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A Unified Model of Dominance Hierarchy Formation and Maintenance

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In many different species it is common for animals to spend large portions of their lives in groups. Such groups need to divide available resources amongst the individuals they contain and this is often achieved by means of a dominance hierarchy. Sometimes hierarchies are stable over a long period of time and new individuals slot into pre-determined positions, but there are many situations where this is not so and a hierarchy is formed out of a group of individuals meeting for the first time. There are several different models both of the formation of such dominance hierarchies and of already existing hierarchies. These models often treat the two phases as entirely separate, whereas in reality, if there is a genuine formation phase to the hierarchy, behaviour in this phase will be governed by the rewards available, which in turn depends upon how the hierarchy operates once it has been formed. This paper describes a method of unifying models of these two distinct phases, assuming that the hierarchy formed is stable. In particular a framework is introduced which allows a variety of different models of each of the two parts to be used in conjunction with each other, thus enabling a wide range of situations to be modelled. Some examples are given to show how this works in practice.

Introduction

Many animals spend all, or important parts of, their lives living in groups which occupy a collective territory. Such groups have a limited amount of resources available to them, which must be divided between the individual members in some way. It is common for a *dominance hierarchy* to form, where the animals arrange themselves into a priority order to divide the available resources, see Alcock (1993) and Hand (1986). Sometimes this hierarchy is linear, so that animal A dominates all others, B dominates all others except A, etc. For different types of group the particular structure varies.

Two important questions about such dominance hierarchies, are

(1) How is the hierarchy formed?
(2) Once formed is the ordering of individuals maintained, and if so how?

Much empirical work has been done to answer the second question. Linear hierarchies are usually stable. Experiments have been carried out where individual fowl have been removed from a population, and reintroduced days later, where they automatically return to their former position (Klopfer, 1973). Coalitions commonly

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help to preserve a hierarchy. These often occur where relatives support each other, although coalitions between non-related individuals have been observed in monkeys (Chapais *et al.*, 1991). There is evidence that dominance hierarchies are maintained by recognizing dominant and non-dominant individuals, by scent in fish, Todd *et al.* (1967) or by voice in birds, Lemon (1967). Various models have also been formulated to answer these two questions. The aim of this paper is to provide a method of unifying models of formation and maintenance into a single model.

MODELS OF DOMINANCE HIERARCHY FORMATION

For many species, animals live in groups which persist through time, so that a new animal simply has to find a position in an already established hierarchy. Often such an animal slots in behind (or ahead of!) its own mother or sisters, in the case of a hierarchy of females (Frank, 1986; Marsden, 1968), and so no formation modelling is required. There is a second type of situation, where groups of individuals form for the first time, such as birds coming together for a lek (Hoglund & Alatalo, 1995; Kokko *et al.*, 1998) or groups of juvenile fish forming a shoal (Issa *et al.*, 1999) where there is no initial ordering and the animals must formulate a dominance order from scratch. In this situation there is a distinct formation phase to the hierarchy which is different in character from the period where a hierarchy has been established, and so has an extra dimension from the modelling point of view.

Together with Cannings and Vickers I have recently written a series of papers considering this question (Broom *et al.* 2000a,b; Broom & Cannings, unpubl.). Starting with a group of 2^n individuals, animals engage in pairwise contests according to a pre-ordained structure. In Broom *et al.* (2000a,b) this was a knockout contest similar to many human competitions such as the Wimbledon Lawn Tennis Championships. At the start of the contest the 2^n players are paired off and play a game in which there is a winner. The winners are then repaired in the next round and this continues until there is one overall winner. Players receive a reward according to which round they were eliminated from the competition (they may also receive costs depending upon what strategies were played in each round). In Broom *et al.* (2000a) players had to play the same strategy in every round they were involved in: in Broom *et al.* (2000b) players could change their strategy from round to round. In Broom & Cannings (unpubl.) a *Swiss tournament*, a structure common in chess tournaments, was used. In each case the players ordered themselves into a dominance structure with a unique dominant individual. The advantage of such contests is that they allow individuals to organize themselves with relatively few costly fights, and these occur between animals which are at the same dominance level at the time. It is not claimed that animals will follow these tournament structures precisely, but that under some circumstances they may prove to be a reasonable approximation.

