

Male reproductive coalitions in the genus *Papio* exhibit substantial variation both within and among populations. In some groups, coalitions are frequent and play a central role in determining access to fertile females, whereas in others they are rare or absent. Even within populations where coalitions occur regularly, participation is strongly biased toward particular age and rank classes of males. Understanding how such coalitions arise, and which males are able to participate in them, has been a long-standing problem in primate behavioral ecology.

After Hall and DeVore's (1965) early observations and description of baboon reproductive coalitions, theoretical interest in baboon reproductive coalitions was further generated due to Trivers' (1971) paper introducing reciprocal altruism, where he suggested that baboon reproductive coalitions were a prime target for observing this mechanism at play in a natural population. Because coalitionary challenges often involve repeated interactions among the same males and potentially repeated opportunities to share reproductive benefits, baboon coalitions were seen as promising candidates for testing predictions about reciprocity. Following this suggestion, Packer (1977) and Smuts (1985) reported patterns in which coalition partners appeared to alternate access to consort females across successful challenges. These observations were interpreted as evidence that males might be reciprocating reproductive opportunities over time, with coalitionary support exchanged for future benefits.

This interpretation was later challenged by Bercovitch (1988), who analyzed a much larger dataset and found little evidence for systematic alternation of reproductive access among coalition partners. Instead, he argued that access to consort females following successful coalitionary challenges was effectively random with respect to coalition membership. Bercovitch further suggested that the costs of coalitionary conflict were minimal, both in terms of injury risk and energetic expenditure. Based on this, he proposed that baboon reproductive coalitions could be explained as instances of by-product mutualism: males participate in coalitions not due to delayed reciprocity, but because coalitionary action provides an immediate chance of gaining access to reproductive opportunities that would otherwise be completely inaccessible through dyadic challenges. Under this interpretation, coalitionary behavior should be selected for even if the likelihood that a given coalitionary male will gain a reproductive opportunity on any given instance is extremely small.

While Bercovitch's interpretation resolved some inconsistencies with the reciprocal altruism hypothesis, it also raised several additional problems. Contrary to claims of negligible costs, multiple studies have documented substantial physiological and injury-related costs associated with coalitionary conflict in baboons (Popp, 1978; Sapolsky, 1983; Smuts, 1985). Additionally, although some populations show approximately random division of reproductive opportunities among coalition partners, others exhibit strongly asymmetrical outcomes, with the higher-ranking coalition member obtaining most or all access to consort females (Collins, 1981; Noe, 1986). Also, if coalitionary participation is low-cost and offers even a small chance of reproductive success, a further puzzle emerges: why are reproductive coalitions usually limited to just two males? Under a purely mutualistic interpretation, additional males should frequently join coalitionary challenges, yet such larger coalitions are observed significantly less often than dyadic ones.

Ronald Noe's work represents another conceptual shift in how these questions were approached. Rather than focusing on the motivational mechanisms underlying coalition participation, Noe's approach was simpler in my view; given known biological constraints, which coalitionary interactions are even possible? His empirical work (Noe & Sluijter, 1990, 1995) demonstrated strong relationships between coalition participation, dominance rank, and age, while his theoretical models (Noe, 1990, 1992, 1994) formalized how these factors constrain coalition formation.

Central to Noë's (1994) model is the observation that fighting ability in male baboons follows a bell-shaped trajectory across the lifespan; increasing during adolescence, peaking in early adulthood, and declining with senescence. Because dominance rank is closely correlated with fighting ability, and because males of different ages coexist within social groups, the distribution of fighting ability across ranks reflects the underlying age structure of the male population. Noë used this relationship to construct rank–fighting ability curves of varying steepness, corresponding to groups with different age compositions. He then examined how the shape of this curve constrains the set of feasible coalitionary interactions.

The model itself is minimalistic by design. Coalitions are restricted to two males challenging a single target male, coalition strength is defined as the sum of the partners' fighting abilities, and coalitions are only considered against higher-ranking opponents. Rather than modeling coalition formation as a behavioral process, Noë assumed that the frequency with which a male participates in coalitions is proportional to the number of feasible partner–target combinations available to him. Under these assumptions, the model produces a robust and counterintuitive prediction: *middle-ranking males should have the greatest number of feasible coalition opportunities*, whereas both high-ranking males (who can dominate other males more easily and does not have to share potential reproductive resources) and very low-ranking males (who contribute little fighting ability) participate less frequently.

