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Self-organizing dominance hierarchies in a wild primate population

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Linear dominance hierarchies, which are common in social animals, can profoundly influence access to limited resources, reproductive opportunities and health. In spite of their importance, the mechanisms that govern the dynamics of such hierarchies remain unclear. Two hypotheses explain how linear hierarchies might emerge and change over time. The 'prior attributes hypothesis' posits that individual differences in fighting ability directly determine dominance ranks. By contrast, the 'social dynamics hypothesis' posits that dominance ranks emerge from social self-organization dynamics such as winner and loser effects. While the prior attributes hypothesis is well supported in the literature, current support for the social dynamics hypothesis is limited to experimental studies that artificially eliminate or minimize individual differences in fighting abilities. Here, we present the first evidence supporting the social dynamics hypothesis in a wild population. Specifically, we test for winner and loser effects on male hierarchy dynamics in wild baboons, using a novel statistical approach based on the Elo rating method for cardinal rank assignment, which enables the detection of winner and loser effects in uncontrolled group settings. Our results demonstrate (i) the presence of winner and loser effects, and (ii) that individual susceptibility to such effects may have a genetic basis. Taken together, our results show that both social self-organization dynamics and prior attributes can combine to influence hierarchy dynamics even when agonistic interactions are strongly influenced by differences in individual attributes. We hypothesize that, despite variation in individual attributes, winner and loser effects exist (i) because these effects could be particularly beneficial when fighting abilities in other group members change over time, and (ii) because the coevolution of prior attributes and winner and loser effects maintains a balance of both effects.

1. Background

How do linear dominance hierarchies arise and what determines the positions of individuals in these hierarchies? These questions are central to our understanding of the evolution of social behaviour because dominance hierarchies, which are common in social animals (e.g. [1–6]), can profoundly influence access to limited resources, and can also influence health and reproduction [7–10]. In addition, it has been suggested that studying the development of linear hierarchies in animals might generate a better understanding of the dynamics of hierarchy formation in humans [11]. However, the proximate mechanisms underlying hierarchy formation are still poorly understood.

Two primary hypotheses propose proximate explanations for how linear hierarchies emerge and change over time. The 'prior attributes hypothesis' posits that individual differences in traits such as body size, fighting ability, personality (e.g. boldness) or social attributes (e.g. family background) directly predict dominance ranks [12], and that individual dominance relationships will be purely based on dyad-level differences in individual attributes. The 'social

dynamics hypothesis' posits that hierarchy formation is based on social processes that go beyond the dyad level. For example, 'winner and loser effects' describe the phenomenon in which winners tend to become more likely to win in subsequent encounters, and losers tend to become more likely to lose [13–16]. Importantly, wins and losses change not only the chances of winning against the current opponent, but also affect the chances of winning against other individuals. Because of this far-reaching impact, winner and loser effects can generate linear dominance hierarchies via self-organization dynamics, even in the absence of individual differences in 'prior attributes' [17–20]. However, the two hypotheses are not mutually exclusive. Even when individual attributes influence the outcome of agonistic interactions, social self-organization dynamics might contribute to the establishment of and change in dominance ranks during an individual's lifetime, and thus play an important role in influencing individual fitness.

While several studies have demonstrated that self-organizing social processes can indeed contribute to hierarchy dynamics (e.g. [11,21]), they have generally relied on experimental designs that artificially eliminate or minimize individual differences in fighting abilities (e.g. by matching age or body size among opponents). This approach can increase the power to detect an impact of non-dyadic social dynamics on hierarchy dynamics, but leaves unclear whether and to what extent such social dynamics shape hierarchy dynamics under natural conditions, where differences between competing individuals in fighting abilities may be small or large.

Here we test whether social dynamics influence male hierarchy dynamics in wild baboons, which exhibit linear dominance hierarchies in combination with pronounced inter-individual differences in traits that are known to influence dominance rank [7,22]. Studying social self-organization dynamics in natural conditions is particularly challenging because of the need for appropriate analytical tools that can deal with the lack of experimental control [23]. To address this challenge, we developed a novel statistical method that focuses on detecting winner and loser effects. Specifically, we extended the Elo rating method [24–26], which was originally developed for the calculation of cardinal dominance ranks. Our extensions of this method allowed us to overcome the key problem that temporal changes in individual attributes can generate behavioural patterns that are also expected for winner and loser effects. For instance, a focal individual that experiences a growth-related increase in fighting ability might start to win and then keep winning against individuals to whom it previously lost, simply because it was growing physically. In this case, the initial win would predict subsequent wins, but there would be no causal effect of winning *per se*; rather, changes in wins and losses would be entirely caused by growth-related changes in fighting ability. In the case of a true winner effect, the same temporal pattern of wins and losses would emerge: an unexpected win would increase future winning chances. This example shows that simply documenting a measurable impact of wins and losses on future wins and losses is necessary but not sufficient to identify winner and loser effects under natural conditions. Our method allows us to overcome this problem by analysing temporal variation in the impact of wins and losses on future wins and losses, and determining whether temporal changes in

the effects of winning and losing can be attributed to variation in winner and loser effects, and not to changes in prior attributes (see §2c(i)).

