource holding potential (RHP; e.g., Parker 1974) expressed via relative difference in size, strength, or fighting abilities (Hammerstein 1981; cervidae: Clutton-Brock et al. 1982; primates: Alberts et al. 2003; Pereira 1995) with rank following an inverted U-shape with age (e.g., Packer 1979; Alberts et al. 2003). However, factors other than RHP may be equally or even more important particularly in permanently group-living species (e.g., Bernstein 1981; Pusey and Packer 1997; Chapais 2004). Apart from genetic influences on aggressiveness and rank (Craig et al. 1965; Kikkawa et al. 1986), 3 general patterns seem to prevail: 1) increasing dominance with age, experience, or tenure (bovidae: Festa-Bianchet 1991; Rutberg 1986; cervidae: Clutton-Brock et al. 1979; herpestidae: Creel et al. 1992; Clutton-Brock et al. 1999; equidae: Lehmann et al. 2003; elephantidae: Archie et al. 2006; hyaenidae: Smale et al. 1997; Engh et al. 2002; primates: Sugiyama 1976; van Noordwijk and van Schaik 2001); 2) decreasing dominance with age (“age-inversed”; primates: Borries et al. 1991; Hrdy SB and Hrdy DB 1976; and possibly herpestidae: Clutton-Brock 2002; procyonidae: Hirsch 2007); and 3) nepotistic hierarchies with kin ranking closely together (hyaenidae: Holekamp and Smale 1991; primates: Kawai 1958).

One way of trying to explain this variance is to search for the ecological basis of these patterns, and in recent years, efforts have focused on predicting these patterns of hierarchies based on the nature of resources and forms of competition (e.g., Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Connor and Whitehead 2005). Such ecological explanations may particularly apply to females for whom access to resources is more strongly limiting reproduction than for males (Trivers 1972) and for whom competition over food might be particularly important. Accordingly, variation in female dominance hierarchies should be fundamentally influenced by the strength of contest competition within and between groups (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). It has been suggested that resources of high quality occurring in well-defined patches or food items with a long handling time should elicit contest competition (Isbell et al. 1998; Koenig and Borries 2006). Such patches or items may be monopolizable leading to differential energy gain and fitness based on dominance rank (Janson and van Schaik 1988), female philopatry, and nepotistic alliances. If in particular contest competition within groups is strong, female dominance hierarchies should be organized along matrilineal with a female and her daughters ranking near to each other (van Schaik 1989).

Such matrilineal hierarchies have been found in various primate species (macaques: Kawai 1958; Bernstein 1969; Missakian 1972; baboons: Hausfater 1975; Dunbar 1980; vervet monkeys: Cheney et al. 1981; capuchin monkeys: Robinson 1981) as well as in hyenas (Holekamp and Smale 1991; Engh et al. 2000). Matrilineal hierarchies can be stable over many years with very rare rebellions (Hausfater et al. 1982). Stability is achieved via coalitional behavior with kin (conservative alliances) and with nonkin (bridging alliances; Chapais et al. 1991; Chapais 1992; Silk 1993; Chapais and Gauthier 2004; for a discussion of terminology and effects of coalitions, see van Schaik et al. 2006). Variation in the structure of matrilineal hierarchies seems to be the result of demographic factors such as the absence of suitable alliance

Address correspondence to M. Broom. E-mail: m.broom@sussex.ac.uk.

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partners in slowly reproducing populations (Hausfater et al. 1987; Data and Beauchamp 1991; Chapais 1995) or differences in the timing of peak reproductive “value” across species (Chapais and Schulman 1980; overview in Chapais 2004).

In contrast, if resources are abundant or not defensible, there is little need or possibility for contest competition. Food patches or food items cannot be monopolized, and differences in resource partitioning or fitness are not expected (Janson and van Schaik 1988). Consequently, dominance hierarchies should be weakly developed or nonexistent (“egalitarian”; van Schaik 1989) as suggested for muriquis (Strier 1999) and mountain baboons (Barrett et al. 1999). Many primate female hierarchies are, however, individualistic following either of 2 patterns. Individualistic hierarchies following an age- or tenure-related pattern have been shown for female ring-tailed lemurs, gorillas, and chimpanzees (e.g., Nakamichi and Koyama 1997; Wittig and Boesch 2003; Robbins et al. 2005; Thompson et al. 2007). Quite likely such a pattern is maintained through winner/loser effects (e.g., Chase et al. 1994; Dugatkin 1997; Beacham 2003) enabling older individuals to remain dominant even if size differences become negligible (Thouless and Guinness 1986; Coté 2000). At the same time such hierarchies might be inherently unstable, if dispersing females change the group composition (Robbins et al. 2005). In contrast to these “age-positive” hierarchies are individualistic patterns in which females rise in rank to top positions in the hierarchy, although they may still be immature and markedly smaller than adult females, and old females are found in the bottom positions (cf. Hrdy 1977, p. 167–174). Thus, the pattern appears to be unrelated to RHP but instead follows an inverse age-graded pattern (Hanuman langurs: Hrdy SB and Hrdy DB 1976; Borries et al. 1991; mantled howler monkeys: Glander 1980; Jones 1980; Phayre’s leaf monkeys: Koenig et al. 2004). Age-inversed hierarchies seem to be even more unstable than age-positive hierarchies because rank may change within a few months and following immigrations.

Although the patterns of hierarchies seem to be rather clear, the initial emergence of different hierarchies and the proposed links to dispersal, demography, and reproductive skew are less well understood. In general, both individualistic forms of hierarchies are characterized by an absence of nepotistic alliances and a lack of stability. Since in several species females disperse and, hence, relatedness is supposedly low, the instability may be due to an absence of suitable alliance partners. However, recent observational and genetic evidence indicates that despite the presence of suitable coalition partners and occasional coalitions with kin (Harcourt and Stewart 1989; Borries 1993; Starin 1994; Watts 1997; Pope 2000; Bradley et al. 2007), stability and a matrilineal hierarchy are not achieved. Likewise, age-inversed hierarchies and female philopatry may co-occur in species such as Hanuman langurs (Koenig and Borries 2001) making it hard to understand why coalitions are rare despite the presence of kin. Instead, in Hanuman langurs, immature females may form revolutionary coalitions (also called “all-up”; cf. van Schaik et al. 2004) with each other and raise to the top positions in the hierarchy (Borries et al. 1991; Apelt 1995). Hrdy SB and Hrdy DB (1976) attempted to explain the presence of an age-inversed pattern based on the “residual reproductive value” such that older females defer to younger ones (for matrilineal societies, see also Combes and Altmann 2001). However, the likelihood of agonistic interactions may be increasing instead of decreasing with low residual reproductive value (Broom et al. 2004 for males). Yielding rank in these groups might only be beneficial if females have a high degree of relatedness (Hrdy 1977). The pattern of relatedness is, however, unclear.

Lastly, in the socioecological model, individualistic hierarchies (age- or tenure-related or age-inversed) are viewed as intermediate between no hierarchies and matrilineal hierarchies

(Sterck et al. 1997). It is thought that the absence of hierarchies relates to an absence of contest competition, whereas matrilineal hierarchies relate to strong within-group competition in which resource partitioning and reproductive skew are strong and benefits via kin support are high. Individualistic hierarchies are suggested to emerge if within-group contest competition is intermediate. Hence, the absence of coalitions and with it long-term stability are explained by weak benefits of supporting kin. Although certainly stronger skew in resource partitioning might lead to higher indirect benefits via kin support and consequently to matrilineal hierarchies, formal tests of these ideas have not been performed due to the lack of adequate data (Koenig 2002; Chapais 2004).