The work shown below builds directly on Noë's (1994) framework by re-deriving the model from its verbal assumptions and implementing an algorithm in Python that generates similar distributions to those generated by Noë in the original paper. By formalizing each assumption mathematically and implementing them as an explicit algorithm that enumerates all feasible partner–target combinations given a specified rank–fighting ability distribution, this approach clarifies which features of Noë's results follow necessarily from structural constraints and which depend on particular parameter choices. This re-derivation provides a transparent foundation for extending the model to address unresolved empirical observations, including payoff asymmetries within coalitions and variation in coalition size.

### Model Explanation / Re-derivation

*Model assumptions from Noë (1994):*

1. Fighting ability and age have a bell shaped relationship
2. The distribution of fighting ability in a group corresponds to the age-fighting ability relationship
3. Fighting ability ( $F$ ) of a coalition is calculated from the fighting abilities of its members
  - a.  $F_{\text{Coalition}} = c(F_{\text{Partner 1}} + F_{\text{Partner 2}})$ ; where  $c$  is a multiplication factor
4. Only two-male coalitions against single targets are formed
5. Any two males can form a successful coalition against another male if their combined fighting ability is higher than the target
6. No males form a coalition against a male of lower fighting ability
7. A male forms coalitions with a frequency proportional to the number of combinations of one partner and one target possible

Initially, I intended on re-deriving the model by hand, however I saw an opportunity to design an algorithm instead. The first step to re-deriving this model is to set up the basic objects in the model. We have a single group of baboons that contains  $N$  adult males. These males are indexed by their dominance rank ( $r$ ):

$$r = 1: \text{highest ranking / strongest male}$$

$$r = N: \text{lowest ranking / weakest male}$$

Each male,  $r$ , has a fighting ability  $F_r$ . Ranks are ordered such that:

$$F_1 > F_2 > \dots > F_N$$

From these two pieces of information we can create a rank-fighting ability curve, which is the mechanism which we use to generate the distributions of partner-target combinations for each male under the assumptions listed above. While not explicitly stated in the model description, it is implicitly assumed that  $F_r$  and by extension  $r$ , decrease as a function of age. The rate of this decrease influences the magnitude of difference in fighting ability between individuals of different  $r$ , which in turn changes the distribution of partner-target combinations the model generates.

The next step is to formalize the seven verbal assumptions listed above into mathematical form, allowing us to more easily design the algorithm which will act as the model derivation.

#### Assumptions 1 & 2:

We actually did a lot of the work in formalizing these two assumptions when we defined the model objects above. Assumption 1 is merely stating that as a juvenile male approaches puberty, his fighting ability increases to its peak in his young adult years. As he ages past his prime years, his fighting ability decreases. While Assumption 2 is saying that the differences in magnitude between males fighting abilities is a function of the age structure of males in the group. If a group is all young males (or old males), the fighting ability curve will be very shallow with small differences in fighting ability between ranks, while the more variation there is in male ages within the group, the steeper the curve will be. These are merely biologically informed parameter limitations which limits the number of partner-target combinations we should observe. The only additional consideration we need to outline mathematically is how we are deciding to bound fighting abilities. In Noe's models, he has  $F_1 = 100$  and each subsequent rank decreases from there, with  $F_N = \{50, 25, 10\}$  depending on if the curve was 'shallow', 'moderate', or 'steep', respectively. From this, we can formally bound fighting ability as follows:

$$0 \leq F_r \leq 100$$

#### Assumption 3:

If two males,  $i$  and  $j$  where ( $i \neq j$ ), were to form a coalition; the fighting ability of that particular coalition is calculated as follows:

$$F_{ij} = c(F_i + F_j)$$

Where  $c$  is an optional synergistic effect. Noe uses  $c = 1$  in his model (neutral synergy) but values greater than or less than 1 can be implemented to represent additional strength for coalitionary allies who coordinate well or decreased fighting ability between allies who do not coordinate well or try to take advantage of one another.

#### Assumption 4:

This assumption limits the interactions to a triadic structure, where two coalition males ( $i$  and  $j$ ) challenge a third male,  $k$ . Additional males cannot join  $i$  and  $j$ , and  $k$  cannot solicit aid to form a counter coalition.

## Only interaction structure permitted:

$$(i, j) \rightarrow k$$

### Assumption 5:

Coalition  $(i, j)$  can defeat  $k$  if and only if:

$$F_{ij} > F_k$$

Noe assumes that coalitions only form if  $F_{ij} > F_k$ . He says nothing about the success probability of the coalition actually beating the consort male. The model treats this as the success condition in that males  $i$  and  $j$  could potentially defeat  $k$ , but says nothing about the probability that this is the outcome will be successful (the coalition is able to oust the consort male). It could be a 1 % chance or a 99% chance, but as long as there is a non-zero chance, this is counted as a successful partner-target combination.