In addition, we aimed to investigate whether an individual's genetic background can influence winner and loser effects. In our study population, variance in genetic background arises from natural admixture between this population of primarily yellow baboons (*Papio cynocephalus*) and neighbouring populations of anubis baboons (*P. anubis*) [27–29]. Yellow and anubis baboons interbreed freely at all known zones of contact, show little evidence of dysgenesis, and produce viable and fertile offspring [28–30]. However, these taxa are morphologically distinct [27,31], and previous work on our population found evidence that males with more anubis admixture have higher mating success [32]. The possibility that genetic variation might affect a suite of traits associated with male agonistic behaviour led us to hypothesize that ancestry might influence winner and loser effects.

2. Material and methods

(a) Analytical framework for identifying winner and loser effects

To assess systematic variability in the extent to which winning and losing predicts future wins and losses, we developed a novel statistical modelling approach that is based on the Elo rating method [24–26]. This method is particularly suitable for our purpose because it tracks changes in winning probabilities for all dyads in a group of individuals. Extensions of the original method allowed us to analyse variation in the impact of wins and losses on future wins and losses while controlling for (i) variation in winning probabilities among dyads and (ii) temporal variation of winning probabilities within dyads. In the following section, we first briefly describe the original Elo rating method to provide context for our approach. Second, we describe our extensions of the Elo rating method. The core of our extensions is a change in the assumption that the central parameter ' k ' of the Elo rating method is a constant: we allow k to vary depending on other variables such as aggression intensity.

(i) The Elo rating method

The Elo rating method was originally developed for calculating cardinal dominance ranks and tracking changes in these ranks over time. In the Elo rating method cardinal dominance ranks are measured by the so-called Elo scores, where higher Elo scores indicate more dominant individuals. The method assumes that the difference in Elo scores between two individuals predicts the probability of each of them winning an agonistic encounter with the other. This means that by tracking outcomes of dominance interactions, the method automatically tracks changes in expected winning probabilities among all dyads of individuals.

Specifically, Elo scores are updated at each observed dominance interaction between two individuals, such that the winner receives a 'winner's bonus', which increases their Elo score, and the loser pays a 'loser's tax', which decreases their Elo score. The absolute amount of the winner's bonus and the loser's tax are equal to each other, and depend on two quantities: (i) the predicted probability that the winner wins (prior to the encounter) and (ii) a predefined constant k (see details below).

Similar to previous studies [24–26], we assumed that given the Elo scores Elo_A and Elo_B of two individuals A and B , the

probability p_A that A wins is given by a sigmoid function:

$$p_A = \frac{1}{1 + \exp(-0.01(\text{Elo}_A - \text{Elo}_B))}. \quad (2.1)$$

The Elo rating method evaluates in consecutive order all observed agonistic interactions. For each interaction, it reassigns Elo scores for all individuals. All individuals C who do not participate in an interaction i are assigned the Elo score of their previous interaction ($\text{Elo}_{C,i} = \text{Elo}_{C,i-1}$). By contrast, the two individuals who interact, A and B , receive new Elo scores: the winners receive a winner's bonus and losers pay an equivalent loser's tax. Specifically, if in an interaction i individual A wins against B with a predicted probability $p_{A,i}$ then new Elo scores $\text{Elo}_{A,i}$ and $\text{Elo}_{B,i}$ are given by

$$\text{Elo}_{A,i} = \text{Elo}_{A,i-1} + (1 - p_{A,i})k \quad (2.2)$$

and

$$\text{Elo}_{B,i} = \text{Elo}_{B,i-1} - (1 - p_{A,i})k. \quad (2.3)$$

Thus, the absolute values of the winner's bonus and the loser's tax are identical because k is a constant. Generally, Elo scores do not change much if the observed outcome was highly expected (i.e. when $p_{A,i}$ is close to 1) and Elo scores change maximally when the outcome was very unexpected (i.e. when $p_{A,i}$ is close to 0). This model makes intuitive sense: expected outcomes indicate that the assigned Elo scores captured the current dominance relationship well, and therefore do not need extensive updating, whereas unexpected outcomes indicate that the assigned Elo scores did not capture the current dominance relationship well, and therefore need updating. The implemented winner's bonus and loser's tax are based on the assumption that current outcomes are predictive of future outcomes (i.e. that winners tend to keep winning and losers tend to keep losing).

The constant k determines the maximum amount of change in Elo scores following a single encounter. When k is set to a small value, single outcomes generally have only a small impact on changes in Elo scores. Small values of k thus assume that single wins and losses are not very predictive of future wins and losses. When k is set to larger values, single outcomes tend to have larger impacts on changes in Elo scores, which implies that single wins and losses should be more predictive of future wins and losses. However, the most appropriate value of k for a given dataset is usually unknown.

Taken together, the structures of equations (2.2) and (2.3) show that Elo scores are updated based on two assumptions: that the impact of wins and losses on future wins and losses (i) varies with the previously predicted chance of winning and (ii) does not vary with any other variable (because k is assumed to be a constant).

