Commentary

Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating

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Dominance is one of the most important concepts in the study of animal social behaviour. Dominance hierarchies in groups arise from dyadic relationships between dominant and subordinate individuals present in a social group (\cite{Drews1993}). High hierarchical rank or social status is often associated with fitness benefits for individuals (e.g. \cite{Cotefesta2001, Holsetal2002, Widdgetal2004, Engelhardtetal2006}), and hierarchies can be found in most animal taxa including insects (e.g. \cite{KolmerHeinz2000}), birds (e.g. \cite{Kurversetal2009}) and mammals (e.g. \cite{KeiperReceveur1992}).

The analysis of dominance has a long-standing history (\cite{Schjelderup-Ebbe1922, Landau1951}), and a great number of methods to assess hierarchies in animal societies are currently available (reviewed in \cite{deVries1998, Baylyetal2006, Whitehead2008}). Although differing in calculation complexity, all ranking methods presently used in studies of behavioural ecology are based on interaction matrices. For this, a specific type of behaviour or interaction, from which the dominance/subordination relationship of a given dyad can be deduced, is tabulated across all individuals (see for example, \cite{Verbaeksetal2007}). This matrix can either be reorganized as a whole in order to optimize a numerical criterion (e.g. I&SI: \cite{deVries1998}; minimizing entries below the matrix diagonal: \cite{MartinBateson1993}), or alternatively, an individual measure of success calculated for each animal present (e.g. David’s score: \cite{David1987}; CBI: \cite{Clutton-Brocketal1979}). In the latter case, a ranking can be generated by ordering the individual scores obtained.

Although calculations of dominance hierarchies are routinely undertaken in many studies of behavioural ecology, and although there have been numerous methodological developments in this area (e.g. \cite{Clutton-Brocketal1979, David1987, deVries1998}), there are still a number of obstacles and limitations scientists have to tackle when analysing dominance relationships. This is mainly
because the methods commonly used can often not be applied to highly dynamic animal societies, or to sparse data sets, and because methods based on interaction matrices need to fulfill certain criteria to generate reliable results. Generally, many researchers may not be aware of some of the problems that are associated with the application of such methods to their data sets, which may in the worst case lead to the misinterpretation of results.

An alternative method that can overcome the shortcomings of matrix-based methods is Elo-rating. Developed by and named after Arpad Elo (Elo 1978), it is used for ratings in chess and other sports (e.g. Hvattum & Arntzen 2010), but has rarely been used in behavioural ecology (but see Rusu & Krackow 2004; Pörschmann et al. 2010). The major difference to commonly used ranking methods is that Elo-rating is based on the sequence in which interactions occur, and continuously updates ratings by looking at interactions sequentially. As a consequence, there is no need to build up complete interaction matrices and to restrict analysis to defined time periods. Ratings (after a given start-up time) can be obtained at any point in time, thus allowing monitoring of dominance ranks on the desired timescale.

The major aim of this paper is to promote Elo-rating among behavioural ecologists by illustrating its advantages over common methods, and by validating its reliability for assessing dominance rank orders, particularly in highly dynamic social systems. By providing the necessary computational tools along with an example (see Supplementary Material), we also make Elo-rating user friendly. In the following, we start with an introduction to the procedures of Elo-rating. We then show that with Elo-rating it is easy to track changes in social hierarchies, which may be overlooked with matrix-based methods, and point out several general advantages of Elo-rating over matrix-based methods. To demonstrate the benefits of Elo-rating empirically, we present the results of a reanalysis of one of our own previously published data sets. Finally, we validate the reliability and robustness of Elo-rating by comparing the performance of this method with those of two currently widely used ranking methods, the I&SI method and the David’s score, using empirical data and reduced data sets that mimic sparse data.

**ELO-RATING PROCEDURE**

Elo-rating, in contrast to commonly used methods, is not based on an interaction matrix, but on the sequence in which interactions occur. At the beginning of the rating process, each individual starts with a predefined rating, for example a value of 1000. The amount chosen here has no effect on the differences in ratings later: the relative distances between individual ratings will remain identical (Albers & de Vries 2001). After each interaction, the ratings of the two participants are updated according to the outcome of the interaction: the winner gains points and the loser loses points. The number of points gained and lost during one interaction depends on the expectation of the outcome (i.e. the probability that the higher-rated individual wins, Elo 1978) prior to this interaction. Expected outcomes lead to smaller changes in ratings than unexpected outcomes (Fig. 1). Depending on whether the higher-rated individual wins or loses an interaction, ratings are updated according to the following formulae.

- Higher-rated individual wins:
  \[ \text{WinnerRating}_{\text{new}} = \text{WinnerRating}_{\text{old}} + (1 - p) \times k \] (1)
  \[ \text{LoserRating}_{\text{new}} = \text{LoserRating}_{\text{old}} - (1 - p) \times k \] (2)

- Lower-rated individual wins (against the expectation):
  \[ \text{WinnerRating}_{\text{new}} = \text{WinnerRating}_{\text{old}} + p \times k \] (3)
  \[ \text{LoserRating}_{\text{new}} = \text{LoserRating}_{\text{old}} - p \times k \] (4)

where \( p \) is the expectation of winning for the higher-rated individual, which is a function of the absolute difference in the ratings of the two interaction partners before the interaction (Fig. 1; see also Elo 1978; Albers & de Vries 2001). \( k \) is a constant and determines the number of rating points that an individual gains or loses after a single encounter. Its value is usually set between 16 and 200 and, once chosen, remains at this value throughout the rating process.

