Relative importance of initial individual differences, agonistic experience, and assessment accuracy during hierarchy formation: A simulation study

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Abstract

This simulation study explores some conditions leading to transitivity within dominance orders. Combinations of three parameters were varied to study their consequences upon hierarchy formation and upon the degree of linearity of resultant structures. The factors studied were (*i*) the importance of initial Resource Holding Potentials (*RHPs)* , (*ii*) changes brought in *RHP*s by successive victories and defeats, and (*iii*) accuracy of *RHP* assessment made by opponents. Results show that initial differences in *RHP* always lead to perfectly transitive chains whose rank order reflects the importance of initial differences. Even when simulated animals make important errors while assessing each other during round robin tournaments, emerging dominance structures are perfectly linear and ranks obtained in the structure are highly correlated with initial values in *RHP*s. Moreover, accumulated experiences of victory and/or defeat alone always lead to perfectly linear hierarchies. Their combination with initial individual differences in *RHP* led to the same conclusion. Even when assessment was far from being perfect, not only perfect chains were formed but initial values in *RHP*s significantly influenced rank order when the contribution of victory and defeat to *RHP* was relatively unimportant. The higher the importance of victory and defeat to *RHP* as compared to that of initial *RHP* values, the lower was the correlation between initial *RHP* values and the ranks order reached by individuals in the resultant hierarchies. In general also, the lower the variation within initial *RHP*s, the lower was the correlation between initial *RHP*s and ranks in the hierarchy. At a given level of initial *RHP* dispersion, increasing the contribution of victory and defeat to *RHP* diminished the correlation between initial *RHP* values and obtained ranks. In addition, inaccurate assessment reduced the overall correlation, especially when dispersion of initial *RHP* values was low and the contribution of victory and defeat was high. These results shed some light on the controversy about the respective roles of initial individual attributes and that of patterns of resolution in the formation of animal hierarchies. We present the emergence of social order within closed systems as those simulated here as a case of self-organization.

Keywords:

Dominance; Hierarchy formation; *RHP*; agonistic experience; Assessment; Self-organization; Simulation.

INTRODUCTION

In many animal species, when a limited number, e.g., N<10, of subjects get together either naturally, e.g., after hatching, or after human intervention, they usually begin to challenge each other agonistically and eventually form a dominance order. After a few weeks, the social structure which the human observer can construct intellectually from the identification of the various dyadic dominance relationships will most often form a highly linear order structure, a hierarchy. The degree of linearity found within the structure will be a function of the number of dominance relationships which respect transitivity, a property of binary relationships (e.g., represented by >) in which, for any given members X, Y, Z part of a set, if X > Y and Y > Z, then X > Z also applies. The Landau *h* (1951a) and Kendall *K* indexes have been alternately used as a measure of degree of linearity within a given set of relationships (Appleby, 1983).

One question of interest over the years has been how such a high degree of linearity is reached within a group.

A first explanation is based on individual characteristics which were present before any structure formation, the so-called "individual differences" or "attributes". It is evident that if one picks up 5 pebbles from the beach and weighs each of them using a precise scale, a perfect hierarchy will always be obtained. Even if there are ties, i.e., pebbles having "exactly" the same weight, their assignation at random to adjacent ranks will result, with a high probability, into a perfectly linear chain.

However, with animals, initial individual differences have been reported to be poor predictors of resultant rank orders (Collias, 1943; Guhl, 1953; King, 1965; Bernstein and Gordon, 1980). Moreover, Landau (1951a) has examined the question theoretically and concluded that initial individual differences could not *fully* account for hierarchy structures in animals. Indeed, in principle, the correlation between initial individual characteristics and rank orders in the structure would have to be very high (r.9) to account for what is observed in real animal dominance orders. Moreover, stringent mathematical conditions would have to be met, which is not the case.

There are many explanations for such a "weak" correlation, apart from the fact that, considering the nature of the data and their level of measurement, the appropriate correlation coefficient was not always applied (Jackson and Winnegrad, 1988; Jackson, 1992; Rothstein, 1992). First, we are not always sure that the variables chosen by the researcher and used to correlate are the ones used by animals to sort themselves out. Second, animals are not pebbles: they can rapidly change state, give, or make available to others more or less accurate information about their own state. Moreover, animals surely make errors when they assess each others, and consequently transitivity within dominance orders may suffer from these imprecisions. Third, there is most likely a carry over process from previous encounters to subsequent ones during the process of hierarchy formation, an explanation initially formulated by Landau (1951b) in his "second model". McBride (1958) made a similar suggestion when he said that chickens, in his study, were influenced by memories of their previous successes and failures.

Instead of holding to the concept of individual differences which poses some difficulties, we shall rather use that of "Resource Holding Potential" (*RHP:* after Parker, 1974). *RHP* was conceived to reflect biophysical states, as well as psychological conditions (Clutton-Brock and Albon, 1979; Robertson, 1986; Beaugrand et al., 1996). According to Parker (1974), *RHP* is affected by factors related to the history of the contestant. Amongst psychological factors due to the history of contestants, prior recent victory or defeat experiences are of interest here. Recent prior victory experience seems to account for an increase in *RHP* while recent defeat experience seems to decrease it in fish (Francis, 1983; Beaugrand and Zayan, 1985; Beacham and Newman, 1987; Beaugrand et al., 1991, 1996) and hens (Cloutier et al., 1996; Zayan, 1987; Martin et al., 1996). Thus, at a given moment in the life of an individual, be it momentarily involved in a tournament to position itself in the hierarchy, its *RHP* would be determined by all the aforementioned factors, including recent victory/defeat experience.