(ii) Extensions of the Elo rating method

In our extensions of the Elo rating method, we relaxed the assumption that k is a constant. We allowed k to vary depending on other variables, such as individual attributes or aggression intensity. As a consequence, the impact of wins and losses on future wins and losses can now vary as a function of other variables. In addition, if k varies among individuals the winner's bonus and the loser's tax within an interaction can now differ. Moreover, for a given winning probability the winners' bonus and the losers' tax can vary over time, e.g. due to temporal changes in aggression intensity.

In our implementation, we aimed to preserve the main property of the Elo rating method that only winners receive a 'bonus' and only losers pay a 'tax'. This requires that k is a positive real number. For that purpose, we modelled k as the response variable of a linear model passed through a logarithmic link

function. Thus, for each interaction i with winner A and loser B , and for a set of n predictor variables x_1, x_2, \dots, x_n , and associated coefficients $\beta_0, \beta_1, \dots, \beta_n$, the new Elo scores are now given by

$$\text{Elo}_{A,i} = \text{Elo}_{A,i-1} + (1 - p_{A,i})\exp(\beta_0 + \beta_1 x_{1,A,i} + \dots + \beta_n x_{n,A,i}) \quad (2.4)$$

and

$$\text{Elo}_{B,i} = \text{Elo}_{B,i-1} - (1 - p_{A,i})\exp(\beta_0 + \beta_1 x_{1,B,i} + \dots + \beta_n x_{n,B,i}). \quad (2.5)$$

In an additional extension to the original Elo rating method, we used maximum-likelihood fitting to (i) generate estimates of a given set of coefficients $\beta_0, \beta_1, \dots, \beta_n$ and (ii) test for the significance of individual predictor variables using likelihood ratio tests. Maximum-likelihood fitting is possible because the likelihood of the observed data (i.e. the result of agonistic encounters) can be calculated, given a set of model parameter estimates (i.e. $\beta_0, \beta_1, \dots, \beta_n$). Specifically, equation (2.1) gives, for each observed agonistic encounter i , the predicted probability $p_{A,i}$ that the winner A wins (and the loser B loses). Thus, the overall log-likelihood $\log L_{\text{all}}$ of the model is given by

$$\log L_{\text{all}} = \sum_{\text{all } i} \log(p_{A,i}), \quad (2.6)$$

and is maximized by a set of parameter estimates that most consistently predicts wins and losses in our dataset.

(b) Data collection

To implement our extensions of the Elo method, we used data on agonistic interactions collected between 1996 and 2011 by the Amboseli Baboon Research Project. Agonistic data consisted of 15 917 observations of decided dyadic agonistic encounters among 152 adult males living in five distinct social groups [33]. These data were collected two to three times per week in each group during 5–6 h visits. Each visit included a full group census to record individual membership, identification of peri-ovulatory females, and a record of the outcomes of all observed agonistic interactions and of observed injuries. Agonistic data were collected *ad libitum* [34] while observers were conducting random-order focal animal sampling on all adult females and juveniles in a given social group. This approach ensured that observers continually moved to new locations within the group in a random order, observing all animals on a regular rotating basis. Thus, our procedure for data collection eliminated the possibility that observers spent more time watching particular subsets of the social group, or moved in a biased manner through the group, detecting only the most dramatic events.

We used data only on decided dyadic encounters, which occurred when a clear winner and loser could be identified. These included three different types of encounters: (i) encounters in which the winner gave only aggressive gestures and the loser gave only submissive gestures, (ii) encounters in which the loser gave submissive gestures and the winner gave no aggressive or submissive gestures, and (iii) encounters in which neither individual gave aggressive or submissive gestures but the winner clearly spatially displaced the loser.

(c) Data analysis and implementation of our extensions to the Elo method

First, we confirmed that the Elo rating method captures known patterns of dominance relationships among male baboons. We observed that in 97.5% of all interactions, the Elo scores correctly predicted the outcome direction (i.e. cases in which the winner had a higher Elo score). This result confirms the existence of linear dominance hierarchies in male baboons and the suitability of using the Elo rating method for calculating cardinal ranks.

