Statistical models of transitive and intransitive dominance structures

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Abstract: We present an approach based on generalized linear models for analysing dominance data. First, dominance is defined as a parameter characterizing the relationship between two individuals, determining the expected number of successes of the first individual in disputes with the other. Second, models known from the literature of two different forms of transitivity are defined in terms of these parameters, and examples of different tests of these models are given. Third, a new model is developed where the traits of individuals involved in the dominance interactions are included as covariates. Finally, we show how two forms of intransitive models of dominance structures can be constructed by including a certain interaction term between the trait variables, and terms taking into account the effect of relatedness between the individuals in the group. We reanalyse several data sets in the literature, and also discuss Appleby's method (1983, Anim. Behav., **31,** 600-608), which is frequently used in analysis of dominance data.

A common practice in studies of animal dominance is to rank a group of individuals in the closest possible order to a transitive hierarchy (e.g. Bulger 1993; van den Bos & De Cock Buning 1994; Gust & Gordon 1994; Jenks et al. 1995). Relationships of these ranks with other properties of the individuals are then tested for in further analysis. This procedure implicitly assumes that the dominance structure is transitive, that is, it is assumed that if some individual i dominates another individual j, and j dominates some third individual k, then this implies that i dominates k.

To address this assumption, several tests have been suggested. The most frequently cited method is that of Appleby (1983), who proposed a test based on Kendall & Gibbons's (1990) work on paired comparisons. The null hypothesis of Appleby's (1983) test is that all individuals are equally likely to win dominance interactions with other members of the group, and this null hypothesis of randomness is rejected in favour of the alternative hypothesis that the dominance structure is transitive, if the test statistic, quantifying the degree of transitivity, is sufficiently large. However, confronted with a significant test result, most researchers using Appleby's (1983) method, conclude that the dominance structure is truly transitive. This is a misinterpretation, however; rejection of the null hypothesis of randomness only implies that the alternative hypothesis is a better description of the dominance structure among the individuals being studied.

Both Boyd & Silk (1983), and Iverson & Sade (1990) present good alternatives to the method of Appleby (1983). These authors present specific parametric models of different forms of transitivity, all of which can be rejected by the data using different tests of goodness of fit. Several other interesting tests can also be made.

In this paper, after first making a basic definition of dominance and the sampling model for the data, we briefly describe some of the models of Boyd & Silk (1983), and Iverson & Sade (1990), and analyse some data sets in the literature using these models. We also present some alternatives to the approach of Boyd & Silk (1983), more directed towards determining the relationship between dominance and measured properties of the individuals involved in the interactions.

Given that there is no logical reason for why dominance structures need to be transitive, and given that several apparently intransitive dominance structures have been reported in the literature (e.g. Lahti et al. 1994), it is rather surprising that no specific models of intransitive dominance structure exist. At the end of the paper, models of two different forms of intransitivity are therefore proposed, and fitted to data.

Basic Definitions

We consider n individuals indexed $i = 1, 2, \ldots, n$. Let N_{ij} be the number of observed disputes between individual i and j, and let X_{ij} be the number of times i is observed to win over j. Since the outcome of single disputes between any two individuals nearly always will be, in part unpredictable or unexplained by a model, it will be essential to think of the data as stochastic. A simple, first choice of sampling model is to assume that the probability that an individual i wins over j in each single dispute remain constant over time and equal to p_{ij}, and that the outcome of successive disputes are independent. The number of successes, X_{ij}, is then binomially distributed with parameters N_{ij} and p_{ij}.

We will refer to the parameter p_{ij} as individual i's *dominance* over j. With this definition, dominance is thus a parameter characterizing the relationship between two individuals, taking any value between 0 and 1. We say that an individual i *dominates* j if $p_{ij} > 1/2$. If $p_{ij} = 1/2$, i and j are *equidominant*. Note that we always have the requirement

$$p_{ij} = 1 - p_{ji}. \tag{1}$$

These are the basic definitions also used by Boyd & Silk (1983) and Iverson & Sade (1990). Analogous definitions have also been employed in studies of prey item selection (van der Meer 1992) and in the psychological literature (Tversky 1969). Note that dominance generally, with this definition, can differ between different forms of interaction, that is, the dominances determining the winning probabilities in, for example, contest competition for food may differ from those dominances determining the outcomes of male interactions in competition for females.