Since dominance relationships formed between pairs of animals are most likely determined by momentary individual *RHP*s, which are modifiable during hierarchy formation by successive experiences lived by the animals, it is not surprising that "individual differences" measured before the onset of the formative period end up being poorly correlated with the resultant hierarchy.

Chase (1982a, 1982b) proposed a model, the *jigsaw puzzle*, which stipulates that hierarchy formation is *uniquely* a developmental process where preceding dominance interactions influence succeeding ones. Since theoretical work and empirical evidences indicated to Chase that individual differences could not be strong enough to explain the structure of common observed hierarchies, in his model, he ignored the role that initial individual differences might play during hierarchy formation, either alone or combined with carry-over effects.

The "jigsaw puzzle" approach developed by Chase (1980, 1982a, 1982b, 1986) describes how hierarchy structures, especially strong transitive ones, emerge from patterns of interaction among individuals in the various triads that make up a larger group. The carry over process aforementioned, i.e., experiences of victory or defeat, could explain and account for the fact that when opponents can choose each other, *Double Dominance (DD)* and, to a lesser extent, *Double Subordinance (DS)* sequences are so frequent during the formation of triads in the hen. Chase suggests that *DD* and *DS* patterns *guarantee* transitivity within triads and within larger groups. Since a pattern of *DD* sequences is a historical process, and a historical process cannot be causative, there must exist "behind" this description of process a more profound mechanism within the brain of the individual animal. It is posited that recent experiences of victory or defeat could play that role.

Transitivity can also be insured by other mechanisms as well, like more "cognitive" ones especially in primates. The highly sophisticated neurosystem possessed by primates seems sensitive to incoherencies and would contribute to have them disappear. Some primates are clearly capable of transitive *logical* inference. In less sophisticated organisms, more simple cognitive mechanisms must also exist. Hens seem to be able to "learn" or to assess on a single trial to avoid an unfamiliar hen when they have no chance of defeating it. Thus, Hogue et al. (1996) have shown that a hen observing its prior dominant being defeated by an unfamiliar one could use that information when confronted in turn by the latter by avoiding it and systematically conceding victory, thus contributing to transitivity within the triad. However, more parsimonious explanations other than cognitive ones must exist to account for transitivity, especially in lower vertebrates which also form stable and highly linear dominance structures while they do not possess a very elaborated neurosystem.

The aim of the present paper is to explore some conditions leading to transitivity within dominance orders. Three parameters will be varied in combination to study their consequences upon hierarchy formation and upon the degree of linearity of resultant structures. The studied factors are (*i*) the importance of initial *RHPs* , (*ii*) the changes brought in *RHP*s by successive victories and defeats, and (*iii*) the accuracy of *RHP* assessment made by opponents.

METHODS

The simulations were performed on a PC-compatible Executive 1000CD Packard Bell (Pentium 100 Mz) under Windows 95. The computer program was written by the author in the FoxPro 2.5 for Windows programming language (FoxPro 2.5 and Windows 95 are registered trademarks of Microsoft).

The present simulation modelling relied on several types of random functions whose algorithms can be found in the "FoxPro language reference manual" (Microsoft, 1993, pages L3-773 to L3-775):

(i) Function ndist returns a normally distributed *N(m, sd)* value with mean "*m*" and standard deviation "*sd*". The algorithm was taken from the "Handbook of Mathematical Functions", National Bureau of Standards, June 1964, Equation 26.2.23, page 933. Its error is < (4.5E-4 * *sd*). In the following text, this function will be represented as *N(m, sd)*.

(ii) Function irand returns a uniformly distributed integer *U(min, max)* between *min* and *max*. It will be referred to as *U(min, max)*. By analysing data generated by these routines, we can affirm that they were indeed random and non-periodic.

To measure the degree of transitivity within resultant hierarchies, the Kendall *K* (Appleby, 1983) index of linearity was applied. The Kendall rank-order correlation coefficient (tau) (Siegel and Castellan, 1988, pp. 245-254) was used to calculate the correlation between initial individual *RHP* values (transformed as ranks) and the final individual ranks is the resultant hierarchy.

Assumptions of the general model

Pairs met at random and each pairing was called a "round". We assumed that a hierarchy formed through a tournament, i.e., each individual met each other in turn in successive rounds. An individual was declared dominant over another when it was victorious on 6 successive rounds over that same opponent. We have regularly applied such a dominance criterion to fish (Beaugrand et al., 1991, 1996) and hens (Cloutier et al., 1995). Once the dominance criterion was reached between any two given opponents, the challenge was stopped. This could correspond to "individual recognition" of prior respective status within a given pair. However, pair members were still authorized to challenge other members of the group, unless the dominance criterion had also been met with them.

