Methodological considerations in measurement of dominance in primates

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The strength of dominance hierarchy in a group of animals needs to be quantitatively measured since it influences many other aspects of social interactions. This article discusses three attempts made by previous researchers to measure the strength of hierarchy. We propose a method which attempts to rectify the lacunae in the previous attempts. Data are used from a group of Japanese macaques housed in a colony. A method to calculate strength of hierarchy has been illustrated and a procedure has been suggested to normalize the dominance scores in order to place the ranks of individuals on an interval scale.

AN animal of a species that lives a solitary life does often come into contact with another conspecific. Since animals in most species have rather limited home ranges, there is a good chance that the other conspecific which the animal encounters is the one that the animal would have met previously. On the other hand, animals that live in a social group know group members individually and their interactions are on a routine basis.

Bernstein and Gordon[1] describe interaction between any two animals as ignoring each other, attacking each other, or engaging in some common activity. The outcome of aggressive interactions could be understood by the encounter characteristics (such as age, sex: older individuals or males are more likely to win), location (an animal in its territory is more likely to win), or previous learning ('trained' winners or losers). However, 'when we note a regularity in the directionality of agonistic encounters, and such regularity cannot be explained by the course of the encounter itself, spatial determinants or broadly learned patterns such as trained winners or losers, then we describe the relationship governing agonistic encounters as a dominance relationship'[1].

Schjelderup-Ebbe[2] was the first biologist to identify and describe the presence of a hierarchical system in animal societies. Since then, hierarchies have been observed in all group-living species. A large number of research papers and reviews have been published, especially on primates, on the concept as well as on the mechanism, maintenance, reversal of dominance systems[3–6].

The members of a social group could be classified into a hierarchy in which the individual ranks are placed merely on an ordinal scale. At a more sophisticated level, the hierarchical difference could be quantified by placing individual ranks on an interval scale. The strength of dominance hierarchy refers to the strength of linearity in dominance relationships among members of a group. There are several types of hierarchies:

(a) *Despotism*: In which one individual may dominate all others with no difference of rank among rest of the group members.
(b) *Egalitarism*: In which each group member may be equally likely to win or lose in an encounter with any other member.
(c) *Complete linearity*: In which the dominance ranks are totally linear.

Most of the non-human primate societies range somewhere between complete egalitarism and complete linearity. A number of researchers have shown that the observed or expected outcome of dominant/subordinate interactions is related to many other aspects of social behaviour. It is therefore useful to determine the strength of a hierarchical system. It is for this reason that several attempts have been made to quantify the dominance relationship among members of a group in various species.

The quantification and analysis of dominance was first attempted by Murchison[7]. He measured social interactions in terms of categories of time and space, and subjected the data to the technique of co-variation. He demonstrated that the initial encounters could result in a polygonal form of dominance, but over a period of time,

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a straight-line dominance as a function of adjustment would emerge. Later, Collias[8] attempted to group the determiners of success in an encounter using the method of path coefficient.

The first systematic attempt to quantify the strength of dominance hierarchy was made by Landau[9]. He proposed the following equation:

$$h = [12/(n^3 - n)]\sum_{a=l}^{n}[V_a - (n-1)/2]^2.$$

In this equation, h refers to the strength of hierarchy, n refers to the number of individuals in a group, and V_a refers to the number of group members which the ath animal dominates. Part of the equation $[12/(n^3 - n)]$ has been used as a constant so that any calculated value of h ranged from 0 to 1. The range of calculated values from 0 to 1 would indicate a total absence of a ranking system to a perfect linear order.