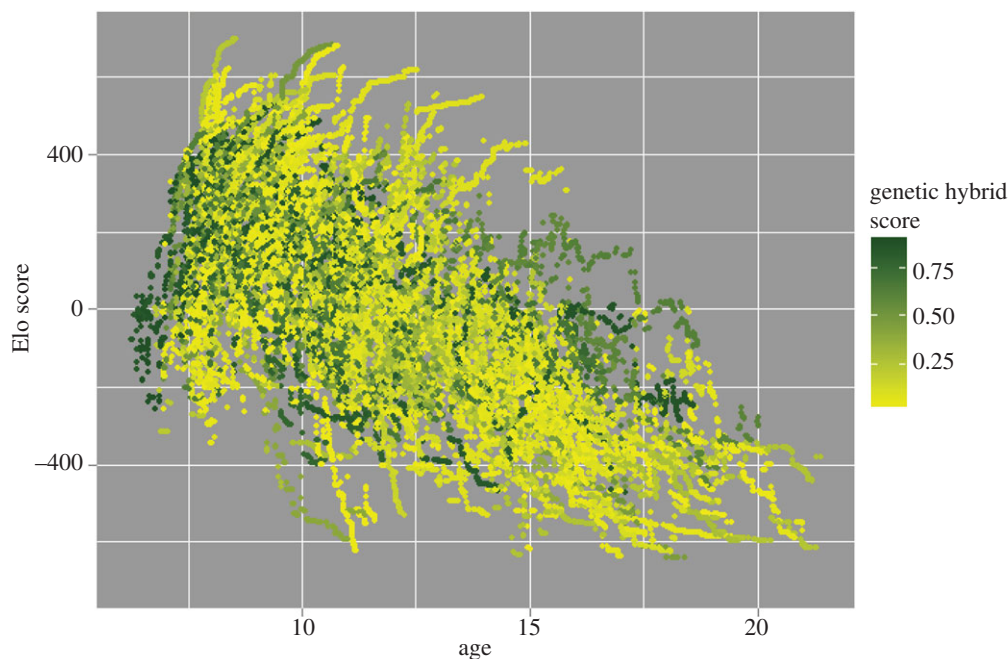


Figure 1. Relationship between age, Elo score and genetic hybrid score (which measures degree of anubis background; see main text). Plotted values are based on all observed agonistic interactions. See the electronic supplementary material, figure S2 for more detailed illustrations for different groups and time periods. (Online version in colour.)

In addition, the relationship between age and Elo scores is consistent with the pattern reported in previous studies: with increasing age young males tend to rise in dominance rank, but rank subsequently tends to decline as individuals age past their prime and senesce (figure 1; electronic supplementary material, figure S2).

Second, documenting winner and loser effects in a natural setting fundamentally depends on ruling out the possibility that temporal variation in the impact of wins and losses on future wins and losses can be attributed to variation in prior attributes, a possible alternative to the ‘social dynamics’ hypothesis. Our approach to this problem relied on the observation that winner and loser effects should be generally stronger when aggression intensity is higher (e.g. because outcomes of more aggressive interactions contain more reliable information on an individual’s relative fighting ability [19,25]). To rule out prior attributes as an explanation for any increase in winner and loser effects when aggression intensity was high, we focused on variation in aggression intensity that was environmentally induced (e.g. that resulted from variation in the availability of mates). If variation in environmentally induced aggression intensity predicted variation in the impact of wins and losses on future wins and losses, winner and loser effects would be implicated rather than prior attributes.

Therefore, the main aim of our analysis was to test whether variation in environmentally induced aggression intensity predicted variation in k , which captures the impact of winning and losing on future wins and losses. Because our observational data did not include a direct measure of variation in environmentally induced aggression intensity, our analysis involved two steps (see flowchart in electronic supplementary material, figure S1). As described in the following section, we first performed an analysis to estimate an index of environmentally induced aggression intensity. In our main analysis, we then used this index, among other variables, as a predictor of k (see section after next, ‘Statistical analysis of agonistic data’).

(i) Estimation of environmentally induced aggression intensity

We expected that environmentally induced aggression intensity would vary between observation days because the competitive regime that males experience—and hence aggression

intensity—should change with the number of adult males and the number of peri-ovulatory females in the group. To quantify this relationship, we used the occurrence of injuries as an indicator of the level of severe aggression. We then estimated an aggression intensity index based on the number of adult males and the presence and number of peri-ovulatory females in a group on a given day.

To do so, we ran a Poisson regression using a logarithmic link function to estimate how the number of males and peri-ovulatory females affected injury risk to males. We modelled the observed number of injuries in adult males in a given group, for a given day, as the response variable ($n = 4383$ group-days in all; 151 with reported injuries). We used three predictor variables: the number of adult males, the presence of peri-ovulatory females (coded as 0 and 1) and the number of peri-ovulatory females (ordinal). We included both the presence and number of peri-ovulatory females to take into account the possibility that injury rate could increase with the presence of peri-ovulatory females, but then decrease with an increasing number of peri-ovulatory females (due to reduced competition). Because we wanted to estimate injury rate per encounter, we included the number of agonistic interactions among adult males as an offset in the model. We conducted our statistical analysis in R [35] using the function ‘glm’. We used the estimated model parameters to calculate an aggression intensity index a_d for each observation day d :

$$a_d = \exp(4.039 - 0.108 n_{m,d} + 0.548 ef_d + 0.070 n_{ef,d}), \quad (2.7)$$

where $n_{m,d}$ is the number of adult males, ef_d indicates the presence of peri-ovulatory females and $n_{ef,d}$ is the number of peri-ovulatory females on day d . This index can be interpreted as the expected number of injuries resulting from each agonistic interaction in a group on a given day. More specifically, this index captures variation in number of injuries that is explained by environmental variation (i.e. variation in number of males and presence and number of peri-ovulatory females). The estimated coefficients (equation (2.7)) essentially indicate that injuries are more likely when more males compete over fewer peri-ovulatory females.

(ii) Statistical analysis of agonistic data

To test the hypothesis that winner and loser effects influenced the outcomes of dominance interactions in the baboons, the main predictor variable in our analysis was the aggression intensity index for the group-day of a given agonistic encounter. Specifically, we predicted that more intense aggression would produce a larger winner's bonus and larger loser's tax, which should result in a positive relationship between the value of the aggression intensity index and the response variable k .