These are not the only models of dominance hierarchy formation. Other models of formation include Mesterton-Gibbons & Dugatkin (1995) which considers the different question of which dominance structure is likely to emerge from a round robin contest where every individual plays each of the others exactly once (in particular what is the probability of a linear dominance hierarchy occurring) and Beaugrand (1997) which considers the influence of a variety of factors in a simulation model.

MODELS OF DOMINANCE HIERARCHY MAINTENANCE

More work has gone into considering the problem of dominance hierarchy maintenance. The concept of reproductive skew was introduced in Vehrencamp (1983), dealing with how mating rights were divided between individuals in a group and in particular whether this division was equitable or not.

An even division of mating rights often occurs in communally breeding birds (Brown, 1987), whereas in other situations this split is more uneven, for instance in the naked mole-rat (Clarke & Faulkes, 1997). Different circumstances can, however, also lead to very different levels of reproductive skew in the same species. In the dwarf mongoose the level of skew is generally high (Rood, 1980), but greater mating rights are available to subordinates as they get older (Creel & Waser, 1994). In ants, colonies with many queens can split their reproduction very differently, depending upon how the queens are related. If they are closely related, the skew is very large, but for unrelated queens the split is far more equitable (Strassmann, 1989; Reeve & Ratnieks, 1993).

The idea of stay and peace incentives was introduced in Keller & Reeve (1994), where dominant individuals allow subordinates limited mating rights in order not to challenge the authority of the dominant or leave the group, which may damage the fitness of the group as a whole and the dominant individual in particular. It is assumed that the dominant individual has complete control of reproductive rights, and allows limited reproductive rights to subordinates out of self interest. Under this assumption the model predicts that higher skew should occur when individuals are close relatives (Reeve & Keller, 1996) and when individuals have less possibilities of leaving the group and mating successfully on their own (as in the younger mongooses of Creel & Waser, 1994). See also Reeve & Emlen (2000) for an extension of this idea to the multi-player case for staying incentives.

A different type of model was introduced in Broom & Ruxton (2001), which considers a situation where individuals of unequal quality must divide available resources amongst themselves and which focuses on contests between pairs of individuals. In this model no individual has direct control over the reproductive rights of others, but dominant individuals exercise dominance over others in direct contests over resources (which may or may not be mating rights). This "quality" could be size, but also could be linked directly to a dominance level.

These two distinct phases of the dominance hierarchy, formation and maintenance, must surely be linked, however. The extent to which an individual should strive to be dominant will depend upon the rewards available to the occupier of that position, so that cases where reproductive skew is high, for example, should lead to violent formation phases, whereas equitable divisions should not.

A Unified Model of Dominance Hierarchy Formation and Maintenance

We now create a mechanism in which a model of dominance hierarchy formation and one of dominance hierarchy maintenance can be unified into a single model, assuming that the hierarchy is stable after formation. This is a reasonable assumption for many models, for instance the reproductive skew models assume that the dominant individual gives away just enough rights to maintain stability. We shall base our construction on a combination of the formation model of Broom *et al.* (2000b) and the resource division model of Broom & Ruxton (2001). Note that we can combine any pair of formation and maintenance models, as long as the hierarchy is stable, the formation model provides the structure (1) and the maintenance model provides the reward division (2), although sometimes the maintenance model has an inbuilt structure, in which case the two structures must match. The major elements of the combined model are as follows.

(1) A dominance structure $\mathbf{D} = (D(i))$. The N animals are divided into m dominance classes so that all animals in class i are dominant to all of those in class j if and only if $i<j$. The number of animals in class i is $D(i)$, so that the vector $\mathbf{D}$ completely defines the dominance structure. Thus if the hierarchy is linear, $m = N$ and $D(i) = 1$ for all i. Typically, $D(1) = 1$ so that there is a single animal which is dominant over all others.

(2) A division of resources $\mathbf{V} = (V(i))$. It is assumed that each animal within dominance class i receives $V(i)$, so that they all receive the same share of the resources available, and that $V(i)$ is decreasing with i.