We postulated that several characteristics of the individual contributed to its disposition for dominance against another opponent but we assumed that they combined within each animal to form some kind of composite factor, *RHP*. Upon meeting at a given round, opponents assessed their respective *RHP*s, and compared these values; the individual assessed as having the larger *RHP* value was given victory at that given round, and its opponent, defeat. When their assessed *RHP*s were equal, victory was decided randomly. Facultatively, at each round, obtaining victory could increase the winner's *RHP* and defeat decrease the loser's *RHP*. We assumed that victory and defeat independently contributed to the *RHPs* of each concerned opponent.

Since the resultant hierarchies were constructed from dominance dyadic relationships and not from the sorting of individuals on their final *RHPs*, individuals with lower final *RHP*s could end up higher in the resultant hierarchy than others with higher ones.

Parameters

The following parameters could be varied through the simulation:

(i) Number of subjects per group to form a hierarchy. We made it vary from 3 to 10 in some simulations. In others, it was fixed at 6 simulated animals.

(ii) Initial values in *RHP*. *RHP* values could all be set to zero, be a balanced series, or form a series of arbitrary numbers obtained by sampling at random from a normal distribution (m, .*5m*), i.e., having a mean value of *m* and a standard deviation of half the value of *m*. Balanced series were composed of signed integers whose sum was equal to zero and which could be ranked without ties (e.g., for 6 animals: 30, 20, 10, -10, -20, -30).

(iii) Victory contribution to *RHP*. This *increase* corresponded to a positive random normal value generated by function *N*(*m*, *sd*) where *m* could vary between 0 (no contribution) and 50 with a standard deviation *sd*=.5*m*.

(iv) Defeat contribution to *RHP*. Same as for victory but implied a *decrease* in *RHP*.

(v) Accuracy of mutual *RHP* assessment. Assessment of the opponent's *RHP* could be accurate or could contain an error of assessment at a given round. When assessment was made to be accurate, each rival obtained the momentary true value of the opponent's *RHP*. When assessment was made to be inaccurate, rivals made errors in assessing the opponent's *RHP*. The error level was at its highest level on the first encounter between a given pair, but gradually diminished as the same pair members repeatedly met again. This was done through a procedure similar to that used by Leimar and Enquist (1984), in which assessment is carried out through a process of successive sampling. As sample size increases, sampling error diminishes and the assessment moves toward the "true" value of the opponent. On their first meeting, the estimate made by one animal of the *RHP* of its rival was equal to the true current value of the rival's *RHP*, plus error E. On any subsequent meeting between the same two animals, the current *RHP* estimate became equal to the average of two values: (i) its estimate of the *RHP* of that same opponent on the previous meeting, and (ii) the true current value of the rival's *RHP*, plus error E. Error E was generated by sampling from random normal function $N(m, sd)$ where m equals the percentage of error (%er) to attain, multiplied by the current rival's *RHP* value, divided by the number of rounds including the current one which involved the same pair members. Standard deviation sd was set to 50% of the value of m. For example, if 100% of initial error is aimed at, and the rival's *RHP* equals 1, error E will be at its maximum on the first round since it will be sampled from distribution $N(100, 50)$. On the 10th round between the same two rivals, error E will have considerably decreased since it will be a random value sampled from distribution $N(2, 1)$.

In the present simulations, variable %er was made to vary between 0 (accurate assessment) and 300%. However, since randomness could generate values as large as 1000 times the current assessed *RHP*, extreme resultant values were truncated at both ends of the resultant distribution by sampling again when values were not within the range of -1.96*(%er)**RHP* to +1.96*(%er)**RHP*.

Steps followed within each simulation

A set of *N* opponents was first formed and an initial *RHP* value was affected to each of them (*N.B.* it could be zero). Pairs were then formed at random by repeatedly sampling from a uniform random distribution two different numbers corresponding to the identity of any two group members that could still encounter. A given pair was not formed nor encountered each other again once it had satisfied the dominance criterion. Facultatively, victory or defeat on a given round could modify individual *RHP*s. The increase and decrease in *RHP* values were independently sampled for each opponent at the end of each round, until all $n*(n-1)/2$ possible pairs had reached the dominance criterion.

A dominance matrix was then completed and individual dominance scores were calculated. The score structure was obtained together with the Kendall *K* index of linearity, together with the Kendall giving the correlation between initial individual *RHP*s and their corresponding positions in the resultant hierarchy. The total number of paired comparisons required to form each hierarchy was also available.

The dominance criterion remained the same for all simulations. Each type of simulation was carried out at least 100 times.

RESULTS

Experience alone

A first series of simulations studied the roles of victory and defeat alone upon hierarchy formation of sets composed of 3 to 10 individuals whose initial *RHP* was initially set at zero. Each victory or defeat was made to bring respectively a random *RHP* increase or decrease to individual *RHP*s. These values were sampled from random normal distribution $N(1, .5)$. At each round, assessment was made to be accurate, i.e., the true momentary *RHP* values were used by the protagonists to decide upon which animal of the pair would obtain victory at that given round. The dominance criterion was 6 consecutive victories.