Model Selection

Before going into the different models, we briefly describe some well known principles in model selection and some basic terminology used in generalized linear models (McCullagh & Nelder 1989). With the definitions above, the dominance structure between all individuals is characterized, if no further assumptions are made, by a total number of $n(n-1)/2$ parameters, that makes up a parameter matrix

$$\begin{bmatrix} - & (1-p_{21}) & \dots & (1-p_{n1}) \\ p_{21} & - & \ddots & (1-p_{n2}) \\ \vdots & \ddots & - & \ddots \\ p_{n1} & p_{n2} & \ddots & - \end{bmatrix}. \tag{2}$$

Model (2) is usually referred to as the full model. Different hypotheses about the unknown dominance structure are statements about the elements of (2) and not about the data directly. It is useful to think of the different hypothesis or models (described in the next section) as different subspaces of the $n(n-1)/2$ dimensional parameter space of the full model. Fitting a specific model to the data by maximum likelihood is done by finding the parameter point in this subspace which maximizes the probability of the data.

It might be noted that for the full model (2), the maximum likelihood estimates of the parameters are simply $\hat{p}_{ij} = X_{ij}/N_{ij}$. These estimators have, as noted by Lahti et al. (1994), some desirable properties in that they are unbiased, which may seem like an attractive feature of this model. However, especially in cases where the data are sparse, the variance of each $\hat{p}_{ij}$ would be very high, and one usually ends up with better estimates of the dominances if prior knowledge about dominance structures in general can be employed.

To assess the goodness of fit of a particular candidate model H_0, the deviance $D(H_0)$, defined as two times the difference between the maximum log likelihood under H_0 and under the full model, is commonly used. With r observations and p_0 unconstrained parameters, and given that H_0 is true, this test statistic is approximately χ^2 distributed, with $r - p_0$ degrees of freedom.

One model H_0 is said to be nested within another model H if it can be obtained by imposing constraints on the parameter space of H. Given that H_0 is true, the change in deviance between the two models, $D(H_0) - D(H)$, is approximately χ^2 distributed, with $p - p_0$ degrees of freedom, where p and p_0 is the number of parameters under H and H_0 respectively. If the change in deviance is sufficiently large H_0 can be rejected in favour of the more general model H.

In count data of the form considered in this paper, dependencies between each individual dispute will typically be present, leading to so called over-dispersion, that is, more variance in each X_{ij} than expected under the binomial model. Over-dispersion will also arise if there is stochastic variation in the underlying parameters, the p_{ij}'s, of the binomial distribution. The amount of overdispersion under a particular fitted model H_0 can be estimated by the deviance, $D(H_0)$, divided by the number of residual degrees of freedom $r - p_0$. In cases where over-dispersion appear to present, in tests between two nested alternative models H_0 and H, it is recommended to use the test statistic,

$$\frac{(D(H_0) - D(H))/(p - p_0)}{D(H_0)/(r - p_0)}, \tag{3}$$

which is approximately F distributed with $p - p_0$ and $r - p_0$ degrees of freedom (SAS Institute Inc. 1996, ch. 10).

Dominance Structure Models

The simplest model in our case, nested within all other alternatives, is that of *randomness*, also referred to as 'chance' by Iverson & Sade (1990). In the parameter space, this model corresponds to the single point $p_{ij} = 1/2$ for all ij. We now describe a range of different models, all nested in between the full model and that of randomness.

A dominance structure such that $p_{ij} > 1/2$ and $p_{jk} > 1/2$ imply $p_{ik} > 1/2$ for all $i \neq j \neq k$, is said to be *weak stochastic transitive* (WST) (Iverson & Sade 1990). The maximum likelihood under WST, which would be needed in, for example, a goodness of fit test, can be obtained by estimating all dominances by $\hat{p}_{ij} = X_{ij}/N_{ij}$, and then setting all $\hat{p}_{ij}$'s violating WST equal to 1/2. The maximum likelihood under WST is then the product of the binomial probabilities evaluated at this point in the parameter space (Tversky 1969).