Appleby[10] carried out a statistical analysis of social dominance in a group of red deer stags. The analysis was based on Kendall[11]. In addition to the demonstration of 'chance' on linearity of hierarchy, Appleby also provided a procedure for the test. For N number of individuals in a group, a matrix of dominance interactions can be constructed in which a row individual (i) dominating a column individual, gets a score of 1. If no interactions were observed among some individuals, each would get a score of half. Then the row totals (S_i) are calculated and the total score of each individual would then indicate the number of animals that the individual dominates. These scores are then used to construct a hierarchy where high score indicates a higher rank. Although Appleby did not provide a procedure for calculation of strength of hierarchy, he did provide a method to calculate whether hierarchy is significant (and hence, beyond 'chance') as follows:

$$d = [N(N-1)(2N-1)]/12 - \tfrac{1}{2}\,\Sigma\,(S_i)^2.$$

If N is up to 10, the probability table of Kendall[11] may be used to check the significance. For higher values of N, the distribution of d approaches c^2 distribution.

The degree of linearity (K) can be calculated as follows:

For odd number of individuals: $K = 1 - [24d/(N^3 - N)]$.

For even number of individuals: $K = 1 - [24d/(N^3 - 4N)]$.

K provides more or less the same value as Landau's h.

Zumpe and Michael[12] calculated dominance index in rhesus monkeys as follows:

1. Per cent aggressive behaviours given, e.g. by animals a and b as 70 and 30% respectively.
2. Per cent submissive behaviour received, e.g. by animals a and b as 80 and 20% respectively.
3. Per cent aggression given and submission received per pair, e.g.

for $a = (70\% + 80\%)/2 = 75\%$,

for $b = (30\% + 20\%)/2 = 25\%$.

4. Dominance rank: Use data from all possible pairwise interactions of N animals.

Rank of $a = b + c + \ldots + n/N$.

Landau: In Landau's index, the value V_a, which is crucial to the calculation of h, is based on the number of animals which the ath animal dominates. It appears as if a dominant animal A over B, would dominate B *all* the time. Actual observations on most species show that this is not the case. The equation as such therefore is biased towards high linearity.

Appleby: In Appleby's procedure, if there were no interactions observed between any two individuals, each was accorded a score of half. It means that regardless of one's relative position in the hierarchy, the expected outcome of an encounter is equiprobable in directionality. This is not the case in most animal species. In a group of 15 monkeys, if rank 1 and 14 never engaged in an agonisitc encounter, the expected outcome, if an encounter occurred, cannot be a fifty per cent chance of winning by rank 14 against rank 1.

In Zumpe and Michael, empty cells in a matrix were not considered at all, and no attempt was made to calculate the strength of hierarchy, although an attempt was made for an interval scale.

We provide a method which, by and large, employs all the three procedures described above, and also attempts to rectify the flaws mentioned in these procedures.

In the measurement of hierarchy, the first step is to collect data on agonistic encounters. In order to understand the pattern in a simple form, all data should be gathered from dyadic interactions. Such interactions occur naturally or they could also be induced by artificial feeding. Zumpe and Michael[12] have indicated the directionality of behaviour in an encounter as:

Direct aggression towards one $\rightarrow$ Dominant
Direct submission towards one $\rightarrow$ Submissive.

Dominant behaviour may include threat, chase, attack, displacement, mount, symbolic mount (placing hand on hindquarters).

Subordinate behaviour may include fear, grimace, run away, submit/crouch, move away, screech, present.

A matrix for all individuals can be prepared for dominance and submission. A few important points to be considered are as follows:

(a) As far as possible, encounters should be dyadic.
(b) Gather as many encounters as possible.
(c) As far as possible, encounters (natural or artificial) should be recorded between all possible pairs. (However, if it is not possible, a method is later provided to fill in such empty cells.)

(d) Data should be gathered in a short time duration (say a couple of weeks at the most) so that the possibility of rank reversal, etc. does not significantly influence the outcome.

We consider the data presented in Table 1 (in the form of matrix) to illustrate the method of calculation of strength of hierarchy. Data were gathered from dyadic aggressive interactions among adult members of a group of Japanese macaque (*Macaca fuscata*) housed in an outdoor colony at Bucknell University, Pennsylvania. The group had a total of 14 individuals out of which six were adult males and four were adult females. Data were gathered over a period of four months and the total number of aggressive encounters amounted to 897. In the above matrix, individuals in rows are ‘dominant’ and those in columns are ‘subordinate’. An entry in a cell indicates the number of fights won by a row individual out of the total number of encounters that occurred between the row and the column individuals.