All of the formation models (Broom *et al.*, 2000a, b; Broom & Cannings, unpubl.) have an inbuilt structure $\mathbf{D}$, and given a fighting cost C and the reward structure $\mathbf{V}$ generate a model of the behaviour during the formation of the dominance hierarchy. The problem is how to choose $\mathbf{V}$. Under the assumption of the dominant individual controlling mating rights and allowing stay and peace incentives (Keller & Reeve, 1994) the theory can automatically generate these values of $\mathbf{V}$, although it may be hard to quantify these. For unknown **V**, we describe a method of generating **V** using only some competition rules from individual contests between animals of different dominance levels, as in Broom & Ruxton (2001). We require two factors which allow us to calculate it.

(3) A pairwise competition rule $\mathbf{R} = R(i,j)$, indicating the reward to an individual of level i involved in a pairwise contest against an individual of level j. $R(i,j) > R(j,i)$ if $i<j$. Such a reward function is devised in Broom & Ruxton (2001) for individuals of different qualities, and can easily be adapted to different dominance ranks.

(4) A frequency of competition measure $\mathbf{F} = F(i,j)$. How many times, on average, will a given pair of animals one of level i and one of level j, compete in the contests from (3)? For instance, if competition is over food items that are discovered, $F(i,j)$ might be constant over all pairs of animals. If the competition is over mates, then it might be very inequitable (a female is unlikely to mate with a male animal of low rank, so contests between high ranking males will occur far more often).

The reward to an individual of rank i, $V(i)$, can then be expressed as some base value added to the reward accrued from the contest described above so that we obtain

$$V(i) = \alpha + \sum_{j=1,\, j\neq i}^{m} F(i,j)R(i,j)D(j) + (D(i)-1)F(i,i)R(i,i)$$

assuming such rewards are additive, where α is the base level.

A PARTICULAR MODEL

As an illustration we use the formation model developed in Broom *et al.* (2000b). In general for this model there are 2^n individuals divided into $m = n + 1$ dominance classes where there is a unique individual of rank $1 (D(1) = 1)$ and the number of individuals of rank i is given by $D(i) = 2^{i-2}$, $i = 2, \ldots, m$.

The frequency of competition depends upon many factors such as species, the resource being competed for and the dispersal of the population. Generally, valuable resources will be fought over at least as frequently by dominant individuals as subordinate ones. Let us suppose for simplicity that $F(i,j) = c\beta^{i+j-2}$ for some $0<\beta\leqslant 1$. Thus the smaller β is, the more such competition is restricted to the most dominant animals (see numerical examples 1 and 2).

Using the resource division model of Broom & Ruxton (2001), individuals compete for resources of value V in asymmetric Hawk–Dove contests (see also Maynard Smith & Parker, 1976) with cost C. Let us assume that $C = \gamma V$, with $\gamma > 1$. Then in every competition between different ranked individuals, one will play Hawk and the other Dove. In Broom & Ruxton (2001) the paradoxical solution (inferior playing Hawk, superior playing Dove) was allowed under some circumstances, due to historical reasons. Here it is clear that a higher ranked individual will have the psychological advantage, so that it seems unlikely that this will occur. Thus, it is assumed that the superior animal will always win, and so

$$R(i,j) = V, \quad i<j, \qquad R(i,j) = 0, \quad i>j.$$

If the two individuals are of equal rank, then the conventional Hawk–Dove game of Maynard Smith (1982) is played, and each plays the mixed strategy, playing Hawk with probability $V/C = 1/\gamma$, with payoff

$$\frac{V(C-V)}{2C} = \frac{(\gamma-1)V}{2\gamma}.$$

Thus we can substitute into the general reward equation to give

$$V(1) = \begin{cases} \alpha + \sum_{j=2}^{m} c\beta^{j-1} V 2^{j-2} & = \alpha + Vc\beta \dfrac{1-(2\beta)^{m-1}}{1-2\beta} \\ (\beta \neq 0.5), & \\ & = \alpha + 0.5Vc(m-1) \\ (\beta = 0.5) & \end{cases}$$