WST differs from so called *strong stochastic transitive* (SST) (Iverson & Sade 1990), which is defined by the constraint that $p_{ij} > 1/2$ and $p_{jk} > 1/2$ imply $p_{ik} \geq \max(p_{ij}, p_{jk})$. SST, being a more restrictive model than WST, is thus nested within WST. It can be seen that under SST the p_{ij}'s increase across each row of the parameter matrix (2), with increasing difference in rank. The estimated parameter matrix in Table II is of this form.

Another simple and perhaps more biologically plausible form of SST arises by assuming that there exist some parameters $\beta_1, \beta_2, \ldots, \beta_n$ characterizing each individual, hypothesized to reflect, for instance, condition, body weight or internal hormone levels, and that the dominance between any pair of individuals is an increasing function of the difference between these parameters only. We can write this model as:

$$g(p_{ij}) = \beta_i - \beta_j. \tag{4}$$

Note that there can be no intercept in this model owing to the requirement of symmetry (1). In generalized linear model terminology, $g(\cdot)$ is called a link function (McCullagh & Nelder 1989). To ensure that the model makes physical sense for all parameter values, it is desirable that $g(\cdot)$ maps the dominances ($0 \geq p_{ij} \geq 1$) onto the whole real line. For the logit choice of link function, $g(p) = \ln(p/(1-p))$, model (4) is referred to as the Bradley-Terry model (Bradley & Terry 1952). For this model, the subordinate individual j always has a possibility of winning in disputes with i. As the difference between the absolute dominances of individual i and j becomes large, however, the probability of this event tends asymptotically towards zero (see Fig. 1). Apart from this property of the model, which may be biologically justified, the exact shape of the logit link-function is, of course, without any further prior knowledge, somewhat arbitrary and subjective.

Despite some of the attractiveness of the Bradley-Terry model, its only application in analysis of animal dominance data has been that of Boyd & Silk (1983) and Haley et al. (1994). Here we describe a fitting procedure based on a different parameterization than the one suggested in their papers, more compatible with commonly used statistical software packages.

Only $n-1$ differences between each individual's 'absolute dominance', β_i, and the 'absolute dominance' of an arbitrarily chosen individual, say individual $i = n$, can be estimated from the data. First note that we can write (4) as

$$\operatorname{logit} p_{ij} = (\beta_i - \beta_n) - (\beta_j - \beta_n). \tag{5}$$

Reparameterising the model by substituting β_i' for $\beta_i - \beta_n$ yields

$$\operatorname{logit} p_{ij} = \beta_i' - \beta_j'. \tag{6}$$

This reduces the number of parameters to $n-1$, since β_n' by definition is zero. Using dummy variables we can write (6) as

$$\operatorname{logit} p_{ij} = \beta_1' x_1 + \beta_2' x_2 + \cdots + \beta_{n-1}' x_{n-1}, \tag{7}$$

where, for sample unit ij, $x_i = 1$, $x_j = -1$, and $x_k = 0$ for all $k \neq i \neq j$, $k \leq n-1$.

Treating the dummy variables as covariates, and the number of successes X_{ij} out of the total number of encounters N_{ij}, as the response variables, the fitting of the model is very similar to standard multiple regression and can now be done using any software package that handles generalized linear models (e.g. the GLIM package or PROC GENMOD in SAS).

Willow-tit example

As an illustration of the Bradley-Terry model and WST we will analyse a data set in Lahti et al. (1994). They observed dominance interactions in 31 flocks of willow-tits, *Parus montanus*, in Northern Finland over several years in the period from October to December. Three apparently intransitive dominance data matrices are available in their paper, one of these is shown in Table I.