![Figure 1. Graphical illustration of Elo-rating principles. Two individuals A (squares) and B (circles) interact four times of which the first three interactions are won by A and the fourth is won by B. The number of points gained/lost depends on the probability that the higher-rated individual wins the interaction (see text for details). The winning probability (p) is a function of the difference in Elo-ratings before the interaction (dotted vertical lines). As the difference in ratings increases with each interaction so does the chance of A winning. A graphical way to obtain the winning chance is depicted in the inset figures. A detailed description of this example can be found in Appendix 1.](image-url)

process. In the short term, $k$ influences the speed with which Elo-ratings increase or decrease. In the long term, however, $k$ appears to have only minor influence on the rankings obtained (Albers & de Vries 2001; C. Neumann et al., unpublished data). For the latter reason, we used an arbitrary fixed $k = 100$ throughout our analyses, even though the choice of $k$ can have interesting implications (see Integrity of Power Assessment).

As Elo-rating estimates competitive abilities by continuously updating an individual’s success, it reflects a cardinal score of success. As such, the differences between ratings are on an interval scale and may thus allow the application of parametric statistics in further analyses. An example, illustrating the process of Elo-rating in more detail, can be found in Appendix 1 (see also Albers & de Vries 2001).

**ADVANTAGES OVER MATRIX-BASED METHODS**

**No Minimum Number of Individuals**

Scientists often face the problem of small sample sizes when it comes to determining dominance hierarchies. In many group-living species, age—sex classes or even complete groups may contain fewer than six individuals. Problems with matrix-based methods therefore start with the calculation of linearity (i.e. if A is dominant over B and B is dominant over C, then A is dominant over C). The commonly used index to assess the degree and statistical significance of linearity (Landau 1951; de Vries 1995) will yield significant results only if there are more than five individuals in the matrix (Appleby 1983), thus preventing, for example, the application of the widely used I&SIs method (de Vries 1998) to small groups.

Elo-rating, however, can be applied to groups of any size with only two individuals required for the calculation of Elo-ratings (see Fig. 1).

**Independence of Demographic Changes**

Biological systems are often very dynamic in regard to group composition. New offspring are born, maturing animals migrate, individuals become the victim of predation, floating individuals may join groups temporarily, or entire groups undergo fission and fusion regularly.

An advantage of Elo-rating is the incorporation of demographic changes such as migration events without interruption of the rating process itself. Whereas matrix-based methods need to discontinue rating and to build up new matrices (which then need a sufficient number of interactions between individuals to produce reliable rankings) after each demographic change, hierarchy determination with Elo-rating can be continued despite demographic changes. This is achieved by giving a new individual the predefined starting value (as defined for all individuals before they are rated for the first time) before the first interaction with another individual. After a few interactions this individual can be ranked in the existing hierarchy (see below). This feature may be particularly advantageous for studies on species that live in large social groups with high reproductive rate, high migration rate and/or high predation rate.

To illustrate this, we plotted the development of Elo-ratings of adult males in a group of crested macaques, *Macaca nigra*, over the course of a month during which three migration events took place (Fig. 2; see below for details of the study population and data collection). In our example, male ZJ migrated into group R2 on 11 March 2007. To include him in the dominance hierarchy, he was assigned the initial score of 1000, and even though he lost his first observed interaction, Elo-rating made it possible to recognize him quickly as the new alpha male. Likewise, individuals that emigrate or die (such as males SJ and YJ in this example) are simply excluded from the rating process from the date of their disappearance without causing any interruption to the rating procedure.

Since Elo-rating does not stop the rating process as a consequence of changes in group composition it circumvents a further drawback of matrix-based methods. Techniques such as I&SIs and David’s score result in values that directly depend on the number of individuals present; thus an observed change in calculated dominance rank or score across two time periods may in fact be a consequence of changes in the number of animals in the group rather than changes in competitive abilities, making a comparison invalid. For example, in the case of the normalized David’s score (cf de Vries et al. 2006), values can range between 0 and $N - 1$, where $N$ is the number of individuals present in the social group. Elo-rating, in contrast, results in ratings that do not depend on the number of individuals present. Given that $k$ is fixed for the entire rating process, the current opponent’s strength is the only variable that influences an individual’s future rating. Hence, the Elo-rating of an individual is independent of the number of individuals and of time periods that need to be created as a consequence of changes in the number of individuals. This feature allows Elo-rating to be used in a longitudinal manner, which is crucial for a wide array of studies, such as those on mechanisms of rank acquisition and maintenance, and determinants of lifetime reproductive success.