A modified version of the basic Landau equation by Singh *et al.*[13] is provided below for calculation of strength of hierarchy:

$$h = [12/(n^3 - n)] \sum_{a=1}^{n} [d_a - (n-1)/2]^2 ,$$

$$\text{where } d_a = \sum_{a=1}^{n} P_a .$$

P_a refers to the proportion of encounters won by an animal against another in a pair-wise encounter. It may be noticed that d_a in the above equation is not a mere replacement of V_a in the original Landau’s equation. D_a itself is a product of a summation process on the basis of proportion of encounters won rather than merely the number of animals dominated by an animal, as it is in the case of V_a in the Landau equation. Since an animal may not win in all encounters against a so-called lower ranking individual (see actual data in Table 1), d_a is a more realistic value than V_a.

The above equation can now be employed for treatment of data in Table 1. The first step is to calculate the proportion (P_a) in each of the cells. The next step is to calculate the d_a value for each animal, which is simply the total of all P_a values in a row. One may apply a check for the accuracy of calculations here. The sum of all d_a values in Table 1 is 45. If the dominance relationships were to be linear, the ten individuals of the group would have dominance scores as 9, 8, 7, 6, 5, 4, 3, 2, 1 and 0, the total of which would be 45. The next step is to calculate $[d_a - (n-1)/2]^2$ for each animal. For example, for Hal, this value would equal $[9 - (10 - 1)/2]^2$ or 20.25. Likewise, these values are calculated for all other individuals. These values are shown in Table 2. The sum of all d_a values is 78.3044. The value of $[12/(10^3 - 10)]$ equals 0.012. The value of h is $78.3044 \times 0.012 = 0.94$. This value represents the strength of dominance hierarchy or a measure of linearity of dominance among the individuals of this group.

In a group of several animals, there is a possibility that some individuals may never engage in pair-wise aggressive encounters at all. In such a situation, some of the cells in the encounter matrix would remain empty. It has been mentioned earlier that Appleby suggested to fill half values in each of such cells. We, however, propose a different method for filling such empty cells. In most non-human primate societies, the dominance hierarchies may not be perfectly linear, but they do tend to be closer

Table 1. Data matrix for number of encounters ‘won’ out of total number of encounters between any two pairs, and P_a and d_a values

	Subordinate										
Dominant	HAL	RIP	TAI	SAM	OLI	MAX	ERO	URS	QUI	BER	d_a
HAL	–	56/56	27/27	5/5	8/8	17/17	9/9	20/20	9/9	2/2	9.00
P_a		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	
RIP	0/56	–	47/49	37/37	29/29	25/25	0/30	10/40	7/21	7/11	5.18
P_a	0		0.96	1.00	1.00	1.00	0	0.25	0.33	0.64	
TAI	0/27	2/49	–	35/35	25/25	2/12	0/9	0/12	0/5	8/27	2.51
P_a	0	0.04		1.00	1.00	0.17	0	0	0	0.30	
SAM	0/5	0/37	0/35	–	12/12	1/9	0/6	0/12	0/15	0/12	1.11
P_a	0	0	0		1.00	0.11	0	0	0	0	
OLI	0/8	0/29	0/25	0/12	–	0/5	0/5	0/7	0/15	0/3	0
P_a	0	0	0	0		0	0	0	0	0	
MAX	0/17	0/25	10/12	8/9	5/5	–	0/12	0/14	0/3	1/16	2.78
P_a	0	0	0.83	0.89	1.00		0	0	0	0.06	
ERO	0/9	30/30	9/9	6/6	5/5	12/12	–	22/22	51/51	37/37	8.00
P_a	0	1.00	1.00	1.00	1.00	1.00		1.00	1.00	1.00	
URS	0/20	30/40	12/12	12/12	7/7	14/14	0/22	–	75/75	17/17	6.75
P_a	0	0.75	1.00	1.00	1.00	1.00	0		1.00	1.00	
QUI	0/9	14/21	5/5	15/15	15/15	3/3	0/15	0/75	–	29/29	5.67
P_a	0	0.67	1.00	1.00	1.00	1.00	0	0		1.00	
BER	0/2	4/11	19/27	12/12	3/3	15/16	0/37	0/17	0/29	–	4.00
P_a	0	0.36	0.70	1.00	1.00	0.94	0	0	0		