In summary, although dispersal, demography, and reproductive skew may account for some of the variation in matrilineal hierarchies (Chapais 2004), much of the variation in these hierarchies remains unexplained. More importantly, it remains unclear why and under what conditions other hierarchies occur, that is, it remains unclear why age-inversed or age-related patterns occur instead of matrilineal patterns (or vice versa), why some dominance hierarchies are inherently stable and others are not, and why some of these hierarchies are stabilized through coalitions and others are not. The current paper approaches this controversy via mathematical modeling. More specifically, we provide a framework for the analysis of the stability and the likelihood of the occurrence of coalitions within a dominance hierarchy in terms of some key features of a population such as relatedness, division of resources, and potential costs of conflicts. Using this framework, we show that the patterns of hierarchies are not just the outcome of the strength of competition or relatedness, but contingent on several factors including the variance of within-group relatedness (affecting the indirect benefits for an alliance partner), costs and likelihood of coalitions (affecting the costs for an alliance partner), resource needs of contenders, and value of ranks for the contenders (both affecting the “willingness” to participate in a contest).

In the following section, we outline our model, based on the interactions of 3 individuals (triads) within a larger group with an established hierarchy. Rather than investigating the formation of hierarchies (e.g., Chase 1974; Broom 2002; Broom and Cannings 2002; Chase et al. 2002) or the formation of coalitions (Mesterton-Gibbons and Sherratt 2007) and the impact of winner/loser effects (e.g., Dugatkin 1998; Johnstone and Dugatkin 2000; Pandit and van Schaik 2003; van Schaik et al. 2004), we focus on the interactions featuring a potential contest that can change the order within the hierarchy, as well as possibly incurring costs to the participants. We identify the different roles of the players, their available strategies, parameter values, and rewards based on a combination of these. We then explore the effect of varying the parameter values on the likelihood of a stable hierarchy and the formation of coalitions. In the subsequent section, we relate our parameter values to real-world situations and then explore some special cases and examples. The final section is a discussion of our model and our conclusions.

GENERAL MODEL

We consider a group of animals where there is a dominance hierarchy and individuals can challenge another individual to improve their place in the hierarchy. If the challenger wins, the contenders swap places. A third individual may observe a challenge in progress and decide to join either side or ignore the contest. The observer’s only incentive to fight is to help out a relative (hence increasing its own inclusive fitness), rather than in the hope of reciprocal action. This is of course a simplification, and reciprocity has received significant attention in the game-theoretic literature, originating with Trivers (1971).

Such behavior is plausible whenever individuals may interact repeatedly, see for instance the extensive work on the classical prisoners' dilemma (Axelrod 1984) and subsequent developments on indirect reciprocity such as Nowak and Sigmund (1998). We impose this restriction for 2 reasons. First, reciprocity would be a lot harder to model as we would need information about the group structure and the likelihood of meetings between certain individuals so that the range of potential strategies would be extensive. Second, it is also likely to be of secondary importance compared with the benefit of assisting relatives in this particular scenario where although reciprocity has been observed (e.g., in chimpanzee and baboon males), coalitions are more likely and more commonly observed in matrilineal hierarchies (Chapais 1995). Thus, in this first instance, we shall ignore it, although it could be a useful addition to later versions of this model.

For simplicity, we assume that the outcome of the contest and the observer's decision do not have an influence on its own position in the hierarchy, although the positions of the principal contestants can be significantly altered. To include such a factor would greatly complicate the model, and the focus of this paper is the consideration of the influence of factors such as the variance of relatedness and the individuals' different life-history stages on hierarchy stability and the likelihood of coalitions. Furthermore, we do not explicitly include any influence of the observer's properties relative to the other individuals, although the formulation of the model is general enough that these could be included (for instance, the probabilities of winning in aggressive contests could be functions of the size of each individual). For simplicity again, in our examples, we treat the probability of winning and hence also the likelihood of intervention, as being independent of the observer's properties. Through this simplification, we hope to clarify the consequences of a third party's interventions, and we obtain predictions in accordance with behavior in real situations based on the key factors that are our primary interest here, involving relatedness, life history, and the general cost to and opportunity of interventions.

We assume that A is of higher rank than B and B challenges A for its position. Observer C must choose to help A, B, or neither (N; see specifications in Table 1). Given the choice made by C, A and B choose strategy H (Hawk) or D (Dove) simultaneously. This is again a significant simplification of real contests where there can sometimes be a lot of signaling between individuals, and a contest may involve a long sequence of choices (e.g., Packer 1977, 1979). In particular, our conclusions may change if C was allowed to alter its decision after the strategies of A and B were revealed; A and B might then logically also be able to update their strategies after a withdrawal as the entry or exit of an individual from a contest is the most obvious cue for a strategic choice. We have chosen the simplest contest which involves the 2 actions of observer choice, followed by strategic choice of the principals. This is mimicking "simple" coalitionary support that goes along with spontaneous outbursts of aggression as seen for example in bonnet macaques (Silk 1992). An individual who plays Hawk is one who is prepared to engage in a physical conflict, and an individual who plays Dove is not. An actual conflict, and thus the chance for third party intervention, only arises when both individuals play Hawk. Hence, if one chooses H and the other D then the H player wins (irrespective of C's choice). Similarly, if both choose D, each wins with equal probability (although this is not crucial, as long as both have some nonzero chance of success). If both choose H, A wins with probability p_A if C supports A, p_B if C supports B, and p_N if C supports neither (where $p_A > p_N > p_B$). Throughout the paper, we will interchangeably refer to C supporting A (or B) and C playing A (or B). If C supports neither A nor B, then we shall say that C plays N. As stated above, these 3 probabilities could depend

Table 1
Players, rules, and parameters

Players	Position
A	High rank
B	Challenger, low rank
C	Observer (no rank specified)
Rules	
B challenges A's position, and C can choose between supporting A, B, or neither (N)	
Given C's choice, A and B simultaneously choose Hawk (H) or Dove (D)	
HVD or DVH	H always wins regardless of C
DVD	A and B win with equal probability
HVH	A's probability of winning: p_A if C supports A, p_B if C supports B, and p_N if C supports neither ($p_A > p_N > p_B$)
Parameters	
κ	Cost for the loser of an HVH contest
$\phi\kappa$ ($0 \leq \phi \leq 1$)	Cost for player C if it supports the loser of an HVH contest
ε	C's extra cost of supporting A or B
V_A (<0)	A's gain if B replaces A
V_B (>0)	B's gain if B replaces A
V_C	C's gain if B replaces A

on the sizes of the 3 competitors and so could be different for each possible subgroup of 3 individuals (triads) within the group. The loser of a HVH contest pays a cost κ , if player C supported this loser, it pays a cost $\phi\kappa$ ($0 \leq \phi \leq 1$). C pays an extra cost ε if it "fights" (i.e., supports A or B) whatever strategies are played. This is another simplification, and it is possible that a larger cost might occur for more violent contests (HVH) than others, for instance; thus, we could consider 4 such cost parameters but providing that the losing cost κ is large compared with the extra cost, we believe that this simplification is reasonable. If B replaces A, then B gains V_B (>0), A gains V_A (<0), and C gains V_C (which represents a gain in inclusive fitness based on its relatedness to A and B). Otherwise, all remain in their current place and so gain 0.