![Figure 2](image-url) Elo-ratings of 10 male crested macaques during March 2007 (group R2). Each line represents one male. Each symbol represents Elo-ratings after they were updated following an interaction of the depicted individual. Note that on 10 March, the residing top-ranking male (SJ) and another high-ranking male (YJ) emigrated from the group and a new male (ZJ) joined the group on 11 March, becoming the group’s new alpha male (see text for details).
However, as in the other methods, true ratings of individuals are known only after a minimum number of interactions involving these individuals have occurred (see also Albers & de Vries 2001). For example (Fig. 2), rank orders that would have been obtained through Elo-rating within the first 2 weeks of ZJ’s group membership would have placed him as ranking below BJ. After 13 days (i.e. eight observed interactions), ZJ reached the top-ranked position in the Elo-ratings. Using all observed interactions from these 2 weeks it was not possible to construct a linear hierarchy, and only after 45 days did we obtain a matrix with a sufficient number of interactions permitting the use of I&SI. However, it is likely that ZJ became alpha male directly upon his arrival in the group even though he lost his very first observed interaction (top entry: see e.g. Sprague et al. 1998) rather than constantly rising through the hierarchy. Albers & de Vries (2001) suggested waiting for at least two interactions before assessing a dominance hierarchy through Elo-rating whenever a new member joins the hierarchy; one against a stronger and one against a weaker opponent. In the case of ZJ, however, we observed him interacting with six of the seven other males present. In our case it thus seems more appropriate to follow Glickman & Doan’s (2010, rating chess players) suggestion to treat first 2 weeks of ZJ’s (2010, rating chess players) interaction matrices for dominance hierarchies.

**Visualization and Monitoring of Hierarchy Dynamics**

Even if group composition is stable, matrices do not allow dynamics to be tracked within social hierarchies, especially if study periods are very short and data insufficient to obtain reliable rankings. In the worst case, a researcher may overlook rank changes when analysing hierarchies at some fixed interval (e.g. monthly).

One of the great advantages of Elo-rating is its ability to visualize dominance relationships on a given timescale, thus allowing monitoring of rank relationship dynamics. As the information about the sequence of interactions is a prerequisite for applying Elo-rating, one can easily create graphs that depict the timescale on the X axis and plot the development of each individual’s ratings on the Y axis. This approach can demonstrate a fundamental feature of Elo-rating, that is, the possibility of obtaining a rank order at any given point in time by ordering the most recently updated ratings for a given set of individuals. For example (Fig. 2), the ordinal rank order among the individuals present on 1 March based on Elo-ratings was SJ (1810 Elo points), BJ (1592), YJ (1317), VJ (1068), KJ (982), TJ (942), RJ (703), CJ (526), Pj (90). By 31 March, however, the ordinal rank order had changed to ZJ (1355), BJ (1262), VJ (994), TJ (950), KJ (892), RJ (600), CJ (592), PJ (53).

Figure 3 gives an example illustrating how Elo-rating can reflect dynamics in rank relationships. In late June 2007, medium-ranked male KJ started losing interactions against several lower-ranked males and dropped to rank 11. As such, his drop to the lowest rank among group males is reflected by a rapid decrease in his Elo-rating by several hundred points in only a few days (Fig. 3). Such dynamics are difficult to track with both I&SI and David’s score since a new matrix would need to be created after such a conspicuous event, requiring sufficient data to obtain reliable rankings.

At the same time, it is common practice to calculate dominance hierarchies based on rather arbitrary time period definitions (e.g. monthly: Silk 1993; Setchell et al. 2008). This might lead to blurring or in the most extreme case even to overlooking dynamics in rank relationships. Elo-rating, with its capacity to visualize dominance relationships graphically, allows identification of such dynamics in rank relationships in great detail. Hierarchies for the example-month June 2007 (Fig. 3) obtained with matrix-based methods lead to illogical rankings; the I&SI algorithm assigns KJ rank 11, whereas David’s score ranks KJ 10th (note that linearity is statistically significant during this month: H′ = 0.50, P = 0.043, total of 205 interactions, 24% unknown relationships). Elo-rating, in contrast, shows that KJ held a medium rank almost throughout the entire month and dropped in rank only during the last week of June.

In Old World monkeys and many other group-living mammals, it is sometimes observed that young males rise in rank before they eventually leave their natal group (e.g. Hamilton & Bulger 1990). A common approach to quantify this phenomenon would be to calculate monthly ranks and correlate them with the time to departure. Doing so for 16 natal male crested macaques using David’s score, however, lends only little support to this phenomenon (Spearman rank correlation: r = 0.642, N = 7, P = 0.139; Fig. 4a). As described below, this may be the consequence of high proportions of unknown relationships leading to less reliable scores. It could also be because David’s scores depend directly on the number of individuals incorporated in the matrix. In contrast, with Elo-rating, the hypothesis that natal males rise in rank before emigration is strongly supported (r = 1, N = 7, P < 0.001; Fig. 4b). We observe an almost linear increase in ratings before the migration date. It appears that males
went through a noticeable surge about 3 months before emigration, and kept rising before their departure. This is, however, a preliminary result and further investigation is warranted. Since Elo-ratings can be obtained at any desired date, even an analysis with higher time resolution (e.g. weekly) is possible (Fig. 4c).

In addition, Elo-rating also allows objective identification and quantitative characterization of hierarchical stability. Again, the graphical features of Elo-rating provide very useful assistance in this respect. Figure 2, for example, shows that individuals KJ and TJ changed their ordinal rank relative to each other five times within 1 month, suggesting some degree of rank instability (see also individuals RJ, TJ and GM in Fig. 3).