We also included four additional predictors: (i) the outcome of an encounter (scored 1 for a win and 0 for a loss), which allowed k to differ for winners and losers; (ii) the degree of anubis ancestry for each individual (i.e. the individual's 'genetic hybrid score'), which was previously estimated based on genotype data from 14 microsatellite markers [28,29,36] and which allowed us to test for possible effects of genetic background on interaction outcomes; (iii) each individual's age (in years), because age is known to affect competitive ability in male baboons [7,22]; and (iv) the number of days 'inactive' (i.e. the number of days since the last observed agonistic encounter involving a given individual), which controlled for variation in the frequency with which males engaged in agonistic interactions (note that this variable was only calculated for residents; for immigrants this variable was set to 0).

We also tested all pairwise interactions of the encounter outcome (win or loss, for each individual) with the other four predictors listed above (aggression intensity index, genetic hybrid score, age and days inactive). These interactions allowed us to test whether these predictors had different effects for winners and losers. Finally, we tested an interaction between the aggression intensity index and hybrid score. This additional interaction was included to investigate the possibility that the relationship between k and competitive context depends on the level of a male's anubis ancestry.

Likelihood calculations were performed separately for each of the five social groups that we studied, and log-likelihood values for each group were summed to obtain the overall log-likelihood for the whole dataset. For all males in all social groups, initial Elo scores were set to zero. This initial value also applied to males who immigrated into the social group at some time during the study period. In addition, individuals who left the group for more than 90 days and then returned to the same group were treated as new immigrants, and their Elo score was set to zero at time of immigration. To avoid any biased Elo scores for immigrants, after each updating of Elo scores we centred all Elo scores of current group members to a mean of zero. This procedure ensured that immigrants were always assigned the average Elo score of the group, but it did not affect the relative ranking of individuals or their predicted winning probabilities.

For the analysis of each group, the first 100 encounters were set as a burn-in period. In all of these encounters values of k were kept at 100; encounters in the burn-in period were excluded from the likelihood calculation. Maximum-likelihood fitting was performed using the function 'optim' in the statistical software R [35]. We used likelihood ratio tests to calculate p -values for each predictor variable. To implement likelihood ratio tests, we used a χ^2 -test with the test statistic D , which is twice the difference in log-likelihoods of the corresponding null model (where the respective parameter was removed) and the full model containing all parameters. Calculations of p -values were initially performed for the full model specified above. Final p -values were calculated after removing non-significant interactions from the model. A variable was assumed to be significant if the corresponding p -value fell below a threshold of 0.05.

3. Results

Our results provide clear evidence of the existence of winner and loser effects in wild male baboons. As predicted,

Table 1. Variables that explain variation in the parameter k , which determines how strongly winning and losing predicts the outcome of future interactions.

parameter	coefficient	D^a	p -value ^b
(intercept)	4.939	667.2	<0.001
aggression intensity index	14.949	4.3	0.040
genetic hybrid score	−0.558	19.4	<0.001
contest outcome	0.255	8.0	0.005
age	−0.020	2.2	0.138
days inactive	0.006	5.4	0.020
age : contest outcome	−0.035	20.0	<0.001

^aThe test statistic D is twice the difference in log-likelihoods of the corresponding null model (where the respective parameter was removed) and the full model that contains all parameters (see the electronic supplementary material, table S1).

^bAll p -values were obtained using likelihood ratio tests based on the test statistic D .

we found a significant positive relationship between the aggression intensity index and the value of k (table 1; figures 2*a* and 3). Therefore, changes in Elo scores—the winner's bonus and the loser's tax—were larger when aggression intensity was higher. In other words, the impact of winning and losing on future wins and losses increased with increasing environmentally induced aggression intensity.

By relaxing the assumption that k is a constant and allowing k to vary, our extensions of the Elo method allowed us to identify several intriguing sources of variance in k (table 1). Most surprisingly, we found that, compared with more yellow-like individuals, more anubis-like individuals had significantly lower values of k (table 1; figures 2*b* and 3). That is, individuals with more anubis background experienced smaller winner's bonuses and smaller loser's taxes.

In addition, the interaction between age and encounter outcome was also a significant predictor of k . Specifically, k -values for both winners and losers were lower for older males, but k -values for winners declined more quickly with age than k -values for losers (figures 2*c* and 3). This provides clear evidence of how the winner's bonus and the loser's tax can differ when we remove the assumption of the original Elo method that k is constant. As a consequence, for the youngest adult males, winning affected the future chance of winning more than losing affected the future chance of losing. The opposite pattern occurred for older individuals.

Finally, we also found that individuals who had not interacted for a long time tended to require more pronounced updating of their Elo scores. Specifically, we found a positive effect on k of the number of days since the last observed agonistic encounter involving a given individual. This is consistent with the idea that Elo scores become out-dated over time.