The estimates of the differences in absolute dominances are given in Table I, and the corresponding estimates of the dominances are shown in Table II. Relying on the assumption that the data is binomially distributed, the Bradley-Terry model (7), when fitted to the willow-tit data, could be rejected ($D = 99.95$, $df = 26 - 7 = 19$, $P < 0.0001$), also with a Bonferroni adjusted α-level of $0.05/31 = 0.0016$.

To test if the data is still consistent with weak stochastic transitivity, different rankings were tried, until the ranking maximizing the likelihood under WST was found. For this ranking, showed in table III, one 'reversal' was still present in the data, between individual number 4, who won 9 out of 9 disputes with individual number 5. This gives a difference between the log likelihood under WST and under the full model (owing to this reversal only) equal to 3.12 and a deviance of $D = 6.23$. With 26 observations and 25 unconstrained parameters under WST, we can thus also reject WST ($D = 6.23$, $df = 1$, $P = 0.01$), again relying on the assumption of binomially distributed data. This result is, however, clearly non-significant if we use the correct Bonferroni adjusted α-level. In other words, taking into account the large number of flocks studied, the observations are as expected under WST.

It might also be noted that the two models produce different rankings in that individual number 5 is moved two steps down in the hierarchy under WST. These ranks may not be very meaningful, however, if the models are truly wrong.

Trait Dependencies

The approaches based on WST and the Bradley-Terry model can both be used to establish a rank order, and the validity of using these model can be assessed using tests of goodness of fit. In many cases, however, the objective of the study is to relate variation in the outcome of interactions between individuals with characteristics of the individuals involved, for example secondary sexual characters, sex, body size, etc. We will first look at how this can be done more directly using a simpler model that circumvents the problem of estimating the entire hierarchy. In the next section we then look at certain interesting extensions of this model that can be made in the direction of intransitive dominance structures.

Assume that for each individual i we have measured a vector of traits (x_i, y_i), say age and sex. A simple model is to let p_{ij} depend on the differences between individual i and j in their trait values, multiplied by some parameters representing the strength of the relation between dominance and each trait. Also assuming a logit link function, this becomes

$$\operatorname{logit} p_{ij} = a(x_i - x_j) + b(y_i - y_j). \tag{8}$$

It might be noted that this model (8) is of Bradley-Terry form, because the characteristics of each individual determining its dominances with other individuals, can be summarized by $\beta_i = ax_i + by_i$.

House sparrow examples

We will reanalyse two data sets (Solberg & Ringsby 1997; Møller 1987) on house sparrows, *Passer domesticus*, that illustrate this approach. Both of these data sets consist of several subpopulations and dominance interactions only occurred within subpopulations. Since we are not interested in estimating the hierarchies within each subpopulation, but only the parameters quantifying the dependencies of the dominances on the trait differences, we can combine all the data and run one single analysis for the combined data sets. This only assumes that the parameters a and b do not differ between subpopulations, which is a reasonable assumption to start with.

In both cases, total badge size and age were determined for each individual. For Solberg & Ringsby's (1997) data, several other morphological traits were also available. Inclusion in the model were based on one-tailed significance values for traits for which clear predictions existed, and on two-tailed Bonferroni adjusted significance levels for other traits not hypothesized to be related to dominance. The change in deviance when each covariate was included in the model was used to calculate significance values. All trait variables were standardized before the analysis, except juveniles and adults which were coded as -1 and 1 respectively. A few missing values were replaced by sample means.

Table IV shows the parameter estimates under the selected model for each data set. We see that the dominances are positively related to the differences in both total badge size and age, as predicted by general theory. In previous analysis of these data sets in Møller (1987) and Solberg & Ringsby

(1997), using Appleby's (1983) method in combination with Spearman rank correlation tests, the dominance ranks were significantly positively correlated with only total badge size, only in Møller's (1987) study.

Total badge size has a larger effect than age on the dominances, and this pattern is consistent across both data sets. There is also a marked difference between the two data sets in the estimated strength of the relationships though. For Solberg & Ringsby's (1997) data, if we substitute the covariate values for juveniles and adults and the parameter estimates into the model equation, we find that the dominance between a pair of individuals that only differ in age, would be $p_{ij} = 0.55$. The corresponding probability for Møller's (1987) data, would be $p_{ij} = 0.67$. For the badge size dependencies, the differences are much larger.