To quantify the degree of hierarchy stability, we propose using the ratio of rank changes per individuals present over a given time period. Formally, the index is expressed as

$$S = \frac{\sum_{i=1}^{d} (C_i \times w_i)}{\sum_{i=1}^{d} N_i}$$

(5)

where $C_i$ is the sum of absolute differences between rankings of 2 consecutive days, $w_i$ is a weighting factor determined as the standardized Elo-rating of the highest-ranked individual involved in a rank change, and $N_i$ is the number of individuals present on both days (see Appendix 2 for further details). Before division, values are summed over the desired time period, that is, $d$ days. $S$ can take values between 0, indicating a stable hierarchy with identical rankings on each day of the analysed time period, and 2/max($N_i$), indicating that the hierarchy is reversing every other day, that is, total instability. Our data suggest that $S$ typically ranges between 0 and 0.5.

To test the validity of this approach we calculated $S$ before and after the immigration of male crested macaques that subsequently achieved high ranks (among the top three). We expected such events to induce instability (e.g. Lange & Leimar 2004; Beehner et al. 2005), thus leading to higher $S$ values than in periods before such incidents. We found less stability, that is, greater $S$ values, during the 4-week periods after the immigration of males that achieved high rank compared to the 4-week periods before (Wilcoxon signed-ranks test: $V = 87, N = 14, P = 0.030$), indicating that hierarchies were less stable after the immigration of a high-ranking male. In contrast, after the immigration of males that subsequently held low ranks, we observed no such difference in stability ($V = 14, N = 7, P = 1.000$).

Such a quantitative approach may be advantageous since, so far, hierarchical instability has been identified in an inconsistent manner.

Independence of Time Periods

It is common practice to obtain hierarchies at some arbitrary fixed time interval (e.g. monthly). Given the dynamics of animal societies, both in group composition and rankings (see above), such an approach is prone to misjudgement of hierarchies for two reasons. First, all individuals incorporated in a dominance matrix must have the opportunity to interact with each other at all times. If group composition changes within the studied interval, for example in fission/fusion societies or when individuals leave and join frequently (floaters), applying matrix-based methods is unjustified. Second, rank changes that occur will be blurred (see the example above, Fig. 3).

With Elo-rating it is possible to pinpoint rankings to a specific day. This is of particular importance when studying events, such as a male's rank at the day his offspring was conceived or born, or tracking the rank development of individuals before and after they migrate.

A related problem to the creation of time periods is the proportion of unknown relationships. When creating relatively short time periods to account for the above-mentioned dynamics, one often faces a high percentage of pairs of individuals that were not observed interacting in a given period. Like any statistical test, ranking methods suffer from decreased power or precision when sample size is low (Appleby 1983; de Vries 1995; Koenig & Borries 2006; Wittemyer & Getz 2006), even though attempts have been made to counter this problem (see de Vries 1995, 1998; de Vries et al. 2006; Wittemyer & Getz 2006).
As we show below, Elo-rating seems less affected by unknown
relationships than matrix-based methods, and is therefore also
operational on very sparse data sets.

Integrity of Power Assessment

Without demonstrating their application, we finally mention
three further advantages of Elo-rating that may refine the precision of
power assessment of individuals: (1) integration of undecided
interactions into the rating process, (2) discrimination of agonistic
interactions of differing quality, and (3) choosing k according to
the study species.

Undecided interactions

Although some matrix-based methods (e.g. David’s score or
Boyd & Silk’s 1983 index) explicitly allow interactions without
unambiguous winners and losers, that is, draws or ties, to be taken
into account when establishing dominance orders, researchers
(=including us) usually choose to discard such observations. Clearly,
agonistic interactions that end without unambiguous winners and
losers contain information about competitive abilities of the indi-
viduals involved and therefore should not be disregarded. When
using Elo-rating, an undecided interaction can be incorporated into
the rating process to the disadvantage of the higher-rated indi-
vidual whose rating will decrease, even though the decrease will be
smaller than had the higher-rated individual lost the interaction
(Albers & de Vries 2001). After a draw the rating for the higher-
rated individual is reduced to Ratingnew = Ratingold − k (p − 0.5),
whereas the rating for the lower-rated individual increases to
Ratingnew = Ratingold + k (p − 0.5). Hence, a draw between two
individuals that had identical ratings before the interaction
(i.e. p = 0.5) will not alter the ratings. In this way, Elo-rating allows
for a more complete power assessment of individuals by including
interactions in the rating process that are just as meaningful as
clear winner–loser interactions.

Agonistic interactions of different quality

Instead of being fixed throughout the rating process, the constant
k could be adjusted according to the quality of the interaction or
the experience of the interacting individuals. For example, one could
distinguish between low- and high-intensity aggression (e.g. Adamo
& Hoy 1995; Lu et al. 2008) and assign interactions involving high-
intensity aggression higher values of k. This procedure results in
greater changes in ratings after such interactions compared to
interactions involving low-intensity aggression.

Choosing k

Previous experience of individuals plays an important role in
the outcome of agonistic encounters in many animal taxa: the
winner of a previous interaction is more likely to win a future
interaction, whereas losers are more likely to lose future inter-
actions (Hsu et al. 2006). A meta-analysis on the magnitude of
such winner/loser effects demonstrated that the likelihood of
winning an interaction is almost doubled for previous winners
whereas for previous losers the likelihood of winning is reduced
almost five-fold (Rutte et al. 2006). Depending on the size of this
effect in the study species, k could therefore be split into a smaller
k_w, for the winner and a larger k_l for the loser to reflect this
phenomenon (de Vries 2009).

Thus, Elo-rating is not limited to decided dominance interac-
tions, but can incorporate undecided interactions and in addition
allows for a detailed hierarchy evaluation by weighting interactions
according to their properties and the magnitude of winner/loser
effects. This surplus of information Elo-rating can utilize allows for
a much finer assessment of dominance relationships.