The results were extremely neat and the same for all sets: they all structured invariably into perfectly transitive hierarchies. Fig. 1 illustrates the structuring of one set of 10 individuals over the 271 rounds that were required to obtain all $n*(n-1)/2$ dominance relationships. Each line of Fig. 1 represents the trajectory of momentary values in *RHP* for one individual over the successive rounds. On each line nine small squares can be found. Each square marks the round at which the dominance criterion was reached by that given individual toward another of the nine opponents. Filled squares represent dominance, while open ones represent submission. A filled square on the trajectory of a dominant animal is placed vis-à-vis an open one on the trajectory of its corresponding submitted opponent. It is the total number of filled squares (i.e., cases of dominance) present on each trajectory which determines the rank order of individuals in the hierarchy, and not the *RHP* value reached by the individual at the end of its trajectory when social stability is reached.

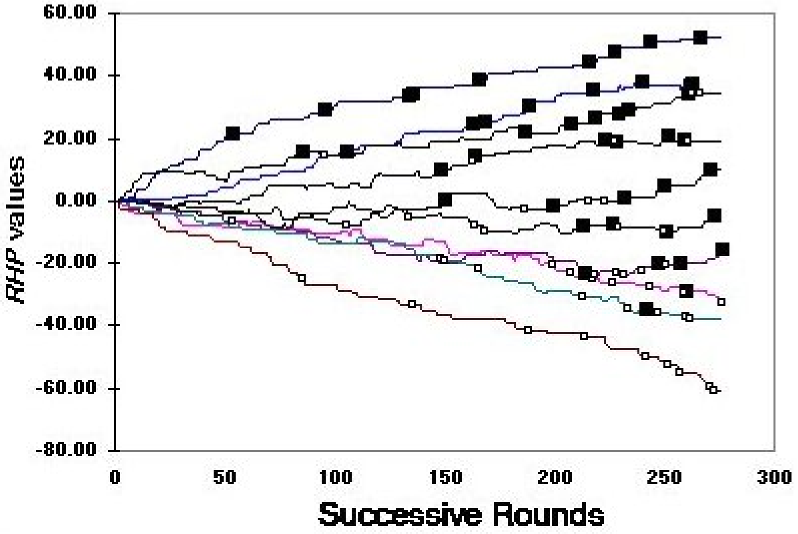

Figure 1. Trajectories of *RHP* values toward perfect linearity in a set of 10 individuals forming a hierarchy. All simulated individuals started with a *RHP* of 0. The structuring required 270 pair encounters or *rounds*. Assessment of the opponent's *RHP* was accurate and victory and defeat contributed to random changes in *RHP* sampled from distribution N(1, .5). Squares which are placed vis-à-vis on the various trajectories indicate the round at which the dominance criterion was reached for this individual against another. Filled squares indicate dominance and empty ones, submission.

Another series of simulations examined whether victory or defeat alone could lead to the same kinds of hierarchies as when both experiences contributed. The parameters were set as before, except that in some simulations victory brought no change in *RHP* while defeat decreased *RHP* by a value sampled from distribution *N*(1, .5). In other simulations, it was the reverse: victory increased *RHP* by *N*(1,.5) while defeat did not diminish *RHP*.

Again, the results are extremely clear: all sets of 3 to 10 individuals formed perfectly linear hierarchies. Final *RHP*s were all positive or negative depending upon which aspect, victory (Fig. 2-a) or defeat (Fig. 2-b) contributed to *RHP*.