Thus, we consider how a population behaves by considering triads. The hierarchy within the whole group or population will be stable if no switching of places can occur for any triad. We will consider what types of hierarchies will result and investigate when coalitions should occur (i.e., C chooses a strategy other than N).

Based on these considerations, one can calculate the rewards to the individuals for each possible combination of strategies (see Table 2), which can then be used to find the optimal strategies of the different participants; the calculations for general p are shown in Appendix 1.

The value of p depends on the choice of C. There are 3 values of p ($p_A > p_N > p_B$) that yield 4 different situations for V_A and 4 for V_B (which will yield $4 \times 4 = 16$ situations). We label these cases A1–A4, B1–B4

$$\begin{aligned}
 \text{A1} : V_A &< \frac{-(1-p_B)\kappa}{p_B}, \\
 \text{A2} : \frac{-(1-p_B)\kappa}{p_B} &< V_A < \frac{-(1-p_N)\kappa}{p_N}, \\
 \text{A3} : \frac{-(1-p_N)\kappa}{p_N} &< V_A < \frac{-(1-p_A)\kappa}{p_A},
 \end{aligned}$$

Table 2
Payoffs for each player for each of the 12 possible combinations of choice by A, B, and C

A choice	B choice	C choice	A payoff	B payoff	C payoff
D	D	A or B	$V_A/2$	$V_B/2$	$V_C/2 - \varepsilon$
D	D	N	$V_A/2$	$V_B/2$	$V_C/2$
H	D	A or B	0	0	$-\varepsilon$
H	D	N	0	0	0
D	H	A or B	V_A	V_B	$V_C - \varepsilon$
D	H	N	V_A	V_B	V_C
H	H	A	$(1 - p_A)(V_A - \kappa)$	$(1 - p_A)V_B - p_A\kappa$	$(1 - p_A)V_C - \varepsilon - (1 - p_A)\varphi\kappa$
H	H	B	$(1 - p_B)(V_A - \kappa)$	$(1 - p_B)V_B - p_B\kappa$	$(1 - p_B)V_C - \varepsilon - p_B\varphi\kappa$
H	H	N	$(1 - p_N)(V_A - \kappa)$	$(1 - p_N)V_B - p_N\kappa$	$(1 - p_N)V_C$

$$A4 : V_A > \frac{-(1 - p_A)\kappa}{p_A},$$

$$B1 : V_B < \frac{p_B\kappa}{(1 - p_B)},$$

$$B2 : \frac{p_B\kappa}{(1 - p_B)} < V_B < \frac{p_N\kappa}{(1 - p_N)},$$

$$B3 : \frac{p_N\kappa}{(1 - p_N)} < V_B < \frac{p_A\kappa}{(1 - p_A)},$$

$$B4 : V_B > \frac{p_A\kappa}{(1 - p_A)}.$$

We consider combinations of A and B conditions to find the optimal choice for C and hence the optimal play for A and B. As outlined in Appendix 2, in total, there are 9 possible scenarios; A/B is one of H/VH, HVD, DVH and this occurs in combination with C playing one of A, B, or N (there are another 3 involving DvD, but from Appendix 1, we know that these will not occur). In fact, 2 of these 9 never occur (C supports A, DVH; C supports B, HVD) leaving 7. Table 3 lists the possibilities where C should support A, B, or N in particular mentioning when a stable hierarchy results (A plays H, B plays D so it stays as it is with probability 1) and where coalitions occur, that is, C does not play N.

VARYING THE PARAMETER VALUES

The effect of the parameters

We now investigate the effect of each of the parameters in turn on the optimal strategies in this 3-player game (results are obtained from Appendix 2 and Table 3):

- Increasing the participation cost for individual C, ε makes N more likely, and A and B less likely.
- Increasing the Hawk versus Hawk loser cost, κ or the proportion of this cost paid by individual C if on the losing side, φ makes N more likely, and A and B less likely.
- Increasing the advantage to A of having the support of C in a Hawk versus Hawk contest, $p_A - p_N$ makes A more likely and N less likely.
- Increasing the advantage to B of having the support of C in a Hawk versus Hawk contest, $p_N - p_B$ makes B more likely and N less likely.
- Increasing the probability of an A victory in a Hawk versus Hawk contest where C does not intervene, p_N makes A more likely, B less likely, and the effect on N varies with other parameters.

- Increasing the reward to individual C in the event of a victory for B, V_C makes A less likely, and B more likely.
- Increasing the modulus of the above reward (and so the importance of the contest to C), $|V_C|$ makes N less likely.
- Increasing the reward to A for a B victory, V_A (i.e., decrease the loss to A) moves the situation from lower numbered to higher numbered A conditions, that is, A1 \rightarrow A2 \rightarrow A3 \rightarrow A4 making N more likely and B (generally) less likely.
- Increasing the reward to B for a B victory, V_B has a similar effect on the B conditions, that is, B1 \rightarrow B2 \rightarrow B3 \rightarrow B4 making N less likely and A (generally) more likely.

In general, whatever the values of the other parameters, there is a value $\varepsilon_{\text{critical}}$ such that if $\varepsilon > \varepsilon_{\text{critical}}$ individual C will not get involved in a coalition and if it is under this critical value, then it will be involved in a coalition (whether this is with A or B is decided by the other parameters). In some cases, this critical value is 0 so that coalitions do not occur, in others, it is some positive number depending on the other parameter values. Here we note that Mesterton-Gibbons and Sherratt (2007) consider a different model of coalition formation where a triad of individuals each independently chooses whether to offer to join a coalition with one or more of the others (or not), where making such an offer is costly, and the division of resources depends on the properties of the individuals (so all 3 or none could be in a coalition). True coalitional contests (2 vs. 1) typically occur when the weaker individuals join together to secure resources and are more likely when variance in fighting ability or the benefit of resources to the winners are largest. The most striking similarity to our model is the existence of 2 critical values of the cost of coalition entry, where different solutions occur when the true cost is above, below, or between these critical values.

Note that the more complex situations may be unlikely to occur in practice. It is likely that $1 - p_B$ and p_A are noticeably greater than $1/2$ (these are the probabilities of the coalition of 2 defeating the single individual in the 2 possible cases) so that both A1 and B4 will require injury costs to be low compared with the value of a high hierarchy position. Ignoring these 2 possibilities, there is only a single region where Hawk versus Hawk contests occur, in B3; A2 if $-\varepsilon/(1 - p_N) < V_C < \varepsilon/p_N$. In all other cases, contests would be settled peacefully in the favor of one of the parties. All regions marked with an asterisk in Table 3 do not occur without A1 or B4.