RELIABILITY AND ROBUSTNESS OF ELO-RATING

So far, we have shown how Elo-rating circumvents the problems
associated with matrix-based methods. However, we have not yet
shown how it compares with other methods in terms of reliability
and robustness. We now compare Elo-rating with two widely used
ranking methods that are based on interaction matrices (I&SI and
David’s score), using our own empirical data. Mimicking a variety of
social systems, we use data collected on two species of macaques
with different aggression patterns, crested macaques (agonistic
interactions frequent, but of low intensity) and rhesus macaques,
Macaca mulatta (agonistic interactions less frequent, but of higher
intensity; de Waal & Luttrell 1989; Thierry 2007), and calculate
dominance hierarchies for females (more stable hierarchies) and
males (more dynamic hierarchies) separately. To facilitate the
assessment of these analyses we first briefly review the two methods
we use for our comparisons.

Short Introduction to I&SI and David’s Score

The I&SI method (de Vries 1998) is an iterative algorithm that tries
to find the rank order that deviates least from a linear rank order. It is
based on observed dominance interactions (e.g. winning/losing an
agonistic interaction) and tries to minimize the number of inconsis-
tencies (I) produced when building a dominance hierarchy, that is,
imimize dyads for which the relationship is not in agreement with
the actual rank order. Subsequently, the strength of inconsistencies
(SI), that is, the rank difference between two individuals that form an
inconsistency, is minimized, under the condition that in the iterated
rank order the number of inconsistencies does not increase. The
result of the I&SI algorithm is an ordinal rank order.

David’s score (David 1987) is an individual measure of success, in
which for each individual a score is calculated based on the outcome
of its agonistic interactions with other members of the social group as
DS = w + w_l − I, where w is the sum of an individual’s winning
proportions and I the summed losing proportions. w_l represents an
individual’s summed winning proportions (i.e. w) weighted by the
values of its interaction partners and, similarly, l equals an individ-
ual’s summed losing proportions (i.e. l) weighted by the values of
its interaction partners (David 1987; Gammell et al. 2003; see de Vries
et al. 2006 for an illustrative example). Thus, David’s score takes the
relative strength of opponents into account, valuing success against
stronger individuals more than success against weaker individuals.

Rank orders generated with I&SI and David’s score are generally
very similar to each other (e.g. Vervaecche et al. 2007, C. Neumann
et al., unpublished data).

Methods

Study populations

For our tests of Elo-rating, we chose two species of macaques, crested
and rhesus. Even though our aim was not to test for species
differences, we nevertheless aimed at gathering a broad data set
including different, but comparable, species. Macaques fit this
condition as the different species are characterized by a common
social organization but at the same time by pronounced differences
in aggression patterns (Thierry 2007).

Data collection

Between 2006 and 2010, we collected data in three groups
(R1, R2, FB) of a population of wild crested macaques in the
Tangkoko-Batuangus Nature Reserve, North Sulawesi, Indonesia
(1'33’N, 125’10’E; e.g. Duboscq et al. 2008; Neumann et al. 2010).
Groups comprised 4–18 adult males and 16–24 adult females and
were completely habituated to human observers and individually

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recognizable. Between 2007 and 2010, data on rhesus macaques were collected in two groups (V, R) on the free-ranging population on Cayo Santiago, Puerto Rico (18°09′N, 65°44′W). The study groups comprised 20–60 females and 16–54 males (e.g. Dubuc et al. 2009; A. Widdig, unpublished data).

We collected data on dyadic dominance interactions, that is, agonistic interactions with unambiguous winner and loser, and displacement (approach/leave) interactions during all-occurrence sampling on focal animals and during ad libitum sampling (Altmann 1974). Overall, our data set comprised a total of 12 740 interactions involving 252 adult individuals. Dominance hierarchies were created separately for the different species, groups and sexes.

Data analysis

Our first aim was to investigate whether dominance rank orders calculated with Elo-rating reflect rankings obtained with more established methods. To answer this, we assessed how similar rank orders generated with Elo-rating are to those obtained with the I&SI method and David’s score. From our data on both macaque species, we created time periods based on sociodemographic events, such as changes between mating and birth season, migration or death of individuals, maturing of subadult individuals and conspicuous status changes (hereafter ‘full data set’, see Table 1) and produced corresponding dominance interaction matrices. Two consecutive time periods of a given species/sex combination did not comprise the same set of individuals in the majority of cases (61 of 66 periods, i.e. 92%).

We tested all 66 matrices for linearity by means of de Vries’s (1995) h’ index. For the 29 matrices for which the linearity test yielded a significant result, we applied de Vries’s (1998) I&SI method. Next, we calculated normalized David’s scores from all matrices following de Vries et al. (2006). Finally, we calculated Elo-ratings from all interactions in each of the group–sex combinations as a whole using Elo-ratings on the last day of each time period for the comparison with I&SI ranks and David’s scores. Elo-ratings were calculated with 1000 as initial value and k was set to 100.