and for other i

$$\begin{aligned} V(i) &= \alpha + \sum_{j=i+1}^{m} c\beta^{i+j-2} V 2^{j-2} + (2^{i-2}-1)c\beta^{2i-2}\frac{\gamma-1}{2\gamma}V \\ &= \begin{cases} \alpha + cV\left(\beta^{2i-1}2^{i-1}\dfrac{1-(2\beta)^{m-i}}{1-2\beta} + (2^{i-2}-1)\beta^{2i-2}\dfrac{\gamma-1}{2\gamma}\right) & (\beta \neq 0.5) \\ \alpha + cV\left((0.5)^{i}(m-i) + ((0.5)^{i} - (0.5)^{2i-2})\dfrac{\gamma-1}{2\gamma}\right) & (\beta = 0.5) \end{cases} \end{aligned}$$

Numerical Examples

We shall consider three examples to see how a unified model can be formed. In each case the results are set out in their general form, and then specific numerical values are chosen to help illustrate the results. These numerical values are rather arbitrary and are not meant to represent any particular real situation, although the relative size of these numerical values is important in some cases (the value of γ is larger in example 1 than example 2, $\beta = 1$ in example 1, and takes the significantly smaller value of 0.5 in example 2).

Example 1. Suppose that we have a dominance hierarchy composed of eight individuals, which was formed according to the knockout model of Broom *et al.* (2000b). Thus $m = 4$ and so we have $D(1) = 1, D(2) = 1, D(3) = 2, D(4) = 4$.

To find the values of $V(i)$ we now need to establish the base value α and the frequency of contests $F(i,j)$. Assuming that we use the simplified formulation of $F(i,j) = c\beta^{i+j-2}$, this reduces to choosing values of β and c.

Let us suppose that contests are over food. It is supposed that each pair of individuals may be equally likely to fight over an item of food, implying that $\beta = 1$; the number of contests between each pair of animals is $F(i,j) = c$, for some c. Also suppose that the proportion of food items found resulting in a contest is f_c, with the remaining $1 - f_c$ uncontested, so that there are $28c$ contests and so another $28c(1 - f_c)/f_c$ items are found by individuals which are not subject to any contest, i.e. an average of $3.5c(1 - f_c)/f_c$ each, so that $\alpha = 3.5cV(1 - f_c)/f_c$. Thus the division of food resources is given by

$$V(1) = \frac{3.5cV(1-f_c)}{f_c} + 7cV,$$

$$V(2) = \frac{3.5cV(1-f_c)}{f_c} + 6cV,$$

$$V(3) = \frac{3.5cV(1-f_c)}{f_c} + cV\left(4 + \frac{\gamma-1}{2\gamma}\right),$$

$$V(4) = \frac{3.5cV(1-f_c)}{f_c} + cV\frac{3(\gamma-1)}{2\gamma}.$$

It is likely that an item of food is worth considerably less than the cost of an injury, so that γ is large; in this case we set $\gamma = 10$. Picking $f_c = 0.5$ gives

$$V(1) = 3.5cV + 7cV = 10.5cV,$$

$$V(2) = 3.5cV + 6cV = 9.5cV,$$

$$V(3) = 3.5cV + 4cV + \frac{9cV}{20} = 7.95cV,$$

$$V(4) = 3.5cV + 0 + 3\frac{9cV}{20} = 4.85cV.$$

The total resources acquired is thus $55.3cV$ and so the proportionate division of food resources is: dominant individual 0.190, the second ranked individual 0.172, the next two individuals 0.144 each and the subordinate individuals 0.088 each.

Violent (Hawk vs. Hawk) contests only occur between individuals of the same rank, with probability 1/100, so the total number of such contests is $(6c+c)\times 1/100 = 7c/100$, which is a proportion 0.0025 of the total number of contests.

Example 2. Consider a situation as in Example 1, except that now contests are over mates. It is reasonable to assume that mates will have a preference for a dominant male, so that higher level contests are more likely to result in the reward of a mate than lower level contests.