Thus, possible behavior is reduced to the following conditions (see also Table 4):

- B1—C plays N, A wins with a stable hierarchy;
- B2— $V_C < \varepsilon$, C plays N, A wins with a stable hierarchy;
- $V_C > \varepsilon$, C supports B, B wins and the hierarchy is altered;
- B3, A3, A4— $V_C < -\varepsilon$, C supports A, A wins with a stable hierarchy;

Table 3
Optimal choices for C and optimal play for A and B

C plays	A plays	B plays	Conditions	Stable hierarchy?	Coalitions?	Needs B4 or A1(?)
A	H Or	D	B3; A3, A4 B3; A1, A2	$V_C + \epsilon < 0$ $(1 - p_N)V_C + \epsilon < 0$	Yes	Yes
A	H Or	H	B4; A3 B4; A1, A2	$p_A V_C + \epsilon + (1 - p_A)\phi\kappa < 0$ $(p_A - p_N)V_C + \epsilon + (1 - p_A)\phi\kappa < 0$	No	Yes *
B	D Or	H	B2; A2, A3, A4 B3, B4; A2	$V_C - \epsilon > 0$ $p_N V_C - \epsilon > 0$	No	Yes
B	H Or	H	B2; A1 B3, B4; A1	$(1 - p_B)V_C - \epsilon - \phi p_B \kappa > 0$ $(p_N - p_B)V_C - \epsilon - \phi p_B \kappa > 0$	No	Yes *
N	H Or Or	D	B1 B2; A2, A3, A4 B2; A1	$V_C - \epsilon < 0$ $(1 - p_B)V_C - \epsilon - \phi p_B \kappa < 0$	Yes	No *
N	D Or Or	H	B3; A3, A4 B4; A4 B4; A3	$V_C + \epsilon > 0$ $p_A V_C + \epsilon + (1 - p_A)\phi\kappa > 0$	No	No * *
N	H Or Or Or	H	B3; A2 B3; A1 B4; A2 B4; A1	$-\epsilon/(1 - p_N) < V_C < \epsilon/p_N$ $-\epsilon/(1 - p_N) < V_C < (\epsilon + \phi p_B \kappa)/(p_N - p_B)$ $-(\epsilon + (1 - p_A)\phi\kappa)/(p_A - p_N) < V_C < \epsilon/p_N$ $-(\epsilon + (1 - p_A)\phi\kappa)/(p_A - p_N) < V_C < (\epsilon + \phi p_B \kappa)/(p_N - p_B)$	No	No * * *

The 7 possible optimal combinations of choices are listed (there are 5 combinations which are in fact never optimal) together with the parameter conditions that give the particular combination. The combinations that are stable, involved a coalition, or result from the more extreme parameter values are also indicated.

- $V_C > -\epsilon$, C plays N, B wins and the hierarchy is altered;
- $B3, A2 - V_C < -\epsilon/(1 - p_N)$, C supports A, A wins with a stable hierarchy;
- $-\epsilon/(1 - p_N) < V_C < \epsilon/p_N$, C plays N, and there is a Hawk-Hawk contest;
- $V_C > \epsilon/p_N$, C supports B, B wins and the hierarchy is altered.

Note that in B3, A2 all 3 possible contests HVD, HVH, and DVH are possible, determined by the choice of C which in turn is determined by its relatedness to A and B.

The meaning of the parameters

How do these general parameter effects influence behavior? Obviously, this will depend on the specific situation of a given pop-

ulation of animals as it may vary in terms of factors affecting the parameter values. In the following, we briefly discuss 4 factors and their effects. We do not aim at a complete evaluation of all possible aspects. Rather, we intend to provide examples which should illustrate the general explanatory value of the parameter effects.

Arboreal versus terrestrial groups

It has been shown recently that arboreal primate groups are characterized by lower rates of agonism and generally less despotic hierarchies (Wheeler BC, Koenig A, in preparation). This finding might coincide with generally higher costs of interference which would make coalitions less likely (see, e.g., Noë and Sluiter 1990). Specifically, in such groups, it might be difficult for a third party to influence fights ($p_A - p_N$ small, $p_N - p_B$ small), losing could be costly, for example, falling from trees (κ large), the chances of the third party paying this cost

Table 4
Conditions on the parameters for stability and coalitions in the nonextreme cases

		Coalitions	
		No	Yes
Stability	No	B3; A3, A4; $V_C > -\epsilon$ B3; A2; $-\epsilon/(1 - p_N) < V_C < \epsilon/p_N$	B2; $V_C > \epsilon$ B3; A2; $V_C > \epsilon/p_N$ B3; A3, A4; $V_C < -\epsilon$
	Yes	B1 B2; $V_C < \epsilon$	B3; A2; $V_C < -\epsilon/(1 - p_N)$

is low because it might not get a chance to fight (ϕ small), the energetic/time payment for trying to interfere will be higher (ϵ large). All these (except ϕ small) will generally make coalitions unattractive and harder to achieve. Variation in group spread (even in terrestrial species) may give a similar result in a different way. If groups need to spread out because of food dispersion or because low predation risk allows them to do so, then the number of occasions that 3 individuals are together for potential contests is reduced (see e.g., Hill and Okayasu 1996). Thus, individuals may be just as likely to enter coalitions if given the opportunity, but these opportunities, and thus the occurrence of coalitions, may be less likely.

The effect of group relatedness

It is generally expected that in groups composed of individuals of low relatedness coalitions are less likely (e.g., van Schaik 1989). However, this prediction seems only partly correct. If the degree of relatedness of A to C is r_A and of B to C is r_B , then $V_C = r_A V_A + r_B V_B$ (remember that $V_A < 0$, $V_B > 0$). If all these relatedness parameters are of similar value, especially if close to 0 (nonrelatives) but also if large (e.g., all sisters), then $|V_C|$ is small and coalitions are unlikely to occur. If there is significant variation in relatedness, then a potential observer is likely to encounter contests between a pair of individuals, one of which is a close relative and one of which is not. If the challenger is the relative, then V_C will likely be large and positive, and if the challenged individual is the relative, then V_C will likely be large and negative, in either case a favorable situation for a coalition. Thus, the more varied the relatedness within a group, the more likely coalitions will be. Applied to nonhuman primates or other group-living animals, this finding means that small groups consisting of a single matriline should be less likely to show coalitionary behavior (e.g., Hill and Okayasu 1996) than groups composed of several matriline. In addition, the number of males and reproductive skew are likely to influence this relationship. If groups contain only a single male, all offspring are paternal half-siblings and relatedness is a function of maternal relatedness, that is, the number of matrilines (Hrdy 1977). If groups contain multiple males, low reproductive skew among these males should lead to several clusters of related and unrelated offspring (depending on the relatedness of males; see also Lukas et al. 2005).

Juvenile resource needs

In many animals with extended juvenility, as for instance in primates, "juveniles" are very susceptible to malnutrition because of somatic and particularly brain growth (Janson and van Schaik 1993; Deaner et al. 2003). If we assume that juveniles are or become dominant, then V_A is large and negative, V_B small and positive, which indicates high stability. In contrast, assuming that juveniles are subordinate, V_A is large and positive, V_B small and negative, which indicates low stability. Note that because $r_A V_A + r_B V_B = V_C$, V_C will tend to be large if the juvenile is subordinate and small if it is dominant; in both cases, this reinforces the tendency above. In particular, a population whereby juveniles automatically slot into high positions will be stable. This is illustrated in Table 5.