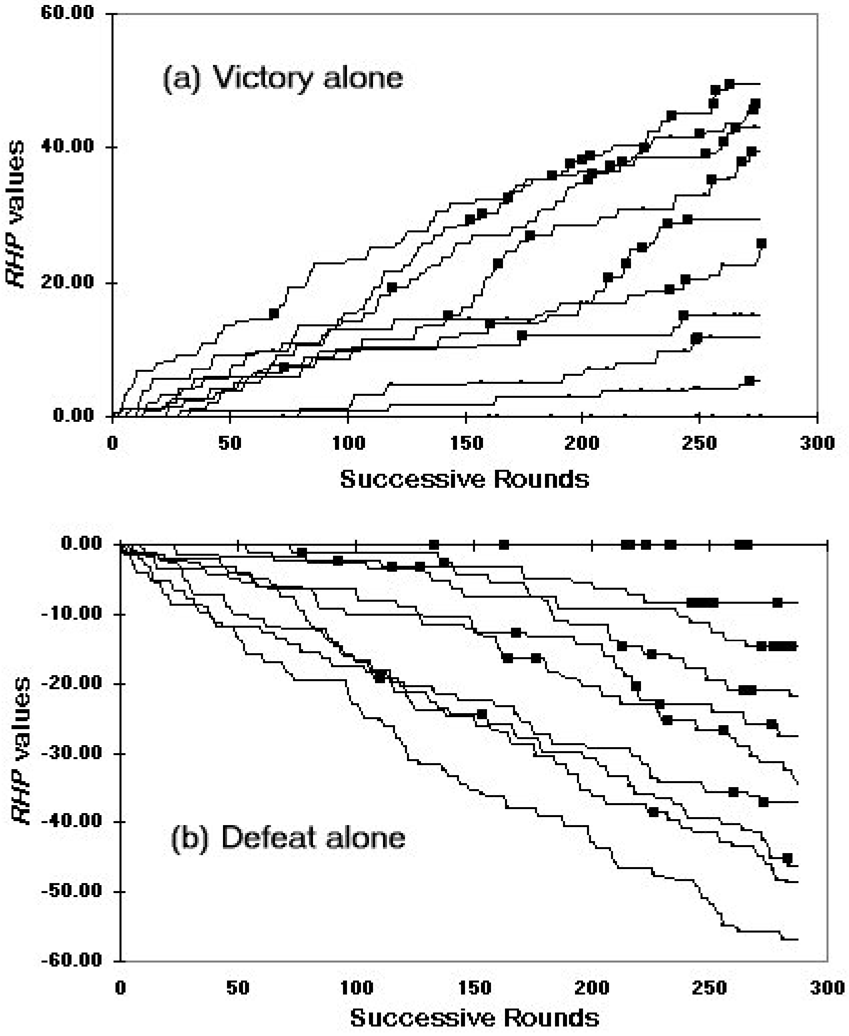

Figure 2. Trajectories of *RHP* values for 10 individuals forming a perfect hierarchy when only victory (a) or defeat (b) brought changes in *RHP*.

Errors in assessment

Errors in assessment of respective *RHP*s were then introduced. Within a set, initial *RHPs* were affected randomly according to normal function *N*(100, 50). Victory or defeat brought a random *RHP* increase or decrease in individual *RHP*s; their values were independently and randomly sampled from normal distribution *N*(1, .5). The dominance criterion was the same as in the previous simulations, i.e., 6 consecutive victories. Sets of 6 animals were simulated 100 times each. Initial error in *RHP* assessment was made to vary from 0 to 300% by steps of 50%. As previously explained, error made on the first encounters was made to decrease as the same opponents repeatedly met again.

Fig. 3 illustrates errors in assessment made on the average by the individuals of the 100 simulated sets when initial error was set to 300%. As can be seen, while the errors in assessment were on the average extremely important on the first encounters, they rapidly regressed to the true momentary value as the same opponents met again. Errors made by a given pair of individuals through the 12 successive rounds are also illustrated on Fig. 3.

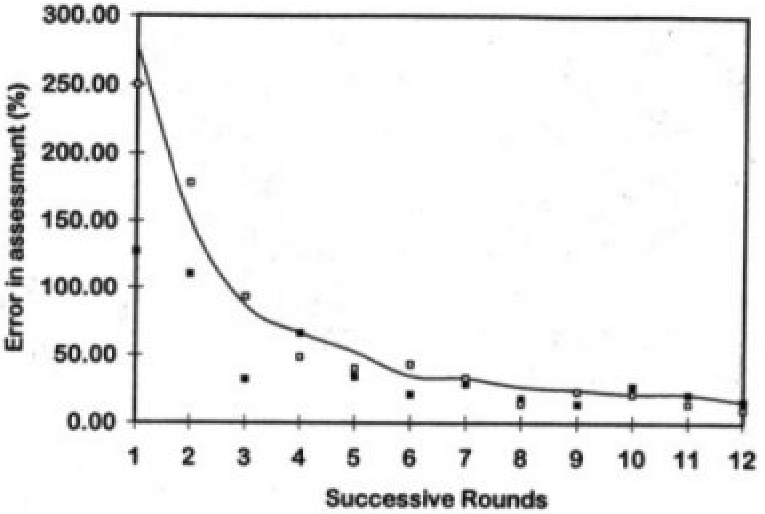

Fig. 3. Mean error in assessment as opponents repeatedly met. Based on 100 sets of six animals where mean initial error percentage was set at 300%. Squares represent assessed values made by a given pair of opponents. Filled squares: future dominant of the pair; empty squares: future subordinate.

Even with important errors of assessment, all simulated structures systematically resulted into perfectly linear and transitive dominance orders. The correlation between initial *RHP*s and the obtained ranks was not affected by initial error level within the range of errors studied when victory or defeat brought random *N*(1, .5) changes in *RHP*. The Kendall of correlation varied on the average between 0.967 and 0.978 but was not systematically associated with the level of initial assessment error.

Relationships between the parameters

We then examined the relative importance of initial values in *RHP*s with respect to modifications in *RHP* brought by successive victories and defeats under conditions of accurate or inaccurate assessment. This was done by noting the correlation between initial individual *RHPs* and the corresponding rank reached by the individuals in the resultant hierarchy while varying the importance of the effects introduced by successive victories and defeats. Only groups of 6 subjects were simulated and their initial *RHPs* were made fixed as balanced series -30, -20, -10, 10, 20, 30. Victory and defeat brought random values normally distributed *N*(*m*, *sd*) with a mean *m* varying from 0 to 100 by steps of 5 and a *sd* equal to half the mean. Two conditions of assessment were examined, one in which it was accurate, and another one in which initial error was set at 100% attenuated as repeated rounds occurred.

For each set of 6, the correlation (Kendall) between initial *RHP*s and resultant rank order was calculated.