### Assumption 6:

Males do not form coalitions against weaker targets in this model. This excludes bridging (coalitions of a high and low-ranking male directed towards a mid-ranking male) and all-down (coalitions of two high-ranking males directed at a lower-ranking male) coalitions from the model. Only all-up coalitions (two lower-ranking males target a higher ranking male) are counted, as this describes the structure of coalitionary pairings in the reproductive context when observed in nature. We can formalize this by saying:

### If male $m$ forms a coalition against $k$ :

$$F_k > F_m$$

Thus, both males must be weaker than their target,  $F_k > F_i$  and  $F_k > F_j$ , and since rank and fighting ability line up, we can say rank  $k$  must be lower (in terms of real integer values) than both ranks  $i$  and  $j$ . For example, if individual  $k = \text{rank } 2$ , then the smaller of the integer values for ranks  $i$  and  $j$  can be at most 3:

$$k < \min(i, j)$$

This condition, along with the condition we formalized in Assumption 5, make up the two primary conditions that must be met for a coalition to be successfully formed in this model. We can call them the **Strength Condition** ( $F_i + F_j > F_k$ ) and the **Direction Condition**  $k < \min(i, j)$ .

### Assumption 7:

The number of coalitions a male participates in is assumed to be proportional to the number of partner-target combinations he has. I see this assumption as the rule which determines how the model calculates the number of potential coalitions a male can form and is how we actually go about generating the model output. We are making no claims about the success of practical coalitions in this model, nor are we making any statements about which coalition partners a particular baboon of a certain rank should choose under different fighting ability curves. This assumption shows we are merely calculating the number of possible coalition partners a given baboon has for each of his potential targets (males ranked above him). This can be formally defined as follows:

$$C(i) = \#\{(j, k) : i \neq j \neq k ; F_i + F_j > F_k ; F_k > F_i \text{ and } F_k > F_j\}$$

where # represents number of elements in the set

Essentially, for each focal individual,  $i$ , in the model, we look at all of the potential targets,  $k$ , that are higher ranked than  $i$ , and then we determine which of the remaining males ( $j \neq i$  or  $k$ ) could feasibly form a successful coalition with  $i$  against  $k$  under the strength and direction conditions. The number of successful coalitions formed for each potential rival male in this set ultimately becomes  $i$ 's y-axis value on the partner-target combination graph.

### Algorithm design

Now that we have formalized all of the assumptions of the original Noe model, we can design an algorithm which will compute the model results for us. If we create a program which starts with a vector of fighting abilities  $\mathbf{F} = \{ \mathbf{F}_1, \mathbf{F}_2, \dots, \mathbf{F}_N \}$  where each male  $i \subset N$  is linked to one of the fighting abilities,  $\mathbf{F}_i$ , within  $\mathbf{F}$  and a synergy factor  $c$ , we can create an algorithm that automatically computes the results of Noe's original model as follows:

1. Initialize counts
  - o For each male  $i$ , set the number of successful coalitions  $i$  can form to 0,  $\mathbf{C}(i) = \mathbf{0}$
2. Loop over all other males in the group
  - o For each potential pairing  $\{i, j\}$  with  $1 \leq i \leq j \leq N$ 
    - i. Compute the coalition strength:  $F_{ij} = F_i + F_j$
    - ii. Determine who they can attack, a target is valid if:
      1.  $k < i$
      2.  $k < j$
      3.  $F_{ij} > F_k$
    - iii. For each target,  $k$ , satisfying all conditions under ii,
      1. Increment the coalition opportunity count for both partners  $i$  and  $j$ 
        - a.  $C(i) += 1$  and  $C(j) += 1$
  - 3. Graph counts
    - o Once the nested loop has gone through and performed calculations for each pairing of male partners and male targets, this data is used to create the graphs of partner-target combinations.

### Potential model extensions:

The re-derivation presented above was intentionally designed to mirror the minimal structure of Noe's (1994) original model as closely as possible, using an algorithm developed in Python rather than a by-hand mathematical approach. By doing so, the resulting distributions of coalition opportunities can be interpreted as direct consequences of the structural constraints imposed by rank, fighting ability, and coalition size. I believe that this same algorithmic framework also allows for a number of natural extensions that relax specific assumptions while preserving the overall logic of the model. Below, I outline several such extensions that can be implemented with minimal modification to the existing code and discuss the qualitative changes in model dynamics they are expected to produce.

### Asymmetrical Payoffs Within Coalitions:

In the current model coalition opportunities are treated symmetrically. Whenever a coalition  $(i, j)$  challenges target,  $k$ , and satisfies the strength and direction conditions, both coalition partners receive equal credit in the coalition opportunity count. This assumes that coalition participation and coalition benefit are equivalent by default, since both males receive an increase in their ‘count’ of successful coalitions. In reality, empiricists have observed that payoffs within coalitions are often highly asymmetrical, with the higher-ranking coalition partner receiving most or all access to the consort female.