4. Discussion

The potential importance of self-organization processes in generating linear dominance hierarchies has been supported by theoretical and experimental studies [11,14,15,17–20,37]. In this study, we showed that such self-organization

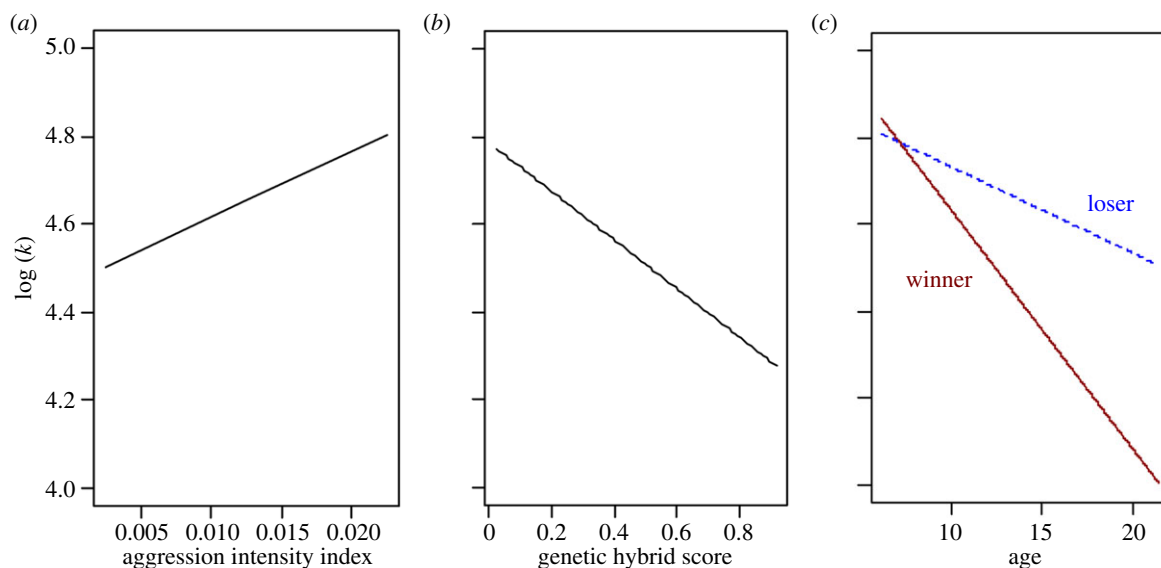


Figure 2. Illustration of the estimated effects on k of (a) aggression intensity, (b) genetic hybrid score (which measures degree of anubis background) and (c) the interaction between age and the outcome of the agonistic interaction, which determines how strongly winning and losing predicts the outcome of future interactions. All depicted effects are calculated for the mean values of all other predictor variables. (Online version in colour.)

processes are also relevant for natural populations in which individuals profoundly differ in fighting abilities. Specifically, we tested the hypothesis that winner and loser effects influence male hierarchy dynamics in wild baboons. The novel statistical method we developed allowed us to quantify variation in the impact of wins and losses on future wins and losses in uncontrolled group settings. We found that the magnitude of these effects was positively correlated with environmentally induced aggression intensity—that is, the effects increase in magnitude when female reproductive availability becomes low relative to male availability (figures 2a and 3), providing strong support for the hypothesis that social self-organizing dynamics play a role in natural groups of wild primates. Furthermore, our approach allowed us to identify additional predictors that explained variation in the impact of wins and losses on future wins and losses, providing further information on agonistic behavioural strategies in our population, and allowing us to formulate novel hypotheses regarding the evolution of winner and loser effects.

Our finding that ancestry affected the impact of winning and losing on future winning chances (figures 2b and 3) indicates effects of genetic background on this phenotype. This effect of genetic background could in principle arise if more anubis-like individuals experienced more short-term fluctuations in their fighting ability (which would reduce the consistency of winning and losing patterns). In this case, prior attribute differences would explain the effects of genetic background. However, the observed genetic background effect is also consistent with genetically determined differences in winner and loser effects between yellow and anubis baboons.

Previous studies in this population revealed effects of ancestry on age at maturation and male mating success [32,36]: more anubis-like males matured earlier and were more likely to participate in consortships with peri-ovulatory females. Tung *et al.* [32] suggested that more anubis-like males might employ more effective mating strategies, such as more effective coalition formation or higher rates of aggression in agonistic interactions. Although our analysis was not designed to specifically test these hypotheses, our

results are more consistent with the coalition hypothesis. If more anubis-like males compete more aggressively for access to peri-ovulatory females, then we would have expected to observe larger winner and loser effects with high levels of anubis genetic ancestry. However, we found the opposite effect, suggesting that more anubis-like males deploy a less aggressive agonistic strategy in dyadic interactions. Recent findings from phylogenetic comparative analyses on male coalitions in mammals suggest that reduced competition intensity might facilitate coalition formation through increased levels of tolerance among males [38,39]. A less aggressive agonistic strategy in more anubis-like males, which is consistent with our results, might allow these males to engage in more effective coalition formation.