We computed Spearman rank correlation coefficients between the rankings and scores for each period. To obtain positive correlation coefficients consistently for all comparisons, we reversed I&SI rank orders (i.e. high-ranking individuals get a high I&SI rank value), since high dominance rank is represented by high David’s scores and Elo-ratings. Thus, if two rankings are identical the correlation coefficient will be 1.00. We present average correlation coefficients with interquartile ranges. All calculations and tests were computed in R 2.12.0 and R 2.13.0 (R Development Core Team 2010). A script and manual to calculate and visualize Elo-ratings with R along with an index. For the 29 matrices for which the linearity test

<table>
<thead>
<tr>
<th>Species</th>
<th>Group</th>
<th>Sex</th>
<th>No. of periods</th>
<th>Duration</th>
<th>No. of individuals</th>
<th>Unknown relationships</th>
<th>Proportion in full data set</th>
<th>Increase in reduced data set</th>
<th>No. of interactions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Macaca mulatta</td>
<td>R</td>
<td>Male</td>
<td>8</td>
<td>3.9 (3.1–4.1)</td>
<td>35 (34–42)</td>
<td>0.82 (0.79–0.88)</td>
<td>0.08 (0.06–0.09)</td>
<td>180 (123–234)</td>
<td>80 (45–119)</td>
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<tr>
<td></td>
<td>V</td>
<td>Female</td>
<td>4</td>
<td>1.8 (1.2–2.5)</td>
<td>22 (19–22)</td>
<td>0.86 (0.84–0.86)</td>
<td>0.03 (0.01–0.07)</td>
<td>106 (76–136)</td>
<td>50 (34–76)</td>
</tr>
<tr>
<td>Macaca nigra</td>
<td>PB</td>
<td>Female</td>
<td>3</td>
<td>4.0 (3.5–7.6)</td>
<td>18 (18–18)</td>
<td>0.25 (0.16–0.30)</td>
<td>0.19 (0.14–0.22)</td>
<td>299 (228–644)</td>
<td>125 (93–158)</td>
</tr>
<tr>
<td></td>
<td>R1</td>
<td>Male</td>
<td>6</td>
<td>2.4 (2.2–3.5)</td>
<td>8 (7–9)</td>
<td>0.36 (0.25–0.40)</td>
<td>0.14 (0.11–0.16)</td>
<td>116 (34–226)</td>
<td>50 (34–118)</td>
</tr>
<tr>
<td></td>
<td>R2</td>
<td>Female</td>
<td>7</td>
<td>6.7 (4.8–7.5)</td>
<td>18 (16–20)</td>
<td>0.50 (0.45–0.56)</td>
<td>0.13 (0.07–0.15)</td>
<td>194 (136–246)</td>
<td>64 (33–181)</td>
</tr>
<tr>
<td></td>
<td>R2</td>
<td>Male</td>
<td>12</td>
<td>3.1 (2.2–4.0)</td>
<td>8 (6–9)</td>
<td>0.26 (0.13–0.34)</td>
<td>0.10 (0.07–0.12)</td>
<td>64 (33–181)</td>
<td>34 (22–70)</td>
</tr>
</tbody>
</table>

Values are presented per species, group and sex. Medians are given with interquartile ranges.

1 Number of time periods created.

2 Duration of time periods in months.

3 Proportion of unknown relationships in the full data matrices and the increase in proportion of unknown relationships in the reduced data set (see text).

4 Number of agonistic interactions in each matrix.

In a second analysis, we explored whether Elo-rating is a robust method under conditions of sparse data and whether the performance of Elo-rating under such conditions is systematically related to the percentage of unknown relationships in the interaction matrix. Note that a sparse matrix is not necessarily a matrix with a higher proportion of unknown relationships. For example, a matrix in which each dyad was observed five times and all entries are above the diagonal (i.e. there are no unknown relationships) is more sparse than a matrix with each dyad being observed 10 times (likewise, no unknown relationships). Whereas the I&SI ranking will be identical in both cases, David’s scores will differ between the two, as will Elo-ratings based on the interactions leading to this matrix.

We created sparse interaction matrices by randomly removing 50% of the observed interactions in each of the 66 time periods (‘reduced data set’: Table 1). These additional matrices were again tested for linearity, resulting in 17 matrices retaining significant linearity and thus justifying the application of the I&SI algorithm. We then calculated for each of the three methods separately correlation coefficients between rankings obtained from full and reduced data sets. For the 49 matrices that did not allow the use of I&SI owing to nonsignificant linearity, we restricted the analysis to Elo-rating and David’s score.

To establish the robustness of the method further, we tested whether Elo-rating is affected by increased proportions of unknown relationships and how it compared to the two other methods. In other words, we investigated whether the methods become less reliable as the proportion of unknown relationships increases. An increase in unknown relationships was generated as a consequence of the random deletion of 50% of all observed interactions (increase per period on average 12.5%, interquartile range 8–17%, ‘reduced data set’: Table 1). We tested for an association between the increase in unknown relationships and the correlation coefficient between ratings from the full and reduced data sets.

Results

Our results show that Elo-ratings correlated highly with both I&SI ranks (median r5 = 0.97, quartiles 0.94–0.99, N = 29 periods) and David’s scores (median r5 = 0.97, quartiles 0.96–0.99, N = 29 periods).