The explanation for the weaker dependency of the dominances on age and badge size in Solberg & Ringsby's (1997) study may be a higher degree of individual recognition due to smaller flock sizes in this study, so that experiences from previous interactions could be used more frequently as a predictor of the true competitive ability of other individuals than visible cues such as age and badge size. An alternative explanation may be that resources were less limited in Solberg & Ringsby's (1997) study, making competition and status signaling less important.

Intransitive, Circular Dominance Structures

A certain type of intransitivity can be incorporated in the model by adding a simple interaction term to (8), involving the difference between the crossproducts $x_i y_j$ and $x_j y_i$ of the trait values of individual i and j. The model then becomes

$$\operatorname{logit} p_{ij} = a(x_i - x_j) + b(y_i - y_j) + c(x_i y_j - x_j y_i), \tag{9}$$

where the new parameter c represents the strength of cross-product interaction. Note that (9) still satisfies the requirement (1) of symmetry.

This model has some interesting properties. Consider an individual j located at some fixed point (x_j, y_j) in the traitspace. To gain a better understanding of the model, it is helpful to ask what trait values (x_i, y_i) some other individual i must have to be equidominant with j. This condition imply that $p_{ij} = 1/2$ so that the lefthand side of (9) is equal to zero. Solving for (x_i, y_i), we then see that the other individual i, must lie on the isoline defined by

$$y_i = \frac{c y_j + a}{c x_j - b} x_i - \frac{a x_j + b y_j}{c x_j - b}. \tag{10}$$

There are many such isolines corresponding to different fixed points (x_j, y_j) (see Fig. 2).

Note that the slope depends on (x_j, y_j), and that the sign of the slopes changes when $x_j = \frac{b}{c}$ and when $y_j = -\frac{a}{c}$. It is also easy to verify that all possible isolines, each going through different fixed points (x_j, y_j), all go through the common point $(x^*, y^*) = (\frac{b}{c}, -\frac{a}{c})$, implying that an individual located at (x^*, y^*) is equidominant with all other individuals in the traitspace.

To see in which direction the dominance increases, it can also be helpful to look at the gradient vector field of the function (9), defined as the sum of the various partial derivatives multiplied by their corresponding unit vectors (Edwards & Penney 1986). The gradient vector, at some point in the traitspace, represents, roughly speaking, the direction in which the dominance increase most rapidly, and its length the rate of increase in dominance in this direction. If we think of (x_j, y_j) as a fixed point in the trait space, and evaluate the partial derivatives of (9) with respect to (x_i, y_i), the gradient vector representing the change in dominance as the position of individual i change, becomes

$$(a + cy_j, b - cx_j) \tag{11}$$

This vector is shown for different points (x_j, y_j) in Fig. 2, with c chosen to be positive. If we consider a hypothetical group of individuals located on a circle around (x^*, y^*), we see that the dominance structure among these individuals can be intransitive, that is, i can dominate j, j can dominate k, at the same time as k dominates i. By examining the gradient vector for different values of c, it can be seen that dominance increases in the clockwise direction for $c > 0$, and in the anticlockwise direction for $c < 0$.

It can also be noted that the 'steepness' of the dominance structure, as indicated by the length of the gradient vector, increases linearly as (x_j, y_j) moves away from (x^*, y^*), while the dominance structure is very 'flat' in the region close to (x^*, y^*).

Another, perhaps simpler way of looking at model (9), is to consider the dominance structure within a subgroup of individuals for which all $y_i = y'$, say all individuals of a certain age. Substituting y' for the y_i and y_j in (9) we find that the dominances within this subgroup are given by

$$\operatorname{logit} p_{ij} = (a + cy')(x_i - x_j), \tag{12}$$

that is, within the subgroup, the dominance structure is transitive and of Bradley-Terry form, with the strength of the dependency on the other trait x being $a + cy'$. Also note that the strength of the dependency on the other trait increases linearly with y' across different subgroups.