Importantly, however, the effect of genetic background we detected could be a direct or an indirect genetic effect. A direct effect would be implicated if the individual's own genetic background affected its own response to winning and losing, for instance by affecting how aggressive an agonistic strategy it uses, as posited above. Alternatively, the genetic effect could be indirect; that is, the individual's genetic background could affect the response of other animals to its wins and losses, which in turn could affect its chances of winning and losing future encounters. For instance, if something about the hybrid morphology—for instance darker coat, somewhat more stocky appearance [27]—resulted in opponents seeing these animals as less predictable than the more common yellow phenotype, this behavioural uncertainty could produce a lower estimated k -value for the hybrid animals. Detectably hybrid animals currently constitute about 25–30% of the Amboseli population [27,29], indicating that they are certainly familiar to all members of the study population. This example highlights the fact that social behavioural phenotypes can depend on both direct and indirect genetic effects [40–42]. Differentiating these effects is beyond the scope of this paper, but would potentially be amenable to quantitative genetic approaches using the 'animal model' to investigate individual variation in k , given a well-linked and large enough pedigree [43,44].

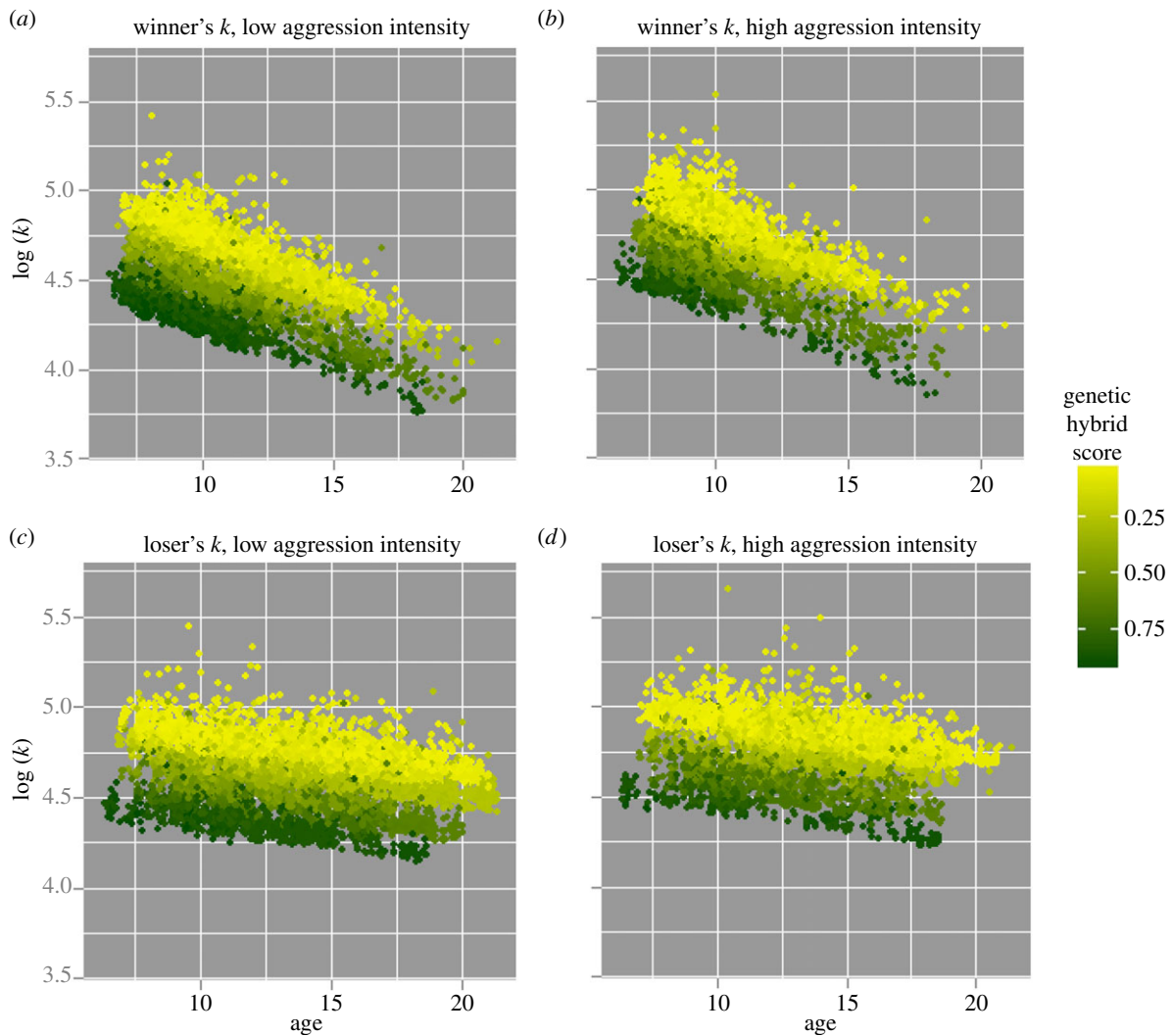


Figure 3. Illustration of the predicted effects on k of aggression intensity, genetic hybrid score, interaction outcome and age, which determines the impact of winning and losing on the outcome of future interactions. Plotted values correspond to all observed agonistic interactions. Aggression intensity index categories correspond to values (a,c) below and (b,d) above the mean. The colour coding illustrates the effect of anubis background; hybrid scores vary continuously. The negative effect of age is more pronounced for (a,b) winners compared with (c,d) losers. Finally, the contrast between (a) and (c) versus (b) and (d) illustrates how values of k increase with increasing aggression intensity. (Online version in colour.)