The effect of difference in skew

Beginning with work in the 1980s (Emlen 1982; Vehrencamp 1983), it has been suggested that skew in energy or reproductive gain depending on dominance is synonymous with despotic societies. Moreover, it was suggested that strong skew in reward is linked to the emergence of matrilineal societies with frequent coalitions (e.g., van Schaik 1989; Sterck et al. 1997). Stronger skew implies that V_B is large and V_A is large and negative. V_C is large and positive if C is related to B and large and negative if C is related to A. Thus, generally N is less likely

Table 5
Situations where one player gives way

	A1	A2	A3	A4
B1	A*	A*	A*	A*
B2	A	A/B	A/B	A/B
B3	A	A/B	A/B	A/B
B4	—	B	B	B*

If A[H]vB[D] is a solution under some parameters in the region, then it is marked A (and A* if no other solution is possible). Similarly, if A[D]vB[H] is a solution, it is marked B (B* if the only solution). Sometimes both are possible, and this is marked A/B. The possibilities of HVH are not considered.

and the hierarchy will be less stable (from a viewpoint of B and C overthrowing A). Applied to the previous example of juveniles, more skewed rewards will tend to make V_C negative (when juveniles are dominant). Thus, C will support A when needed. In general, this supports the claim that in despotic societies with strong skew, coalitions are more likely than in groups with less skew (van Schaik 1989).

Note that we do not consider the possibility that fighting ability may be affected by rank; if an individual is stronger, it may be more likely to acquire higher rank, but possession of this rank does not increase its strength (e.g., due to greater access to resources). In real populations, higher rank may well lead to higher strength, but we are primarily looking at the occurrence and the effects of coalitions, and we ignore this potential feedback for the sake of simplicity. Rank may of course affect attitude and strategy (so we assume if both evolutionarily stable strategies of Hawk versus Dove are possible in a contest, the default is that the higher rank plays Hawk).

SPECIAL CASES

Evenly matched individuals

In this section, we make the most simplistic assumption, that of individuals of equal abilities, in order to illustrate the effects of some of the key parameters in as clear a way as possible while maintaining some generality.

Consider the case where all animals are of equal strength, that is, $p_N = 1/2$ and $p_A = 1 - p_B$. We shall consider within this the cases where gaining the higher position is of equal value to the protagonists ($V_A + V_B = 0$), where it is more valuable to the challenger ($V_A + V_B > 0$) and more valuable to the holder ($V_A + V_B < 0$). We suppose that $(1 - p_A)/p_A = \chi$, so $\chi < 1$, and assume without loss of generality that $\kappa = 1$ (see Table 6, and the working in Appendix 3).

In general, these examples support the assumption that the value of the higher position strongly influences the stability with a situation with $V_A + V_B < 0$ more likely to be stable than one with $V_A + V_B > 0$. However, it is also clear from Table 6 that stable and unstable situations can exist under all 3 conditions, that is, when the higher rank is of equal value to the protagonists, more valuable to the challenger, and more valuable to the holder.

Age-inversed versus matrilineal hierarchies

For each situation, of course, the stability depends on the rewards to be gained by both protagonists and any possible third party. Thus, as we have argued above in a very general way, the composition of the entire group must be specified to see if a particular relationship between 2 animals is stable. In particular, the whole hierarchy is stable only if, picking a potential challenger, challengee, and observer, the situation is stable for all possible such triples. Thus, different types of

Table 6
Possible stable hierarchies and the conditions for their occurrence for evenly matched individuals

C plays	A plays	B plays	Conditions
A	H	D	$1 < V_B < 1/\chi, -1 < V_A, V_C < -\epsilon$ (1)
A	H	D	$1 < V_B < 1/\chi, V_A < -1, V_C < -2\epsilon$ (2)
N	H	D	$V_B < \chi$ (3)
N	H	D	$\chi < V_B < 1, -1/\chi < V_A, V_C < \epsilon$ (4)
N	H	D	$\chi < V_B < 1, V_A < -1/\chi, V_C < (\epsilon + \phi\kappa p_B)/(1 - p_B)$ (5)

Working for these results is shown in Appendix 3. The numbers in the last column are used for reference from both the main text and Appendix 3.

hierarchies may be stable for different species; indeed, some species might have many stable configurations, others few.

Thus, as has been argued previously, dominance relationships and hierarchies should indeed be population (or even group) specific (e.g., van Schaik 1989). However, stable, coalitionary, matrilineal dominance hierarchies are not simply the result of strong feeding competition. As the following examples show, matrilineal and age-inversed hierarchies can emerge in different situations. For some cases, there is more than one possible hierarchy, and which occurs may depend on the history of the specific group. In other cases, only one of the hierarchies is possible, with some situations favorable to one type of hierarchy and others to another.

To illustrate these ideas, we consider 6 very simple examples—generally, we suppose all individuals are evenly matched so $p_N = 1/2$, we choose $p_A = 3/4$ (so $p_B = 1/4$ given evenly matched animals) so that $\chi = (1 - p_A)/p_A = 1/3$; and we further choose the number of individuals to be 4 (2 mother and daughter pairs M1, J1 and M2, J2). Now consider 2 scenarios:

- Case 1—places 1 and 2 in the hierarchy are worth a constant amount k more than places 3 and 4 to all participants.
- Case 2—places 1 and 2 are worth $2k$ more to the daughters J1, J2, but only $1/2 k$ more to the mothers.

For each case, there are 3 hierarchies that we consider:

- H1—J1 and J2 in the top places, M1 and M2 in the bottom places;
- H2—J1 and M1 in the top places, J2 and M2 in the bottom places;
- H3—M1 and M2 in the top places, J1 and J2 in the bottom places.

In H1, the most unstable situation is when M1(M2) challenges J2(J1) in the presence of J1(J2), in H2, it is when J2 challenges M1 in the presence of M2 (others are equally unstable in case 1 but not in case 2), and in H3, it is when

J1(J2) challenges M2(M1) in the presence of M1(M2). We consider when these result in a change in the hierarchy (see Table 7, with working in Appendix 4). For very small values of k , all hierarchies are stable, and for very large values of k , none are stable. The more interesting (and realistic) behavior occurs for intermediate values of k .

In Case 2, hierarchy H1 with daughters at the top is stable and hierarchies H2 and H3 are not. In Case 1, all 3 hierarchies are stable when $0.3 < \epsilon$ and unstable otherwise. In Case 2, there is one stable hierarchy (juveniles at top—this case is where they benefit more), and in Case 1, all 3 are stable under certain circumstances. Thus, hierarchies H2 and H3 are stable under precisely the same circumstances. Note that this is under the assumption of equal strength; if strength is variable and heritable, then the stability of H1 and H3 will tend to be diminished and that of H2 enhanced, with the result that in reality hierarchy H3 will generally be less likely to be stable than H2.

DISCUSSION

With this analysis, we intended to shed light on the variation in hierarchies among group-living animals via mathematical modeling. Based on the interaction of 3 players, 12 outcomes were identified, although only 7 of these actually occurred under optimal play. We found the conditions under which each of these possibilities would occur and explored the effect of changing each of our model parameters. The different relationships were summarized in 1 of 4 different categories: relationships can be stable 1) with or 2) without coalitionary support or relationships can be unstable 3) with or 4) without coalitionary support. The exact choice of strategies and hence the observable outcome in terms of consistent or inconsistent dominance relationships is determined by several factors, which are discussed below (summarized in Table 8).

In discussing these factors, we acknowledge here that our model includes several simplifications, which might have affected some of the outcomes. As such our approach should be viewed as preliminary and we encourage more complex models in the future. We also acknowledge that the effects of some influencing factors have been predicted, modeled, or shown before. But other factors have not been taken into account thus far. Importantly, the combination of 5 factors shown in Table 8 together with their predicted effects represents an entirely novel result. In combination with RHP, these 5 factors should allow us to explain variation in dominance hierarchies among primates and other group-living animals.