We found that Elo-ratings from the full data set correlated highly with Elo-ratings from the randomly reduced data set (Table 2). The performance of Elo-rating is virtually identical to that of I&SI and slightly higher than David’s score (Table 2). Similarly, Elo-rating produced strong correlations with slightly higher correlation coefficients compared to those obtained with David’s
Data sets are limited in the number of interactions observed. Furthermore, our results indicate that Elo-rating is very robust when rankings generated with David Elo-rating produces dominance rank orders that closely resemble dominance interactions in crested and rhesus macaques show that data set based on observations of free-ranging animals. Our results on the first study to test the reliability of Elo-rating with an extensive data set when using David’s score (r_s = −0.52, N = 17, P = 0.031; Fig. 5). Controlling for the initial proportion of unknown relationships by means of a partial Spearman correlation test leads to similar results (Elo-rating: r_s = −0.02, N = 17, P = 0.927; I&SI: r_s = −0.39, N = 17, P = 0.110; David’s score: r_s = −0.59, N = 17, P = 0.006).

Overall, our results indicate that Elo-rating produces rank orders very similar to those obtained with I&SI and David’s score. In addition, results of our tests suggest that rankings from Elo-rating and I&SI (given a significant linearity test) remain stable in sparse data sets, whereas David’s score seems to create less reliable hierarchies in sparse data sets as a result of an increase in unknown relationships.

Discussion

Even though there is abundant literature available that compares the concordance of different methods for the assessment of dominance ranks or scores (e.g. Bayly et al. 2006; Bang et al. 2010), this is the first study to test the reliability of Elo-rating with an extensive data set based on observations of free-ranging animals. Our results on dominance interactions in crested and rhesus macaques show that Elo-rating produces dominance rank orders that closely resemble rankings generated with David’s score and the I&SI method. Furthermore, our results indicate that Elo-rating is very robust when data sets are limited in the number of interactions observed. Elo-rating (and I&SI) even seems to produce more reliable dominance hierarchies than David’s score when the proportion of unknown relationships is high. One could argue that this effect is due to the initial proportion of unknown relationships, that is, a relatively high proportion of unknown relationships in a ‘full’ matrix leads to some uncertainty in the ranking, which may make the scores from the further reduced matrix even less reliable. However, when controlling for the initial proportion of unknown relationships, our results show that the robustness of Elo-rating (and I&SI) is not attributable to this factor.

USING ELO-RATING: AN EXAMPLE

We here demonstrate in an empirical example how Elo-rating can improve study results because of its immunity to detrimental effects of assessing dominance status. Data for this example derive from a previous study in which we investigated the relationship between dominance status and acoustic features of loud calls in male crested macaques (Neumann et al. 2010). We analysed seven acoustic parameters and found three of them to be related to dominance status. However, because of frequent migration events and rank changes, and consequently short time periods with high percentages of unknown relationships, we were able to classify dominance only broadly into three rank categories (high, medium, low).

We reanalysed our original data, using general linear mixed models (R package lme4: Bates et al. 2011; see Neumann et al. 2010 for details of the acoustic analysis and model specifications), and fitted separate models for each acoustic parameter, using Elo-ratings from the day a loud call was recorded as predictor variable instead of rank categories. We additionally fitted models using monthly David’s scores as predictor of dominance status.

In addition to the three parameters that we originally found to be affected by dominance rank, using Elo-rating as predictor revealed two more acoustic parameters to be significant at P < 0.05 (corrected for multiple testing after Benjamini & Hochberg (1995); P values were assessed with the package languageR (Baayen 2011)). Using Akaike’s information criterion (AIC) to assess how well the models fitted the data (see, e.g. Johnson & Omland 2004), we found that of the five models yielding significant effects of Elo-rating, four had smaller AIC values and thus fitted our data better than the respective models using rank categories as predictor. Surprisingly, when using David’s scores as predictor, in none of the models did we find significant effects of dominance status after correction for multiple testing.

Table 2

<table>
<thead>
<tr>
<th>Linearity</th>
<th>N</th>
<th>Elo-rating</th>
<th>David’s score</th>
<th>I&amp;SI</th>
</tr>
</thead>
<tbody>
<tr>
<td>+</td>
<td>17</td>
<td>0.98 (0.97–0.99)</td>
<td>0.96 (0.95–0.98)</td>
<td>0.98 (0.95–1.00)</td>
</tr>
<tr>
<td>–</td>
<td>49</td>
<td>0.94 (0.89–0.98)</td>
<td>0.92 (0.86–0.95)</td>
<td></td>
</tr>
</tbody>
</table>

Medians are given with interquartile ranges. Linearity in the reduced data set: + linearity test yielded significant h’ index, i.e. P ≤ 0.05 (de Vries 1995); – linearity test did not yield significant h’ index, i.e. P > 0.05.

Figure 5. Correlation between the increase in unknown relationships and the performance of (a) Elo-rating, (b) David’s score and (c) I&SI. The increase in unknown relationships was induced by randomly removing 50% of data points and performance is expressed as the correlation coefficient between rankings from the full and reduced data sets. Elo-ratings and I&SI ranks are not influenced by higher percentages of unknown relationships, whereas the performance of David’s score decreases when unknown relationships increase.
GENERAL DISCUSSION

We have shown that Elo-rating has several important advantages over common methods, such as the potential to: (1) monitor the dynamics of hierarchies and extract rank scores flexibly at any given point in time; (2) detect rank changes; (3) objectively identify hierarchy stability; (4) visualize hierarchy dynamics; (5) incorporate demographic changes into the rating procedure; (6) compare periods differing in demographic composition; (7) incorporate undecided interactions; and (8) objectively adjust the rating process based on species-specific information.