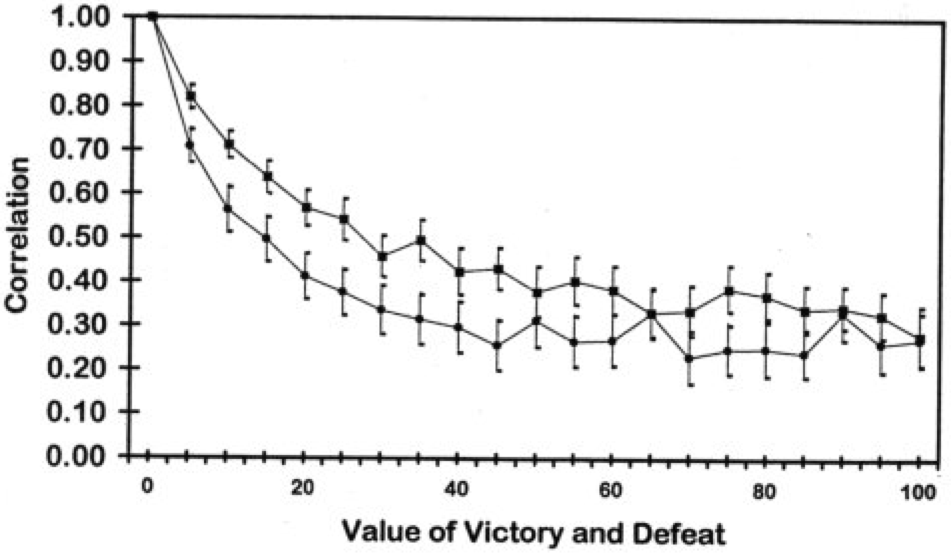

Fig. 4. Correlation between initial RHP values and rank in the resultant hierarchy as a function of importance of changes in RHP brought by victory and defeat. These values were independently and randomly sampled from *N*(mean, S.D.) distributions, where mean varied between zero and 100 units in RHP by steps of five, and S.D. = 0.5 mean. Filled squares correspond to accurate assessment, and circles to 100% error in initial assessment. 95% confidence intervals are indicated.

Under conditions of accurate assessment all 2100 resultant hierarchies were perfectly linear. Under 100% error in assessment, one out of the 2100 resultant structures was circular, with a Kendall K index of 0.886. The values of victory and defeat were on this occasion 100 *RHP* units. The obtained individual score structure was in this case 5:4:3:1:1:1. We have tried to replicate this results by repeating the simulations 1000 times but all sets ended up structured into perfectly linear hierarchies. It suggests that the probability of obtaining circular structures under these conditions is real but extremely low.

Fig. 4 illustrates the mean correlations between initial *RHP*s and rank orders in the resultant hierarchies as more importance was given to victory and defeat. As could be expected, initial individual differences in *RHP*s alone (when victory and defeat did not bring any change in *RHP* and assessment was accurate) led to hierarchies in which the correlation between initial *RHP*s and final rank was perfect. This corresponds to the first point on Fig. 4. When assessment was initially highly inaccurate (100% error in assessment) but victory and defeat did not contribute to *RHP*, the correlation between initial *RHP*s and rank orders was also perfect. Fig. 4 also illustrates that, under both conditions of assessment, increasing the relative importance of victory/defeat contribution to *RHP* as compared to that of initial *RHP*, had for effect to decreased the correlation between initial *RHP* and rank order in the resultant hierarchy. Confidence intervals at 95% on Fig. 4 overlap, indicating that the two corresponding correlation distributions were not statistically significant.

With 6 individuals, the Kendall rank-order correlation coefficient must be larger than 0.733 to be statistically significant at *P*<.028 (Table R*i*, Siegel and Castellan, 1988). Thus, in the present simulation, the influence of the balanced *RHP* series "30, 20, 10, -10, -20, -30" could be neutralized by changes of approximately 10 *RHP* units (or more) brought together by victory and defeat.

We further examined this aspect in a series of simulation where initial *RHP* was normally distributed around a mean of 100, and standard deviation increased from 5 to 50 by steps of 5. In these simulations, victory and defeat also brought changes in *RHP* normally distributed *N*(*m*, *sd*), where *m* increased from 5 to 20 by steps of 5, and *sd*=.5*m*. These 40 conditions were simulated under accurate and 100% error of assessment for sets of 6 simulated individuals, each replicated 100 times.

All 8,000 hierarchies of 6 individuals came out perfectly linear. Fig. 5 illustrates the relationship between *RHP* dispersion, value of victory and defeat, and error of assessment in regards to the correlation between initial *RHP* and rank order in the resultant hierarchy. The lower the variation within initial *RHP*s, the lower the correlation between initial *RHP*s and ranks in the hierarchy. At a given level of initial *RHP* dispersion (*sd*), increasing the contribution of victory and defeat to *RHP* diminished the correlation between initial *RHP*s and obtained ranks. In addition, inaccurate assessment reduced the overall correlation, especially when dispersion of initial *RHP* values was low and the contribution of victory and defeat was high.