In addition to demonstrating the existence of winner and loser effects and identifying predictors of the intensity of these effects, our analysis allowed us to gain some insight into the mechanisms underlying winner and loser effects in male baboons. One potential mechanism would be a change in fighting ability resulting from injury [15]. This mechanism is consistent with our result showing that the impact of wins and losses on future wins and losses increased with increasing aggression intensity (assayed by injury rates). However, while changes in fighting ability from injuries could produce loser effects (because injuries are likely to reduce fighting ability), they should not generate winner effects (because injuries are unlikely to result in *increased* fighting ability). Our results indicate that increased aggression intensity leads to a similar increase in *both* winner effects and loser effects (the interaction between the aggression intensity index and encounter outcome was not significant; $p = 0.33$; electronic supplementary material, table S1). This finding demonstrates the existence of other mechanisms that do not include changes in actual fighting abilities. Such a mechanism probably involves changes in *perceived* fighting ability, which then modulate future agonistic behaviour and associated winning probabilities [14,37,45].

We also found that an interaction between age and encounter outcome significantly affected the impact of winning and losing on future winning chances (figures 2c and 3). This interaction effect could be explained by the prior attributes hypothesis, in the absence of any winner and loser effects. Specifically, it could be explained by a situation in which growth- and ageing-related changes in fighting ability determine individual dominance ranks. For instance, younger males generally experience a growth-related increase in fighting ability (which is consistent with their quickly rising Elo scores; figure 1). For such males, unexpected winning events would be more likely to reflect true changes in fighting ability than unexpected losing events. As a consequence, losing events should have a relatively weak impact on the future chances of winning, whereas winning experiences should have a relatively strong impact on the future winning chances, without the need to invoke winner and loser effects. The opposite pattern is expected for older individuals, who tend to decline in fighting ability. The combination of both opposing patterns could lead to the interaction effect that we observed between age and encounter outcome.

However, while the effect of age and encounter outcome can be explained without winner and loser effects, our results

are consistent with the idea that individuals use age information to flexibly adjust the strength of winner and loser effects. Theoretical work on the evolution of winner and loser effects has demonstrated that these effects can evolve when individuals are uncertain about their relative fighting ability, because outcomes of agonistic interactions provide new information about this quantity [37,46]. Notably, current work on winner and loser effects generally ignores the fact that the relative fighting abilities of individuals change over time (e.g. due to growth, ageing or changes in the composition of a social group). However, if relative fighting abilities change over time, information on relative fighting ability can become out-dated if it is not updated over time. As a consequence, competitors should be constantly prepared to revise their estimation of their relative fighting ability. They thus need to decide whether newly obtained information is reliable enough to support such a revision. An obvious (but potentially costly) solution to this problem is to gather more information through additional interactions. A less costly alternative would be to combine information on the outcome of a conflict with information on the age (or other characteristics) of the interacting individuals. Our results demonstrate that such a combination is indeed able to provide better predictions of the future chances of winning. Whether baboons use information about age to adjust winner and loser effects requires further investigation. However, more generally we hypothesize that the evolution of winner and loser effects should be accompanied by the evolution of behavioural strategies that dynamically adjust the strength of winner and loser effects. Such dynamic adjustments will have the effect of optimizing the estimation of relative individual fighting ability, which will increase the benefit–cost ratio of agonistic behaviour.

More generally, we expect that the evolution of linear dominance hierarchies is shaped by a coevolution of individual (prior) attributes and winner and loser effects that favours a combination of both. Theoretical work on the evolution of winner and loser effects assumed a fixed distribution of individual attributes that impact winning chances in addition to winner and loser effects [37,46]. However, if both individual attributes and winner and loser effects are heritable, then both could evolve simultaneously. We hypothesize that scenarios in which only individual attributes or only winner and loser effects determine hierarchy formation are not evolutionarily stable. If hierarchy

formation is dominated by (heritable) individual attributes, then natural selection will reduce inter-individual variation in these attributes, which increases uncertainty in estimating relative fighting abilities [47], and therefore should facilitate the evolution of winner and loser effects [37,46]. However, these dynamics should not lead to a complete domination of winner and loser effects, because winner and loser effects tend to decrease the correlation between individual attributes and dominance rank, which would reduce selection on individual attributes. In addition, it is likely that additional factors, such as developmentally or environmentally determined variation in individual attributes, influence the balance between individual attributes and winner and loser effects.

Clearly, many open questions remain to be answered to achieve a better understanding of the evolution of winner and loser effects and linear dominance hierarchies. We hope that our proposed methodological advancement will motivate further development of our approach, which in turn will enable more studies on winner and loser effects in animals in natural settings. In addition, we emphasize the need for more formal theory that investigates (i) the evolution of behavioural strategies that implement temporally variable winner and loser effects, and (ii) the coevolution of prior attributes and winner and loser effects.

Ethics. This research was approved by the IACUC at Princeton University and at Duke University, and adhered to all the laws and guidelines of Kenya.

Data accessibility. The datasets supporting this article are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.d0g0d>.

Competing interests. We declare we have no competing interests.

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