Determinants of coalitions and stability

Previous verbal as well as mathematical models for nonhuman primates have stressed the importance of female dispersal patterns, of strength in reproductive skew (van Schaik 1989; Sterck et al. 1997; van Schaik et al. 2004), and of demography (Hausfater et al. 1987; Datta and Beauchamp 1991) in forming

Table 7
Effects of the values of rank positions on the stability of rank positions summarizing the conditions for 4 individuals (2 mothers M1 and M2 and 2 daughters J1 and J2) for 2 scenarios of rank value and 3 different dominance hierarchies

	Difference in rank value: 1,2 minus 3,4	H1 (age-inversed)	H2 (matrilineal)	H3 (age-graded)
C1	k for all	A3, B2 Stable or unstable ^a	A3, B2 Stable or unstable ^a	A3, B2 Stable or unstable ^a
C2	$2k$ for daughters, $1/2 k$ for mothers	A2, B1 Stable	A4, B3 Unstable	A4, B3 Unstable
Unequal strength		Decrease stability	Increase stability	Decrease stability

The general impact of unequal strength is indicated in the bottom row. Calculations for these results are shown in Appendix 4.

^a Stable when $0.3 < \epsilon$.

Table 8
Predicted effects of 5 factors on the structure of female dominance hierarchies

Factor	Predictor variables	Predictions			Reference
		Condition	Consequence of intervention	Hierarchy	
Strength of competition	Food abundance and distribution predation pressure	Low reproductive skew	Low indirect fitness benefits	Individualistic	van Schaik (1989)
Demography	Life history	Slowly reproducing	Few suitable coalition partners	Individualistic	Datta and Beauchamp (1991)
Relatedness	Dispersal pattern ¹	Low variance in relatedness	Low indirect fitness benefits	Individualistic	¹ van Schaik (1989); this study
Possibility of intervention	Male reproductive skew Group size Weaponry ² Complexity of habitat ³ Complexity of spatial structure of a group Group spread	High costs/low likelihood of intervention	Low indirect fitness benefits	Individualistic	² Packer et al. (2001); ³ Whitehead and Connor (2005); this study
Value of resources and rank	Residual reproductive value Life history	Low value Fast growth rate	Lower values for older individuals Higher values for young individuals	Age-inversed	Hrdy SB and Hrdy DB (1976) This study

Presumed variables, conditions, and their consequences are outlined for individualistic hierarchies. Matrilineal hierarchies are expected for the alternate conditions of the first 4 factors. Which of the 2 forms of individualistic hierarchies (age-positive or age-inversed; see also Introduction) are formed, is determined by the conditions of the fifth factor. Conditions for age-inversed hierarchies are outlined.

kin alliances and matrilineal hierarchies. Our results, however, indicate that philopatry in itself (as distinct from relatedness) seems not to be a primary factor. Instead, it is the variance in relatedness within a given group that seems to drive the likelihood of coalitions (Table 8). If it is low, regardless of all individuals in a group being nonrelated or closely related, none would benefit from coalitionary behavior (neglecting reciprocity). In fact, limited dispersal can lead to stronger competition among relatives reducing or eliminating the benefits of cooperation (West et al. 2002). Instead, if groups are composed of some closely and some distantly or unrelated individuals, close relatives might benefit from coalition formation. Variance in relatedness will be determined by a combination of the actual dispersal pattern (e.g., Stewart and Harcourt 1987; Starin 1994; Pope 2000; Bradley et al. 2007), group size, number of males, and reproductive skew among males (e.g., Hrdy 1977; Altmann et al. 1996; Lukas et al. 2005).

Our results also stress the importance of the possibility of interventions and the costs of interventions for the third contender C and with it the likelihood for rank stability. In each case, there was a critical value of the cost of entering a coalition, depending on the other parameters, whereby a third individual would enter into a coalition if and only if the true cost was less than the critical value. Thus, this parameter is very influential and has an easily testable and interpretable effect.

In species with dangerous weaponry such as lions, in which costs of fighting are high, more symmetrical, less stable dominance relationships are expected and were indeed found (Hammerstein 1981; Packer et al. 2001). However, for most species (with less dangerous weaponry), the possibility of encounters and with it the likelihood of coalitionary behavior may depend on the likelihood of 2 or more contenders meeting each other and the costs of intervention (Table 8). In a complex 3-dimensional arboreal environment, the possibility of forming coalitions can be quite low, simply because coordination of potential allies is difficult. An arboreal environment furthermore

includes the risk of falling increasing the costs of intervention. Support for this idea comes from savannah baboons, in which a high-ranking male consorting a female is easily defeated by coalitions of 2 low rankers while on the ground but not while in the trees (Smuts 1985; Noë and Sluijter 1990). The same logic of an impact of the complexity of the habitat applies to the argument that alliances are more likely in marine than terrestrial animals because the ability of alliances to out-manuever stronger opponents is higher in the 3 dimensional marine environment than in the 2 dimensional terrestrial one (Whitehead and Connor 2005).

Beyond the effect of the complexity of the habitat, the simple spread of a group or the positioning of individuals may prevent or facilitate the possibility of coalitions (Table 8). For instance, in groups of wedge-capped capuchin monkeys, juveniles as well as the highest ranking female cluster centrally (Robinson 1981). Presumably because of this positioning, the alpha female frequently supports (related) juveniles in conflicts, whereas other more peripheral females hardly ever support their juvenile relatives (O'Brien and Robinson 1993). Similarly, frequency of aggression and interventions is drastically reduced in troops of Japanese macaques that are dispersed over a greater area (Hill and Okayasu 1996).

Life history and dominance hierarchies

Although the above considerations will help to strengthen the predictions for the emergence of individualistic versus matrilineal hierarchies, the occurrence of age-inversed hierarchies still remains unexplained. Many individualistic hierarchies are characterized through infrequent interventions (for reasons, see above). In addition, in some species, coalitions between females may be disrupted and made ineffective by interventions of males (Harcourt and Stewart 1989; Watts 1997). Thus, the stabilizing effect of all-down coalitions within matrilineal is essentially missing (Chapais and Gauthier 2004). As pointed out previously the stability and age structure of such hierarchies may closely relate

to the value of ranks for the contenders. In varying the probabilities of the Hawk–Hawk contest and the value of ranks, we found that various situations can lead to stable or unstable hierarchies. Particularly, juvenile individuals on top is a stable situation if the top position is more valuable for them. Translated into the real world, this could be interpreted as age-dependent value of high rank or a stronger effect of a higher rank for younger individuals (or those who need more resources etc.; Table 8).

Historically, Hrdy SB and Hrdy DB (1976) suggested that age-inversed hierarchies are the result of differences in reproductive values, where older females with a lower residual value yield to younger (related) females. But variation in the value of rank might also relate to the variation in life history or more specifically growth rates. So far, age-inversed hierarchies have been found or suggested mostly for folivorous species. Folivorous primate species have generally faster growth rates than other species (Leigh 1994; but see Godfrey et al. 2004). Assuming that faster growth rates mean a higher allocation of energy to growth, folivorous juveniles should value a high rank more than frugivores. This in turn would make revolutionary coalitions or more aggressive competition more profitable. These conditions seem to fit revolutionary coalitions of juvenile females as observed in Hanuman langurs (Borries et al. 1991; Apelt 1995). Similarly, in savannah baboons with a strong sexual dimorphism, subadult males experience a much more pronounced growth spurt as compared with macaques (Pereira 1995). This coincides with the fact that compared with macaques, in baboons, subadult ranks are less dependent on coalitions with their mother. Hence, it seems that growth pattern influences the way in which subadult individuals compete (Pereira 1995).