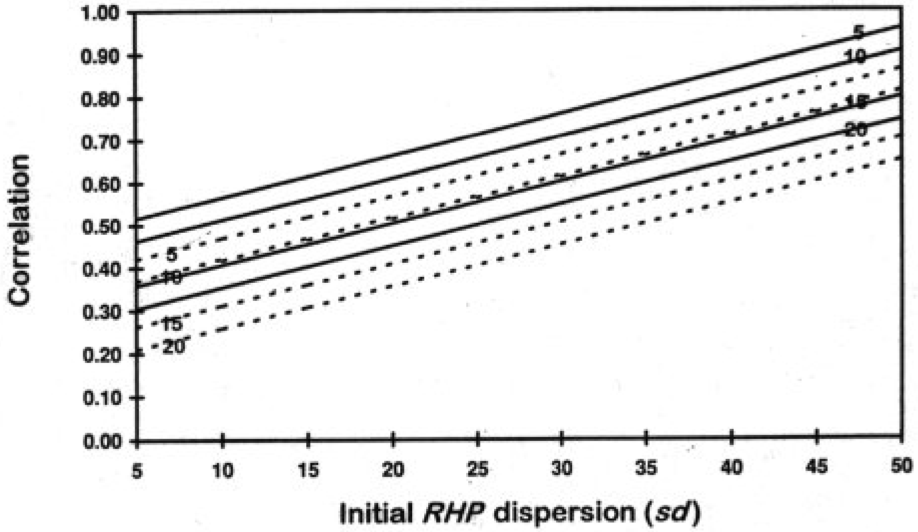

Fig. 5. Correlation between initial RHP values and ranks in the resultant hierarchy as a function of: (1) the importance of dispersion (S.D.) of initial RHP values where varied from 5 to 50 (the abcissa); (2) changes in RHP brought by victory and defeat (5, 10, 15 and 20 RHP units) and (3) initial error in assessment (0, 100%). Value of victory and defeat is indicated on each line. Heavy lines correspond to accurate assessment, while dashed ones to 100% error in initial assessment.

Table 1 illustrates one case of 6 individuals forming a perfectly linear hierarchy. In this case, the correlation between initial individual *RHP*s and final *RHP*s was rather poor (=0.33). Furthermore, the ranks of individual based on their dominance score, i.e., on the number of individuals each dominated in the final hierarchy, did not perfectly coincide for individuals C and D with their ranking according to their final *RHP* (=0.87). This is accountable by the fact that, once the dominance criterion was reached for that pair, their respective *RHP*s changed due to their meeting with other members of the group.

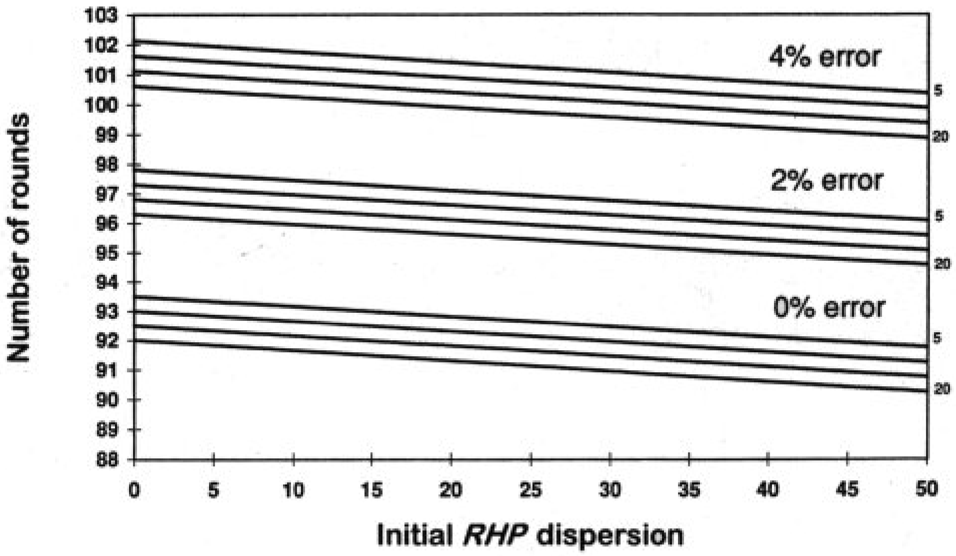

Fig. 6. Number of rounds required to form hierarchies as a function of: (1) dispersion of initial RHPs *N*(100, S.D.), where S.D. varied from zero to 50 in steps of five (on the abcissa); (2) changes in RHP brought by victory and defeat (5, 10, 15 and 20 RHP units); (3) error in assessment with three levels: 0 (accurate assessment), 2 and 4%.