Estimating the extra parameter c representing the strength of the cross-product interaction in (9), is no more difficult than fitting model (7) and (8). From that point of view, $x_i y_j - x_j y_i$ is just another covariate.

Woodland caribou example

We shall see what type of biology model (9) may involve, by reanalysing a data set on woodland caribou, *Rangifer tarandus caribou*, (Barrette & Vandal 1986, Tables 1 and 3). The outcome of 5245 disputes between 20 individuals over various resources were recorded, during a period starting in late February and ending in late April. We included three trait variables that are available from Barrette & Vandal's (1986) paper: sex, age, and antler size. In addition we included cross-product interaction terms between sex and age, and between sex and antler size. The parameter estimates under this model are given in Table V.

The main effects are as expected; the dominances increase both with differences in age and antler size, and males dominate females. The estimated magnitudes of the main effect indicate that antler size is most important in determining the dominances.

There is also an interesting cross-product interaction between sex and antler size. In Fig. 3b it can be seen that the females are distributed further away from the centre point (x^*, y^*) than the males. Since the 'steepness' of the dominance structure increases with distance from the centre point, this means that the dominances are more dependent on antler size among females, than among males. This can also be seen by substituting estimated parameter values into (12). One possible explanation for this can be that access to resources, during springtime, may be more important to birth-giving females than males, which would make competition for food among females more intense, and thereby more dependent on antler size.

The cross-product interaction of sex with age (Fig. 3a) indicates that the dependency on age, however, for a given antler size, is weaker among females than males. The dominances are almost independent of age within females, when antler size is controlled for.

It can also be seen that, among the actual individuals studied, the dominance structure is still transitive, according to the fitted model. We would only have intransitivity if the individuals were distributed on both sides of all possible isolines, that is, around the centre point (x^*, y^*).

Relatedness

One additional variable that may explain a large part of the variation in many data sets, is the relatedness between individuals. We may for example expect mothers to be less dominant towards their own young than towards unrelated juveniles. If the relatedness between all individuals are known, we can incorporate this in the model as follows. For each sample unit ij, let the covariate

$$r_{ij} = \begin{cases} 1 & \text{if } i \text{ is the offspring of } j \\ -1 & \text{if } j \text{ is the offspring of } i \\ 0 & \text{if } i \text{ and } j \text{ are unrelated.} \end{cases} \tag{13}$$

If we then add an extra term dr_{ij} to, for example, (8), the model becomes

$$\operatorname{logit} p_{ij} = a(x_i - x_j) + b(y_i - y_j) + dr_{ij}. \tag{14}$$

The parameter d represents the difference between the logit of, say, a mother's dominance over her own offspring and her dominance over unrelated juveniles. Note that, regardless of whether cross-product interactions are present, the model can no longer be written in Bradley-Terry form and may also, as shown in the example below, be intransitive, once r_{ij} is included as a covariate.

Example

Table VI shows the parameter estimates obtained by fitting the model with an extra relatedness term to the data of Barrette & Vandal (1986). As expected, the estimate of d is positive, indicating that mothers are less dominant to their own young, than toward unrelated individuals. The effect of relatedness is also much larger than the effects of differences in sex, age and antler size. Based on the parameter estimates under the fitted model, the dominance of an average adult female over a average juvenile would be $p_{ij} = 0.65$, while the dominance over her own offspring would be $p_{ij} = 0.10$.

In other words, relatedness can thus create intransitivities in the dominance structure, with juveniles dominating their own mothers. It must be remembered, however, that these dominances only refer to a specific form of feeding behaviour. They do not necessarily relate to dominances in other forms of behaviour for which the mothers may still dominate their young.

It might be noted that when the relatedness term r_{ij} was included, the cross-product interaction between sex and age became non-significant, and this term was therefore excluded from the model.