to linearity. An individual who wins most fights (and is considered dominant) is more likely to win a fight that has not occurred with an individual who has lost most fights (and is considered subordinate). Let us presume that in the present study group, the animals QUI and TAI as well as the animals SAM and BER never encountered each other. The respective cells in this case may be made empty. In order to fill P_a values in these cells, the following procedure may be followed. The d_a score of QUI leaving out her P_a value from TAI is 4.67. Similarly, the d_a score of TAI leaving out his P_a value from QUI is 2.51. If QUI and TAI were to engage in an encounter, the probability of QUI winning the encounter would be 4.67/(4.67 + 2.51) = 0.65. The probability of TAI winning the encounter would be 2.51/(4.67 + 2.51) = 0.35. These respective values can then be added to the earlier d_a values for each of these two animals to obtain their final d_a value. Using a similar procedure, the probability of winning an encounter by SAM against BER and by BER against SAM would be 0.27 and 0.73 respectively. After calculating the new d_a values for the empty cells on the above mentioned proportional basis, the d_a values and $[d_a - (n - 1)/2]^2$ are given in Table 2. The sum of these d_a values is 74.9226, which multiplied by 0.012 provides an h value of 0.90. Table 2 also gives d_a values calculated after assigning a score of 0.50 in the empty cells, regardless of the probability of an animal winning an encounter against the other (as suggested by Appleby). Now, the calculated value of h would be 71.7667 × 0.012 = 0.86. It may be noticed that the value of h being 0.90 is much closer to the actual strength (h = 0.94) than the value of h being 0.86. The method suggested by Appleby, therefore, unnecessarily biases the results towards low linearity.

Before we go further with this analysis, let us make a check of this value of h = 0.94 using the method of Appleby.

$$d = [N(N-1)\ (2N-1)]/12 - ½\ \Sigma\ (S_i)^2,$$

Each d_a here equals (S_i) of Appleby.

$$d = [10(10-1)\ (2 \times 10 - 1)]/12 - ½ \times 280.80 \text{ or}$$
$$d = 142.5 - 140.40 = 2.10$$

Degree of linearity:

$$K = 1 - [24 \times 2.10/(10^3 - 40)] \text{ or } K = 1 - 0.0525 = 0.947.$$

Appleby's K value of 0.947 is the same as h value of 0.94 calculated above (the small difference may be accounted for rounding-off the P_a values to two decimal points).

Notice an important feature of the $[d_a - (n - 1)/2]^2$ values of all animals. The scores of highest and lowest ranking individuals are highest (e.g. 20.25 for HAL with a d_a value of 9 as well as for OLI with a d_a value of 0). The scores (from dominants to subordinates) start from a high to low, reach zero and rise again. One could also obtain two different totals on each side of zero and compare the strength of linearity among dominants (all individuals before zero) and subordinates (all individuals after zero).