Further suppose that no matings will go uncontested, so that $\alpha = 0$. The division of resources is given by

$$V(1) = 0 + cV(\beta + 2\beta^2 + 4\beta^3),$$

$$V(2) = 0 + cV(0 + 2\beta^3 + 4\beta^4),$$

$$V(3) = 0 + cV(0 + 0 + \frac{\gamma-1}{2\gamma}\beta^4 + 4\beta^5),$$

$$V(4) = 0 + cV(0 + 0 + 0 + 3\frac{\gamma-1}{2\gamma}\beta)^6.$$

In this case, mating opportunities are more valuable than food items, and so we shall set $\gamma = 2$. We pick $\beta = 0.5$ to illustrate this numerically, yielding

$$V(1) = 1.5cV, \quad V(2) = 0.5cV,$$

$$V(3) = 0.1406cV, \quad V(4) = 0.0117cV.$$

The total resources acquired is thus $2.328cV$ and so the division of mating rights is; dominant individual 0.644, β individual 0.215, the next two individuals 0.060 each and the subordinate individuals 0.005 each. Violent contests only occur between individuals of the same rank, with probability 1/4, so the total number of such contests is $0.0391c$, which is a proportion 0.0169 of the total number of contests.

The values of $V(i)$ found above are directly related to the rewards V_i in Broom *et al.* (2000b) where $V(i+1) = V_i$. Thus we can now use these to find the formation behaviour given by that model.

Using the dynamic programming method from Broom *et al.* (2000b) and Broom & Cannings (unpubl.) we can find both the probability of individuals playing Hawk at each stage and also the expected reward to each individual at every stage, and thus at the start of the contest. Supposing that $c = 2$ we obtain $V(1) = 3V$, $V(2) = V$, $V(3) = 9V/32$ and $V(4) = 3V/128$. These generate the probability of individuals playing Hawk in each round using the recurrence relation:

$$p_k = mid(0, 1, z_k)\text{where}$$

$$z_1 = \frac{V(1) - V(2)}{\gamma V},$$

$$z_k = \frac{z_{k-1}}{2} + \frac{V(k) - V(k+1)}{\gamma V} - \frac{1}{2}p_{k-1}^2$$

$p_1 = 1$ (since $\gamma = 2$) so that the contest between the top two individuals to decide which is dominant is always Hawk–Hawk.

$p_2 = 0.3594$ meaning that individuals play Hawk much less frequently in contests to decide which individuals contest this final round.

$p_3 = 0.2440$, so that early contests are relatively peaceful.

The expected rewards at each stage can also be found. We obtain an expected reward for each individual at the start of the contest as $0.2079V$. The expected total number of Hawk–Hawk contests is

$$1 + 2\times 0.3594^2 + 4\times 0.2440^2 = 1.4965$$

so that in this particular example, almost all of the violent contests will occur in the formation phase, and after that there will be relatively little conflict (the total in the maintenance phase is 0.0782). The behaviour predicted here is typical of some hierarchies, for example that found in juvenile crayfish (Issa *et al.*, 1999).

Example 1 *continued*. How does the level of violence in the formation phase in Example 2 compare to that of Example 1? For a fair comparison we pick c to make the total reward available the same in both examples, giving $c = 0.0842$ in Example 1. Thus $V(1) = 0.8841V$,

$V(2)=0.7999V$, $V(3)=0.6694V$, $V(4)=0.4084V$; using $\gamma = 10$, the value chosen in Example 1, we obtain $p_1 = 0.00842, p_2 = 0.01722, p_3 = 0.03456$ and the total number of Hawk–Hawk contests is 0.00544 which is much less than in Example 1, as we would expect.

Naturally the above methodology could also be incorporated into other formation models, for instance Broom & Cannings (unpubl.), if that model was more applicable for a particular example. Similarly if we used a maintenance model which generated the values of $V(i)$ directly for an assumed structure, and this structure matched one of those from one of the formation models, then these could also be combined. A good example of this is as follows.