Discussion

The methods presented here offer several advantages compared to the more frequently used method of Appleby (1983). One difference between our approach and that of Appleby (1983) is in the choice of null hypothesis. In our and Iverson & Sade's (1990) notation, Appleby's (1983) null hypothesis is that all individuals are equidominant ($p_{ij} = 1/2$ for all pairs of i and j). Appleby (1983) tests this against the alternative hypothesis that there is some (unspecified) form of transitivity in the dominance structure. A similar approach was adopted by de Vries (1995) who also suggested some improvements by taking into account possible biases in the test statistic due to unknown relationships. In both of these methods the only conclusion that can be drawn from a significant test result is that the alternative hypothesis is a better description of the data than the null hypothesis of randomness.

In contrast to these approaches, we assume specific forms of transitivity, which in turn can be tested against specific extended models including the possibilities of intransitive dominance structures, or against the full model through a goodness of fit test. By testing the goodness of fit of WST, intransitivities in the data can be detected. Rejection of WST does not provide much insight into what causes the reversals in the data, however. In these cases, the model with cross-product interactions, and the one including effects of relatedness, represents two alternative specific and much more informative explanations.

In cases where no traits are measured it may be useful to fit the Bradley-Terry model (7) to the data and then do a goodness of fit test to see if this form of transitivity is acceptable. It should be mentioned that for the Bradley-Terry model convergence of the parameter estimates will not always be guaranteed (Boyd & Silk 1983). For example, if the highest ranking individual always wins encounters with all other individuals in the group, the maximum likelihood estimate of β_i' would tend to infinity. In cases where several of the X_{ij}'s are small, tests based on the deviance function also have to be interpreted with care (McCullagh & Nelder 1989, p. 120)

We have only analysed a small number of data sets and cross-product interactions were only present in one of those. In studies where a large number of traits are measured on each individual, say k traits, the number of possible cross-product interactions would be $k(k-1)/2$. In such cases it will be important to make predictions from general theory, before doing the analysis, in order to avoid making ad-hoc hypotheses about non-existing relationships.

Even though the models with trait dependencies (8) and cross-product interactions (9) presented here possibly can produce several new insights in analysis of dominance structures, the approach based on these models is not completely free of problems. In most cases, only some of the properties affecting the dominances are measured, while other properties (e.g. internal hormone levels) typically will be unknown. We can think of these additional unknown properties $\epsilon_1, \epsilon_2, \ldots, \epsilon_n$ of the individuals in the group as stochastic variables, producing an extra $\epsilon_i - \epsilon_j$ term in the model equation for $\operatorname{logit} p_{ij}$. The effect of this extra stochastic term would be more over-dispersion in the data. While this normally can be controlled for, the problem is that this form of error structure also would generate positive covariances between the elements across each row and column of the data matrix, and these dependencies between the sample units would violate the assumptions usually made in generalized linear models (McCullagh & Nelder 1989, p. 324). In cases where there is a large amount of over-dispersion in the data (see e.g. Table VI), part of which may be of this form, the standard errors of the estimates and significance of the various tests will therefore have to be interpreted with some care.

Acknowledgements

We wish to thank Kjetil Hindar for comments on an early version of the manuscript and Steinar Engen for helpful discussion. EJS and THR received financial support from the Norwegian Research Council and the Norwegian Directorate for Nature Management.

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Table I: The dominance data matrix of eight willow tits taken from Lahti et al. (1994) Table 1, flock C. The numbers are the number of observed victories X_{ij} of individual i in encounters with j. The estimated differences of each individual's absolute dominance to the dominance of individual number five, $\beta_i' = \beta_i - \beta_5$ is shown in the rightmost column.

${}_i\backslash^j$	1	2	3	4	5	6	7	8	$\hat{\beta}_i'$
1	-	16	4	2	16	8	18	10	4.53
2		-	7	2	11	14	23	5	2.78
3	4	2	-	2	18	20	5	9	2.72
4					-	21	12	11	0.55
5				-	9				0
6		2				-	26	10	-0.14
7		1	4	9	3	7	-	17	-0.43
8						2	5	-	-1.88

Table II: The maximum likelihood estimates of the dominances, $\hat{p}_{ij}$, for the Bradley-Terry model fitted to the willow-tit data.