A procedure could be used to standardize the scores and to construct an interval scale for ranks of individuals. This procedure involves calculation of p (proportions) and z (standard scores) for each of the dominance scores (Table 3). Since there is a possibility that the lowest rank individual may get a dominance score of zero (if it never wins any encounter), the resulting zero value of p cannot then be converted into a z score. Therefore, a constant value of 0.5 can be added to the dominance scores of all individuals to obtain d_{aa}. The p values can be obtained by d_{aa}/n, where d_{aa} is the dominance score and n is the number of individuals. The obtained p values can be converted to z scores (standard scores) from statistical tables. In order to construct a standardized interval scale, the lowest z score (usually the highest minus value, in this case – 1.64) can be considered an arbitrary zero. This value can now be added to all other z scores (see scale

Table 2. d_a values obtained from the original scores and after filling empty cells using the method of proportions and Appleby's method

	Original score		After filling proportional scores in empty cells		After filling 0.5 values in empty cells	
Animal	d_a	$[d_a-(n-1/2)]^2$	d_a	$[d_a-(n-1/2)]^2$	d_a	$[d_a-(n-1/2)]^2$
HAL	9.00	20.2500	9.00	20.2500	9.00	20.2500
RIP	5.18	0.4624	5.18	0.4624	5.18	0.4624
TAI	2.51	3.9601	2.86	2.6896	3.01	2.2201
SAM	1.11	11.4921	1.38	9.7344	1.88	6.8644
OLI	0	20.2500	0	20.2500	0	20.2500
MAX	2.78	2.9584	2.78	2.9584	2.78	2.9584
ERO	8.00	12.2500	8.00	12.2500	8.00	12.2500
URS	6.75	5.0625	6.75	5.0625	6.75	5.0625
QUI	5.67	1.3689	5.32	0.6724	5.17	0.4589
BER	4.00	0.2500	3.73	0.5929	3.50	1.0000
Total	45	78.3044	45	74.9226	45.27	71.7667
h		0.94		0.90		0.86

Table 3. Procedure for calculation of standardized interval scale

	HAL	RIP	TAI	SAM	OLI	MAX	ERO	URS	QUI	BER
d_a	9.00	5.18	2.51	1.11	0	2.78	8.00	6.75	5.67	4.00
$d_{aa} = d_a + 0.5$	9.50	5.68	3.01	1.61	0.50	3.28	8.50	7.25	6.17	4.50
p	0.95	0.57	0.30	0.16	0.05	0.33	0.85	0.73	0.62	0.45
z	1.64	0.18	– 0.52	– 0.99	– 1.64	– 0.44	1.04	0.61	0.31	– 0.13
Scale score	3.28	1.82	1.12	0.65	0	1.20	2.68	2.25	1.95	1.51
Rank	1	5	8	9	10	7	2	3	4	6

score in Table 3). These scale scores can be used to obtain an interval scale (Figure 1).

Some problems with the procedure are as follows:

1. Non-transitivity: In a situation where *A* dominates *B* dominates *C* dominates *A*, it may appear that the predicted values for empty cells may not be correct. It is not the case since lack of linearity will automatically make the predicted scores close to 0.5 for animals in the pair. It may be noticed from Table 1 and from the dominance ranks assigned in Table 3 that there is no transitivity in the dominance relationship of the group members in the present study. This is actually the case with most socially living species.
2. Protected threat, proximity effect: These situations do influence the outcome of an encounter. However, such effects are only temporary and such data may not be included in the first table of interactions. Pair-wise encounters should be considered only when these are independent.

With slight modifications in the list of behaviours considered 'dominant' or 'subordinate', the method described above can be used to determine strength of hierarchy in any animal species living in social groups. The procedure of preparation of a matrix for agonistic interactions may vary for different species; however, once such a matrix is prepared, the present methods of calculation of actual hierarchical strength is applicable for all animal species. It may yield reliable comparisons across species as well as within a species in different habitats. Since the hierarchical strength is also related to many other aspects of sociality, the *h* value may become one of the diagnostic keys to understand social organization in a species. The relationship of *h* may also be established for species in different phylogenetic groups, or for species and ecological variables such as uneven food supply, harsh environments, etc.

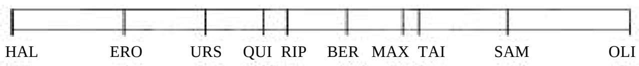

Figure 1. Rank of individuals on an interval scale.

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