Example 3. Keller & Reeve (1994) defined the levels of stay and peace incentives for a group of two individuals based upon a number of factors:

x, the reproductive success of the subordinate if it leaves the group,

k, the total group output if the subordinate stays, the reproductive success of an established single individual is 1,

r, the coefficient of relatedness between the two individuals, and

f, the probability that the subordinate individual wins an escalated contest (it is assumed that the loser of such a contest dies and so receives zero as itself, although its payoff will gain an indirect contribution from its related victor).

The stay incentive (p_s) and the peace incentive (p_p) are evaluated as follows:

$$p_s = \frac{x - r(k-1)}{k(1-r)}, \qquad p_p = \frac{f + r(1-f-k)}{k(1-r)}.$$

Thus the proportion of reproductive rights of the subordinate is $\max(p_s, p_p)$. So for a group of two, the payoffs to the dominant and subordinate are

$$V(1) = k(1 - \max(p_s, p_p)),$$

$$V(2) = k\ \max(p_s, p_p).$$

We now assume that these two individuals fight a formation contest of the Hawk–Dove variety to decide which of them is dominant. If both players play Hawk, then one dies, the winner receiving 1 (as a lone individual), the (indirect) payoff to the loser being r, so the expected reward is

$$E[H,H] = \frac{1+r}{2}.$$

If both play Dove, each wins with probability 0.5, both survive, and so

$$E[D,D] = \frac{k(1+r)}{2}.$$

If one plays Hawk and the other Dove, the Hawk-player wins and so

$$E[H,D] = k(1 - \max(p_s,p_p)) + rk\max(p_s,p_p),$$

$$E[D,H] = rk(1 - \max(p_s,p_p)) + k\max(p_s,p_p).$$

This gives the probability of playing Hawk in the formation phase as

$$p(H) = \min\left(1, \frac{k(1 - 2\max(p_s,p_p))(1-r)}{(k-1)(1+r)}\right)$$

with the sensible assumption that no dominant gives away more that half its mating rights, i.e. $1 - 2\max(p_s,p_p) \geqslant 0$.

For example suppose that the two individuals are unrelated (so that $r = 0$) $f = 0.25, x = 1$ (the subordinate is the equal of the dominant so as capable of reproducing as a lone individual, but with a psychological disadvantage due to the initial contest) and $k = 3$ (the individuals perform better as a pair than on their own). The stay incentive is $1/3$ and the peace incentive is $1/12$, so that the proportion of reproductive rights allocated to the subordinate animal is $1/3$. This yields the probability of playing Hawk in the formation phase, which here is a single contest between two individuals, as 0.5 and so the probability of an escalated contest is 0.25. Note that in general if $x = 1$ then $p_s > p_p$ and the equation for $p(H)$ reduces to

$$p(H) = \frac{k-2}{k-1}$$

($k \geqslant 2$, otherwise no sufficient incentive can be offered to keep the subordinate in the group).

THE REPRODUCTIVE SKEW OF THE MODEL

The reproductive skew of a population generated by any formation model can be calculated using the formula of Pamilo & Crozier (1996) which defined reproductive skew S as

$$S = \frac{n - Q_E}{n - 1}, \quad Q_E = \frac{1}{\sum p_k^2},$$

where p_k is the reproductive contribution of the k-th breeder, which is the fraction of the total reward that individual receives and so is related to the reward structure **V** and the dominance structure **D**. High S (near 1) means high reproductive skew, and low S (near 0) means low reproductive skew. The value of S for Example 2 above is found from

$$Q_E = \frac{1}{0.644^2 + 0.215^2 + 2(0.060^2) + 4(0.005^2)}$$

$$= 2.134$$

and so $S = 0.838$.

Similarly, the value of Q_E for Example 1 is 7.264 giving the lower value of S of 0.105 (note that the way this example has been formulated, the skew is not "reproductive").