This extension can be implemented by replacing the simple increment of coalition counts with a payoff allocation rule. Instead of incrementing  $C(i)$  and  $C(j)$  by one for each successful partner–target combination, each coalition could generate a payoff that is divided asymmetrically between partners based on rank, fighting ability, or a fixed proportion. The set of feasible coalitions would remain unchanged, however we would be able to generate a different ‘reward’ distribution based on this extension. Introducing payoff asymmetry would decouple coalition participation from coalition benefit. While middle-ranking males may continue to have the greatest number of feasible coalition opportunities, the expected reproductive benefits of coalition participation may become more and more skewed toward higher-ranking males. This extension provides a straightforward way to reconcile Noe’s structural predictions with empirical observations of highly unequal coalition payoffs.

#### Probabilistic Coalition Success:

Noe’s original model treats coalition success as deterministic. Once a partner-target combination meets both of the strength and direction conditions, we count it as broadly successful. In reality, even if both of these conditions are met, there is always a chance that the coalition could lose against the consort male. I think this is an important dynamic to consider, because no conflict is guaranteed to go one way and this can influence fitness outcomes greatly.

We could implement this extension by replacing the deterministic handling of coalition success with a probabilistic one, where the probability of success increases with the difference between coalition strength and target fighting ability. Instead of counting only coalitions that satisfy the inequality  $F_i + F_j > F_k$ , the algorithm can accumulate expected success values based on a probability function that we define.

Introducing probabilistic outcomes for coalition success in ousting consort males would probably help smooth the sharp boundaries between feasible and infeasible coalitionary pairings. Coalitions with small strength advantages would contribute less to the distribution of coalition success, while strong coalitions would still greatly influence the distribution structure. This extension should capture variability in coalition outcomes while still preserving the core logic of the coalition success algorithm.

#### Coalition Participation Costs:

Currently, the model assumes that coalition formation is cost-free, although empirical evidence suggests this may not be the case. There is potential for significant cost in terms of energy expenditure, wounding, or in severe cases, mortality, as a result of coalitionary endeavors. Adding these costs into the model could help us make predictions about coalitional feasibility beyond fighting ability alone.

We can introduce costs by subtracting a fixed cost, or in a more complex implementation, a target-dependent cost from the payoff associated with each coalition opportunity. For example, this could be implemented by increasing cost as the rank of the target male increases, representing the increasing danger of fighting higher and higher ranked individuals. As with payoff asymmetry, this extension can be implemented by modifying how coalition outcomes are accumulated, without altering the underlying structure of the feasibility conditions. By including costs, I would expect the model dynamic to change in terms of the number of viable coalition opportunities. More specifically, these should decrease depending on the magnitude of the cost.

### Multi-Male Coalitions:

Currently, male coalitions can only consist of two males challenging a single target. While dyadic coalitions are by far the most common type of reproductive coalition observed in baboons, reproductive coalitions of three or more males targeting a single consort male do occur. By allowing coalition size to vary within the model, we could investigate whether dyadic coalitions emerge as a consequence of structural constraints rather than being imposed *a priori*.

This extension can be implemented by generalizing the coalition strength function to include more than two males. Instead of calculating coalition strength as the sum of two fighting abilities, the algorithm would allow coalitions of size  $m \geq 2$ , with total strength defined as the sum of the fighting abilities of all coalition members, potentially scaled by a coordination factor that decreases with coalition size. This would need to be implemented alongside some factor which decreases the probability of gaining fitness as coalition size grows, since the probability of overthrowing the consort male increases as coalition size increases, but there are more males in the coalition to compete with over access to the fertile female once the coalition is successful in ousting the consort.

These extensions build directly off the algorithmic re-derivation of Noe (1994) while maintaining the same basic logic of the original model. The core feasibility structure generated by rank and fighting ability provides a clean baseline, and by adding payoff asymmetry, probabilistic success, coalition costs, and variable coalition size, the model can be pushed in directions that map more closely onto the major empirical puzzles that motivated this field of theoretical effort in the first place. Importantly, each extension is implemented by modifying how coalition outcomes are calculated and accumulated rather than by fundamentally changing the structure of the partner–target enumeration algorithm, meaning that any changes in the resulting distributions can be interpreted as direct consequences of the added biological or behavioral realism. Taken together, this provides a transparent framework for moving from “which coalitions are possible?” to “which coalitions should occur, and for whom are they beneficial?”, and sets up a clear path for comparing model predictions to observed patterns of coalition participation, payoff division, and coalition size variation across *Papio* populations.