In general, our results show that previous assumptions (e.g., Sterck et al. 1997) for a simple dichotomy or gradual 1-dimensional variation from unstable, noncoalitional hierarchies to stable, coalitional (matrilateral) hierarchies are too simplistic. In addition to RHP, reproductive skew, and demography, the emergence of different dominance relationships and hierarchies as exemplified by age-related, age-inverse, or matrilineal hierarchies seems to depend on 3 additional factors:

1. the variance in relatedness modified by dispersal patterns, the size of groups, and the number of males and their reproductive skew;
2. the costs and the likelihood of interventions depending on, for example, weaponry, complexity of the environment, and group spread; and
3. the value of resources and rank in different life stages which might be linked to the residual reproductive value and to the life history of a species (Table 8).

In order to test for the importance of the individual parameters such as variance in relatedness or growth rates, it would be necessary to conduct comparative analyses within and across animal orders. Some of the necessary factors are unfortunately hardly available, for example, group spread or genetic makeup, but particularly with the growing number of studies incorporating genetics, it should be possible to test some of the parameters in the near future.

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APPENDIX 1

Model payoffs and optimal strategies

Letting q_1 be the probability that A plays H, q_2 the probability that B plays H, in a conflict where A wins an HVH contest with probability p (so $p = p_A$ if C has chosen A, p_B if it chooses B, p_N otherwise):
A's reward

$$R_A = q_1 q_2 ((1-p)V_A - (1-p)\kappa) + (1-q_1)q_2 V_A + (1-q_1)(1-q_2)V_A/2 = V_A/2 - q_1 V_A/2 + q_2 V_A/2 + q_1 q_2 \{(1/2-p)V_A - (1-p)\kappa\}.$$

B's reward

$$R_B = q_1 q_2 ((1-p)V_B - p\kappa) + (1-q_1)q_2 V_B + (1-q_1)(1-q_2)V_B/2 = V_B/2 - q_1 V_B/2 + q_2 V_B/2 + q_1 q_2 \{(1/2-p)V_B - p\kappa\}.$$

These formulas then yield the following expressions:

$$\frac{\partial R_A}{\partial q_1} = -V_A/2 + q_2 [(1/2-p)V_A - (1-p)\kappa],$$

$$\frac{\partial R_B}{\partial q_2} = -V_B/2 + q_1 [(1/2-p)V_B - p\kappa].$$

If $-pV_A - (1-p)\kappa > 0$, $(1-p)V_B - p\kappa > 0$, then $\frac{\partial R_A}{\partial q_1} > 0$, $\frac{\partial R_B}{\partial q_2} > 0 \quad \forall q_1, q_2 \in (0, 1)$ so $q_1 = 1, q_2 = 1$ is optimal.

⇒ SOLUTION A plays H, B plays H

If $-pV_A - (1-p)\kappa > 0$, $(1-p)V_B - p\kappa < 0$,

⇒ $\frac{\partial R_A}{\partial q_1} > 0 \Rightarrow q_1 = 1$ is best, when $\frac{\partial R_B}{\partial q_2} < 0 \Rightarrow q_2 = 0$ is optimal.

⇒ SOLUTION A plays H, B plays D

If $-pV_A - (1-p)\kappa < 0$, $(1-p)V_B - p\kappa > 0$,

⇒ $\frac{\partial R_B}{\partial q_2} > 0 \Rightarrow q_2 = 1$ is best, when $\frac{\partial R_A}{\partial q_1} < 0 \Rightarrow q_1 = 0$ is optimal.

⇒ SOLUTION A plays D, B plays H

If $-pV_A - (1-p)\kappa < 0$, $(1-p)V_B - p\kappa < 0$,

Then, if $q_1 = 1, q_2 = 0$ we obtain $\frac{\partial R_A}{\partial q_1} > 0, \frac{\partial R_B}{\partial q_2} < 0$ and if $q_1 = 0, q_2 = 1$ we obtain

$\frac{\partial R_A}{\partial q_1} < 0, \frac{\partial R_B}{\partial q_2} > 0$ so that both of these solutions are stable.

No stable mixed solution can exist (there is one unstable equilibrium) so either A plays D, B plays H or A plays H, B plays D are the solutions. Whereas either of these are theoretically possible because A holds the dominant position the “natural” solution is A plays H, B plays D. This is very similar to the owner-intruder game (Maynard Smith 1982) where there is an asymmetry between a territory owner and its challenger and an individual plays Hawk as the owner but Dove as the intruder (the Bourgeois strategy), as generally occurs in reality for well-matched opponents. It is far less common in a real situation for a dominant individual to give way to a subordinate, rather than vice versa. If this were not the case, then stable dominance hierarchies would be rare.

Thus, we have solutions

$(1-p)V_B - p\kappa < 0 \Rightarrow$ A plays H, B plays D.

If $(1-p)V_B - p\kappa > 0$, then if $-pV_A - (1-p)\kappa > 0 \Rightarrow$ A plays H, B plays H.

If $(1-p)V_B - p\kappa > 0$, then if $-pV_A - (1-p)\kappa < 0 \Rightarrow$ A plays D, B plays H.

APPENDIX 2

A and B conditions and optimal play

In the following appendix, we consider the combinations of A and B conditions to find the optimal choice for C and hence the optimal play for A and B.

B1; whatever C does $(1-p)V_B - p\kappa < 0 \Rightarrow$ A plays H, B plays D, which then means C maximizes its payoff by playing N.

B2; A2, A3, or A4—in B2, if C supports A or N, then A plays H, B plays D. If C supports B, then A plays D, B plays H in each of A2, A3, or A4.

⇒ C rewards are $(V_C - \epsilon)[B]$, $0[N]$, $-\epsilon[A] \Rightarrow$ N is better than A and is best if $V_C - \epsilon < 0$ otherwise C should support B if $V_C - \epsilon > 0$.

B2; A1—If C supports B here, then A plays H, B plays H and C's possible rewards are

$(1-p_B)V_C - \epsilon - j p_B k [B]$, $0[N]$, $-\epsilon[A]$ p N is best if

$(1-p_B)V_C - \epsilon - j p_B k < 0$ and B is best if $(1-p_B)V_C - \epsilon - j p_B k > 0$.

B3; A3 or A4—in B3 if C supports A then A plays H, B plays D. If C supports B or N then A plays D, B plays H in A3 or A4
 ⇒ C rewards are $V_C - \varepsilon [B], V_C [N], -\varepsilon [A]$ p C plays N if $V_C + \varepsilon > 0$ and A if $V_C + \varepsilon < 0$.

B3; A2—If C supports A, then as above, if C supports B, then A plays D, B plays H, and if C plays N, then A and B play H ⇒ C rewards are $-\varepsilon [A], V_C - \varepsilon [B], (1 - p_N)V_C [N]$.

If $V_C > 0$, then B is better than A and B is best if $V_C - \varepsilon > (1 - p_N)V_C \Rightarrow p_N V_C - \varepsilon > 0$.