Usually, a higher level of reproductive skew leads to more violence in the formation phase. Considering the knockout model used for Examples 1 and 2, it can be shown that increasing the level of skew always leads to at least as many plays of Hawk for either two or four players (this is not universally true for larger numbers of players). Note that this does not necessarily imply an increase in Hawk vs. Hawk contests, which is the true measure of actual violence rather than just violent intent. The two-player case being trivial, we consider four players ($n = 2$).

$$Q_E = \frac{1}{\left(\frac{V(1)}{V(1)+V(2)+2V(3)}\right)^2 + \left(\frac{V(2)}{V(1)+V(2)+2V(3)}\right)^2 + 2\left(\frac{V(3)}{V(1)+V(2)+2V(3)}\right)^2}$$

$$= \frac{K^2}{2V(1)^2 + 6V(3)^2 + K^2 + 4V(1)V(3) - 2KV(1) - 4KV(3)},$$

where $K = V(1) + V(2) + 2V(3)$ is the total reward available. Keeping this reward fixed, and assuming the relationship $V(1) > V(2) > V(3) > 0$, it is easy to show that Q_E is decreased (and so the skew is increased) by increasing $V(1)$ or by decreasing $V(3)$.

Assuming that

$$p_1 = \frac{V(1) - V(2)}{C} < 1,$$

$$p_2 = \frac{V(1) - V(2)}{2C} + \frac{V(2) - V(3)}{C} - \frac{1}{2}\left(\frac{V(1) - V(2)}{C}\right)^2 < 1$$

(ensuring that there is scope to increase or decrease the incidence of Hawk plays in each round) the total number of Hawk plays is

$$\begin{aligned} &2p_1 + 4p_2 \\ &= 2\frac{V(1) - V(2)}{C} + 4\left(\frac{V(1) - V(2)}{2C} + \frac{V(2) - V(3)}{C} - \frac{1}{2}\left(\frac{V(1) - V(2)}{C}\right)^2\right) \\ &= 4\frac{V(1) - V(3)}{C} - 2\left(\frac{2(V(1) + V(3)) - K}{C}\right)^2 \end{aligned}$$

which is decreasing with $V(3)$ and increasing with $V(1)$. Thus an increased reproductive skew always increases the number of Hawk plays in this case.

Discussion

There exist several models and much empirical work on the subject of how animals should behave when in a dominance hierarchy. This behaviour is different if the dominant individual has total control of reproductive rights, than if it has not. In many species a stable hierarchy exists throughout time, and new individuals slot into pre-allocated positions without any conflict. Such a situation is more likely to occur when a group is made up of relatives, and here the likelihood of control by the dominant individual is greater. However in other species, a hierarchy has to form from scratch at the start of every breeding season. For such a species, the type of behaviour and the rewards available in an established dominance hierarchy can also have a significant influence upon the formation of the hierarchy. This paper describes a method of integrating a model of dominance hierarchy formation with a model of dominance hierarchy maintenance, for any such pair of models, provided that the maintenance model yields a stable hierarchy and has, or can generate, a set of rewards for all of the individuals in the hierarchy, and the formation model has an unambiguous structure (which must match that of the maintenance model if it possesses one).

Some examples are given which show how to combine different pairs of models. Often the level of aggression during the formation phase of a dominance hierarchy is much greater than that when the hierarchy has been formed. This is due to the fact that asymmetric contests generally involve less aggression than symmetric ones, so that as long as the initial discrepancies between the strength of the animals are not large, but that the psychological effect of an animal's position in the hierarchy is significant, then the contests in the formation phase are more symmetric than those in the maintenance phase. The level of skew in the division of rewards in the population does not seem to have a great effect upon the level of violence involved after the formation phase, but can have a large effect upon the level of violence during the formation phase, since this determines what the individuals are fighting for, and at a time when they are relatively well matched. This is in agreement with many real situations where the knowledge of the relative dominance of individuals often means that disputes are decided quickly in the favour of the dominant. This division of rewards is in turn determined by what resources are being divided. Food is likely to be more evenly divided than mates, for instance. Using the formulation of Pamilo & Crozier (1996) the resource division can be summarized to give a single numerical value of the (reproductive) skew of the group. Such skew will increase as the value of β or α/cV decreases.

This paper provides a formulation for how distinct phases of a dominance hierarchy can be linked together. In particular, for different species, different models in each phase may be appropriate. However, as long as they possess the required features, any such pair can be linked together, and the results of the maintenance phase can then be used to determine what behaviour should occur when the hierarchy is formed.

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