We furthermore showed that Elo-rating could increase the power of analyses and explain more variation in our data under certain circumstances. Whether a reanalysis using Elo-rating (as described above) will recover unexplained variation in general or not will mostly depend on how severe the potential negative effects of the data were on the ranks derived from matrices. For example, analysing a data set based on a single matrix with few unknown relationships will probably give very robust results, using either David’s score or I&S-I. Elo-rating, in such a case, will probably replicate the results obtained already, but not necessarily improve model fit. In contrast, a cross-sectional study on several groups, varying in the number of individuals and/or with high proportions of unknown relationships as in our example above), may warrant a reanalysis using Elo-rating. We can see, however, one context in which Elo-rating may not be the first choice to assess rank relationships. Unlike the I&S-I method (given its application is feasible), Elo-ratings do not necessarily reflect the rank order corresponding to a linear hierarchy in which an alpha individual is dominant (cf. Drews 1993) over all other individuals and a beta individual is dominant over all other individuals except the alpha, and so on (de Vries 1998). Such a feature of a ranking algorithm may be desirable when, for example, investigating the relationship between parental and offspring rank (Dewbury 1990; East et al. 2009; reviewed in Holekamp & Smale 1991). Such a situation is found in the matrilineal rank organization of many Old World monkeys, which is characterized by a linear structure in which a daughter ranks below her mother, and among all daughters of one mother the youngest one ranks highest (Kawamura 1958; Missakian 1972; but see Silk et al. 1981). Elo-rating nevertheless produces rankings close to a linear hierarchy (see above), and may therefore still allow for appropriate rank assessment in such cases, especially when the I&S-I method cannot be applied because of data limitations.

In conclusion, all the advantages mentioned in this paper make Elo-rating a useful tool for assessing and monitoring changes in dominance relationships, particularly in highly dynamic animal systems.

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Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2011.07.016.

References


In this section, we give a detailed example of how Elo-ratings are calculated. Figure and equation references refer to the main article.

To illustrate the principles of Elo-rating, it is useful to consider the basic unit of any dominance hierarchy, the dyad. In the example presented here, two individuals A and B interact through a sequence of four interactions. At the start of this sequence their competitive abilities are unknown and thus there is no knowledge of their ratings, and both A and B are assigned an initial rating of 1000. At this stage of the rating process, both individuals are expected to be equally likely to win an interaction between each other since there is not yet a higher-rated individual, i.e. \( p = 0.5 \). If A wins the first interaction against B, the ratings will be updated to \( E_{A} = 1000 + (1 - 0.5) \times 100 = 1050 \) (equation (1)) and \( E_{B} = 1000 - (1 - 0.5) \times 100 = 950 \) (equation (2); Fig. 1: Interaction 1). Individual A thus gained 50 points whereas B lost 50 points. Given that A has won the first interaction, A is expected to win the next interaction against B with \( p = 0.64 \) owing to the rating difference between A and B of 100 (Fig. 1: Interaction 2, inset). If A wins the second interaction, ratings will be updated as follows: \( E_{A} = 1050 + (1 - 0.64) \times 100 = 1086 \) (equation (1)) and \( E_{B} = 950 - (1 - 0.64) \times 100 = 914 \) (equation (2)). In a third interaction between A and B, the expectation of individual A winning this leads to \( E_{A} = 1086 + (1 - 0.73) \times 100 = 1113 \) and \( E_{B} = 914 - (1 - 0.73) \times 100 = 887 \) (equations (1) and (2)). Note that the expected probability of winning against B decreases as the increasing difference between A’s and B’s ratings, while at the same time, the number of points won and lost by each individual decreases (50, 36, 27, respectively). If, however, in a fourth interaction, B wins against A then the expectation (A is expected to


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APPENDIX 1

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win with $p = 0.79$), the number of points gained and lost rises to 79, and the new ratings are $\text{Elo}_A = 1113 - 0.79 \times 100 = 1034$ (equation (4)) and $\text{Elo}_B = 887 + 0.79 \times 100 = 966$ (equation (3), Fig. 1: Interaction 4).

APPENDIX 2

The calculation of $S$ is based on the assumption that it is justified to extrapolate Elo-ratings linearly for days during which individuals were present but not observed. Therefore, $S$ is clearly an approximate index.

We introduced a weighting factor to account for the notion that the higher in the hierarchy a rank change occurs, the more effect such a rank change has on stability. In other words, a rank reversal among the two highest-ranked individuals will have a stronger impact on the stability index than a rank reversal between the two lowest-ranking individuals.

The weighting factor $w_i$, by which the sum of rank changes $C_i$ is multiplied, is the standardized Elo-rating of the highest-rated individual involved in a rank change. Standardized Elo-ratings are set between 0 and 1, for the lowest- and highest-rated individual present on a given day, respectively. Ratings of the remaining individuals are scaled in between. Thereby the differences between standardized and original ratings are proportional to each other. A rank reversal among the two highest-ranked individuals will therefore be weighted by $w_i = 1$, whereas a rank reversal among the two lowest-ranking individuals will be weighted by a value near 0. Note that in the latter case the value of $w_i$ depends on the standardized Elo-rating of the second lowest-ranked individual and therefore does not equal 0.

Additionally, when one individual left, we raised the ranks of all individuals below by one, thus defining $C_i = 0$ in such a case, given that rank changes other than those induced by one individual leaving the hierarchy did not occur.