If $V_C < 0$, then A is better than B and A is best if $(1 - p_N)V_C + \varepsilon < 0$.
 Between these limits, N is best.

B3; A1—If C supports A the situation is again as above, if C supports B or N then A plays H and B plays H

⇒ C rewards are $-\varepsilon [A], (1 - p_N)V_C [N], (1 - p_B)V_C - \varepsilon - \phi p_B \kappa [B]$.
 B is better than A if $(1 - p_B)V_C - \phi p_B \kappa > 0 \Rightarrow V_C > 0 \Rightarrow$ N is better than A
 ⇒ B is best if B is better than N (and $V_C > 0 \Rightarrow (p_N - p_B)V_C - \varepsilon - \phi p_B \kappa > 0$.

A is better than N if $-\varepsilon - (1 - p_N)V_C > 0 \Rightarrow V_C < 0 \Rightarrow$ N is better than B (because $p_N > p_B$) ⇒ A is best if A is better than N, that is, $\varepsilon + (1 - p_N)V_C < 0 - N$ is best between these 2 limits.

B4; A4—B always plays H, A always plays D ⇒ C plays N (gains V_C not $V_C - \varepsilon$).

B4; A3—B plays H, A plays H if C supports A, otherwise A plays D. C's rewards are $(1 - p_A)V_C - \varepsilon - (1 - p_A)\phi \kappa [A], V_C [N], (V_C - \varepsilon) [B]$ ⇒ C supports A if $p_A V_C + \varepsilon + (1 - p_A)\phi \kappa < 0$, otherwise C plays N.

B4; A2—B plays H, A plays H if C plays A or N, otherwise A plays D so C's rewards are $(1 - p_A)V_C - \varepsilon - (1 - p_A)\phi \kappa [A], (1 - p_N)V_C [N], V_C - \varepsilon [B]$.

$V_C > 0 \Rightarrow$ N is better than A ⇒ B is best if $p_N V_C - \varepsilon > 0$.
 $V_C < 0 \Rightarrow$ N is better than B ⇒ A is best if $(p_A - p_N)V_C + \varepsilon + (1 - p_A)\phi \kappa < 0$.

N is best between these limits.

B4; A1—B plays H and A plays H whatever C plays—possible C rewards are $(1 - p_A)V_C - \varepsilon - (1 - p_A)\phi \kappa [A], (1 - p_N)V_C [N], (1 - p_B)V_C - \varepsilon - \phi p_B \kappa [B]$.

$V_C > 0 \Rightarrow$ N is better than A ⇒ B is best if $(p_N - p_B)V_C - \varepsilon - \phi p_B \kappa > 0$.

$V_C < 0 \Rightarrow$ N is better than B ⇒ A is best if $(p_A - p_N)V_C + \varepsilon + (1 - p_A)\phi \kappa < 0$.

N is best between these 2 limits.

APPENDIX 3

Calculations for special cases

Cases A1–A4, B1–B4 reduce to

A1 : $V_A < -1/\chi,$

A2 : $-1/\chi < V_A < -1,$

A3 : $-1 < V_A < -\chi,$

A4 : $-\chi < V_A,$

B1 : $V_B < \chi,$

B2 : $\chi < V_B < 1,$

B3 : $1 < V_B < 1/\chi,$

B4 : $1/\chi < V_B.$

A stable hierarchy occurs in the following cases (see Table 6).

Case 1

$V_A + V_B = 0$, then A1 ⇔ B4, A2 ⇔ B3, A3 ⇔ B2, A4 ⇔ B1.

$V_B < \chi \Rightarrow$ always stable (see situation 3 in Table 6).

$\chi < V_B < 1 \Rightarrow$ stable if $V_C < \varepsilon$, that is, that the third individual is not sufficiently related to the attacker and does not get involved (situation 4 in Table 6).

$1 < V_B < 1/\chi \Rightarrow$ stable if $V_C < -2\varepsilon$, that is, it needs the third individual to be its relative and to support it (situation 2 in Table 6).

Thus, as the potential value of moving up the hierarchy increases, the stability declines.

Case 2

$V_A + V_B > 0 - V_C = r_A V_A + r_B V_B$, so that the higher $V_A + V_B$ generally the higher V_C as well which makes supporting A less likely and supporting B more likely. This is in addition to the fact that B would be generally more likely to win (due to being more aggressive as its reward is greater than A's).

In particular considering the “off-diagonal” regions with $V_A + V_B > 0$; A2, B4; A3, B3; A4, B2; $(1 < -V_A < 1/\chi < V_B; \chi < -V_A < 1 < V_B < 1/\chi$ and $-V_A < \chi < V_B < 1)$, the stable possibilities are $1 < V_B < 1/\chi, -1 < V_A < -\chi; V_C < -\varepsilon$ (situation 1 in Table 6). $\chi < V_B < 1/, -\chi < V_A; V_C < \varepsilon$ (situation 4 in Table 6).

V_C is more likely to be positive than not and will be quite large and positive for some animals (i.e., relatives of B) so that long-term stability is unlikely.

Case 3

$V_A + V_B < 0$ because $V_C = r_A V_A + r_B V_B$, V_C is more likely to be negative and there will be a tendency to support A not B. In particular, picking the appropriate off-diagonal regions A1, B3 ($1 < V_B < 1/\chi < -V_A$), A2, B2 ($\chi < V_B < 1 < -V_A < 1/\chi$), A3, B1 ($V_B < \chi < -V_A < 1$), the stable possibilities are $1 < V_B < 1/\chi, V_A < -1/\chi, V_C < -2\varepsilon$ (situation 2 in Table 6), $\chi < V_B < 1, -1/\chi < V_A < 1, V_C < \varepsilon$ (situation 4 in Table 6), $V_B < \chi, -1 < V_A < -\chi$, any V_C (situation 3 in Table 6).

The third of these is always stable and the second may be stable within a group given most V_C 's are negative, although the first case is less likely. Thus, stability here is much more likely to occur.

APPENDIX 4

Simple hierarchies with 4 individuals

Picking arbitrarily the value $k = 0.6$ gives

Case 1; H1— $V_A = -k, V_B = k \Rightarrow V_C = 1/2 k$ (in our chosen case) ⇒ we are in A3, B2 with $V_C = 0.3$ so from Table 3, C, A, B play B, D, H if $0.3 > \varepsilon$ and N, H, D if $0.3 < \varepsilon$.

Case 2; H1— $V_A = -2k, V_B = 1/2 k, V_C = 1/4 k \Rightarrow$ we are in A2, B1 so that C, A, B play N, H, D.

Case 1; H2— $V_A = -k, V_B = k \Rightarrow V_C = 1/2 k \Rightarrow$ we are in A3, B2 with the same result as Case 1; H1.

Case 2; H2— $V_A = -1/2 k, V_B = 2k \Rightarrow V_C = k \Rightarrow$ we are in A4, B3 ⇒ $V_C = 0.6$ which gives C, A, B play N, D, H whenever $V_C > -\varepsilon$ (always true in our chosen case).

Case 1; H3— $V_A = -k, V_B = k \Rightarrow V_C = 1/2 k \Rightarrow$ we are again in A3, B2 with the same result as Case 1; H1.

Case 2; H3— $V_A = -1/2 k, V_B = 2k \Rightarrow V_C = k \Rightarrow$ we are again in A4, B3 ⇒ $V_C = 0.6$ which gives the same result as Case 2; H2.

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