$_i\backslash^j$	1	2	3	4	5	6	7	8
1		0.85	0.86	0.98	0.99	0.99	0.99	1.00
2	0.15		0.51	0.90	0.94	0.95	0.96	0.99
3	0.14	0.49		0.90	0.94	0.95	0.96	0.99
4	0.02	0.10	0.10		0.63	0.67	0.73	0.92
5	0.01	0.06	0.06	0.37		0.53	0.61	0.87
6	0.01	0.05	0.05	0.33	0.47		0.57	0.85
7	0.01	0.04	0.04	0.27	0.39	0.43		0.81
8	0.00	0.01	0.01	0.08	0.13	0.15	0.19	

Table III: The maximum likelihood ranking under weak stochastic transitivity for the willow-tit data. Note that one 'reversal' (*) between individual 4 and 5 is still present.

$_i\backslash^j$	1	2	3	4	6	7	5	8
1	-	16	4	16	8	18	2	10
2		-	7	11	14	23	2	5
3	4	2	-	18	20	5	2	9
4				-	21	12	0*	11
6		2			-	26		10
7		1	4	3	7	-	9	17
5				9*		-		
8					2	5		-

Table IV: Parameter estimates, change in deviance and significance values for traits included in the model, for Solberg & Ringsby's (1997) and Møller's (1987) data sets. Over-dispersion estimates representing the factor by which the standard deviation of the response the variable X_{ij} exceeds the expected standard deviation under the binomial assumption, are also given.

	Solberg				Møller			
Trait	Estimate $\pm$ SE	χ^2	df	P	Estimate $\pm$ SE	χ^2	df	P
Age	0.10 ± 0.06	2.9	1	0.04	0.34 ± 0.15	4.85	1	0.02
Total badge size	0.22 ± 0.07	10.7	1	0.0005	2.46 ± 0.33	55.55	1	0.0001
Visible badge size	-0.23 ± 0.07	10.8	1	0.001				
Over-dispersion	1.52				2.57			

Table V: Analysis of Barrette & Vandal's (1986) data set.

Trait	Estimate	χ^2	df	P
Sex	1.00 ± 0.15	40.1	1	0.0001
Age	0.55 ± 0.14	14.4	1	0.0001
Antler size	1.19 ± 0.18	40.8	1	0.0001
Sex × Age	-0.43 ± 0.15	8.4	1	0.004
Sex × Antler size	0.46 ± 0.16	8.2	1	0.004
Over-dispersion	4.51			

Table VI: Analysis of Barrette & Vandal's (1986) data set with the relatedness between all individual taken into account.

Trait	Estimate	χ^2	df	P
Sex	0.99 ± 0.16	39.4	1	0.0001
Age	0.81 ± 0.18	20.2	1	0.0001
Antler size	1.26 ± 0.19	45.3	1	0.0001
Sex $\times$ Antler size	0.52 ± 0.16	10.0	1	0.0016
Relatedness	2.71 ± 0.62	19.1	1	0.0001
Over-dispersion	4.33			

Figure 1: The relationship between p_{ij} and the difference in the 'absolute dominances', $\beta_i - \beta_j$, under the Bradley-Terry model, with the logit choice of link-function. Note that for $\beta_i = \beta_j$, $p_{ij} = 1/2$, for $\beta_i \gg \beta_j$, p_{ij} tends to 1, and for $\beta_i \ll \beta_j$, p_{ij} tends to 0.

Figure 2: An intransitive dominance structure. Pairs of individuals lying on the isolines are equidominant. For positive c, individuals become increasingly dominant in the clockwise direction. The gradient vector field is represented by the arrows.

Figure 3: Graphical interpretation of cross-product interactions. Each dot represent a single individual. Individuals lying on the isolines are equidominant. The direction of increasing dominance is indicated by the arrows. (a) Sex versus age: among females (sex $= -1$), the dominances are only weakly dependent on age, while the dominances increase with age among the males (sex $= 1$); at the same time, irrespective of antler size, males dominate females. (b) Among both males and females, dominance increase with antler size. The dependency on antler size is stronger among females however. Some individuals of the same sex and age class coincide on the graphs.