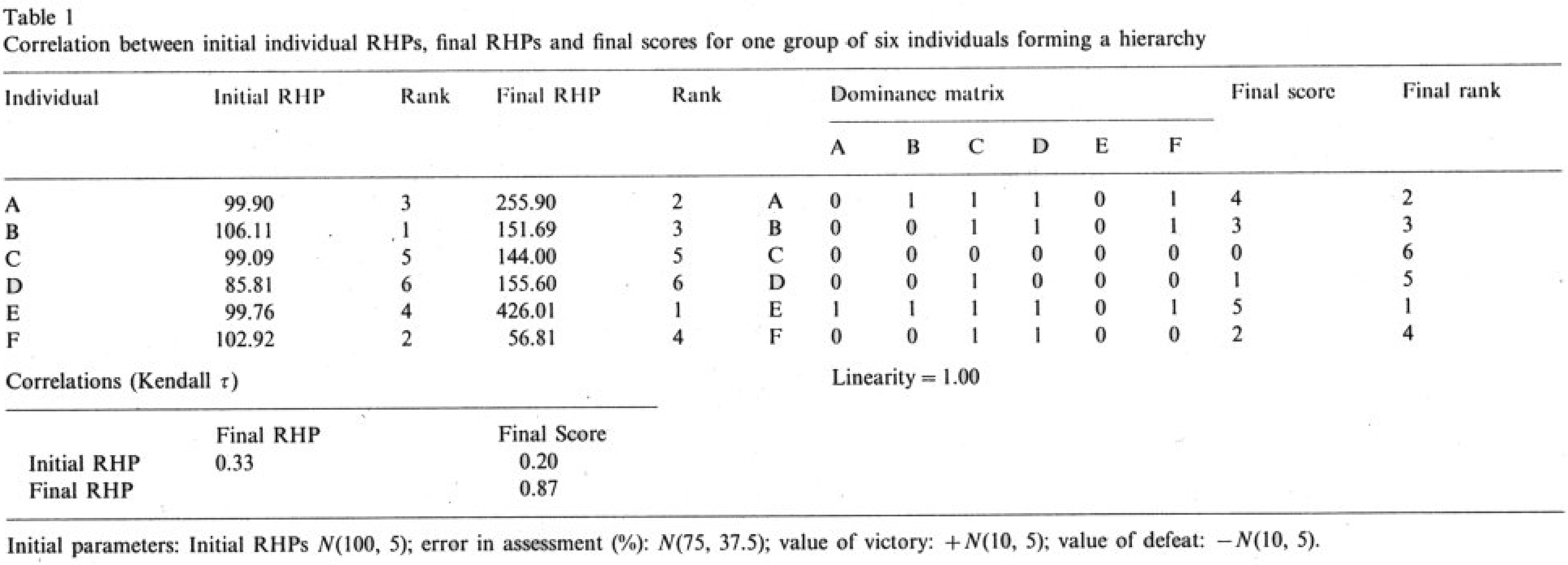

Table 1
Correlation between initial individual RHPs, final RHPs and final scores for one group of six individuals forming a hierarchy

Individual	Initial RHP	Rank	Final RHP	Rank		Dominance matrix						Final score	Final rank
						A	B	C	D	E	F		
A	99.90	3	255.90	2	A	0	1	1	1	0	1	4	2
B	106.11	1	151.69	3	B	0	0	1	1	0	1	3	3
C	99.09	5	144.00	5	C	0	0	0	0	0	0	0	6
D	85.81	6	155.60	6	D	0	0	1	0	0	0	1	5
E	99.76	4	426.01	1	E	1	1	1	1	0	1	5	1
F	102.92	2	56.81	4	F	0	0	1	1	0	0	2	4

Linearity = 1.00

Correlations (Kendall τ)

	Final RHP	Final Score
Initial RHP	0.33	0.20
Final RHP		0.87

Initial parameters: Initial RHPs $N(100, 5)$; error in assessment (%): $N(75, 37.5)$; value of victory: $+N(10, 5)$; value of defeat: $-N(10, 5)$.

Determinants of the required number of "rounds"

In the present study, the number of pair encounters required by a given group to complete hierarchy formation could serve as an index of the "cost"

implied, given the value of various aspects that could affect the momentary value of individual *RHP*s. Three parameters were thus varied in a further simulation: (1) dispersion (*sd*) of initial *RHP*s sampled from a $N(100, sd)$ distribution, with *sd* passing from 0 to 50 in steps of 10; (2) value of victory and defeat, sampled from distribution $N(m, .5m)$ where *m* passed from 5 to 20, and (3) error in assessment obtained by randomly sampling from distribution $N(m, .5m)$, where *m* increased from 0 to 100% in steps of 2%. The resulting number of rounds was then analysed using multiple linear regression. Figure 6 illustrates the effects for 0%, 2% and 4% of %er values only, but they are representative of other levels of assessment error levels. Keeping assessment error and value of victory/defeat constant, increasing variability within initial *RHP*s slightly but significantly decreased (T=-9.732, P<0.001) the total number of rounds required to obtain a hierarchy. At a given level of initial *RHP* dispersion and for a given error level in assessment, increasing the importance of victory and defeat significantly decreased (T=-9.466, P<0.001) the number of required rounds.

Finally, given a level of RHP dispersion and contribution to *RHP* by successive

victories and defeats, increasing error in assessment increases (T=12.453, P<0.001) the number of required rounds to reach complete hierarchy. Examining weights of the resultant regression model, error in assessment seemed to be the most important factor affecting the number of rounds (=.238), followed equally by *RHP* dispersion (=-.186) and contribution of victory and defeat (=-.180).

Thus, factors which contributed to momentary differences in *RHP* between individuals, also diminished the number of encounters which were required for a group to form a complete hierarchy. Table 2 presents a synopsis of the results obtained by this research.

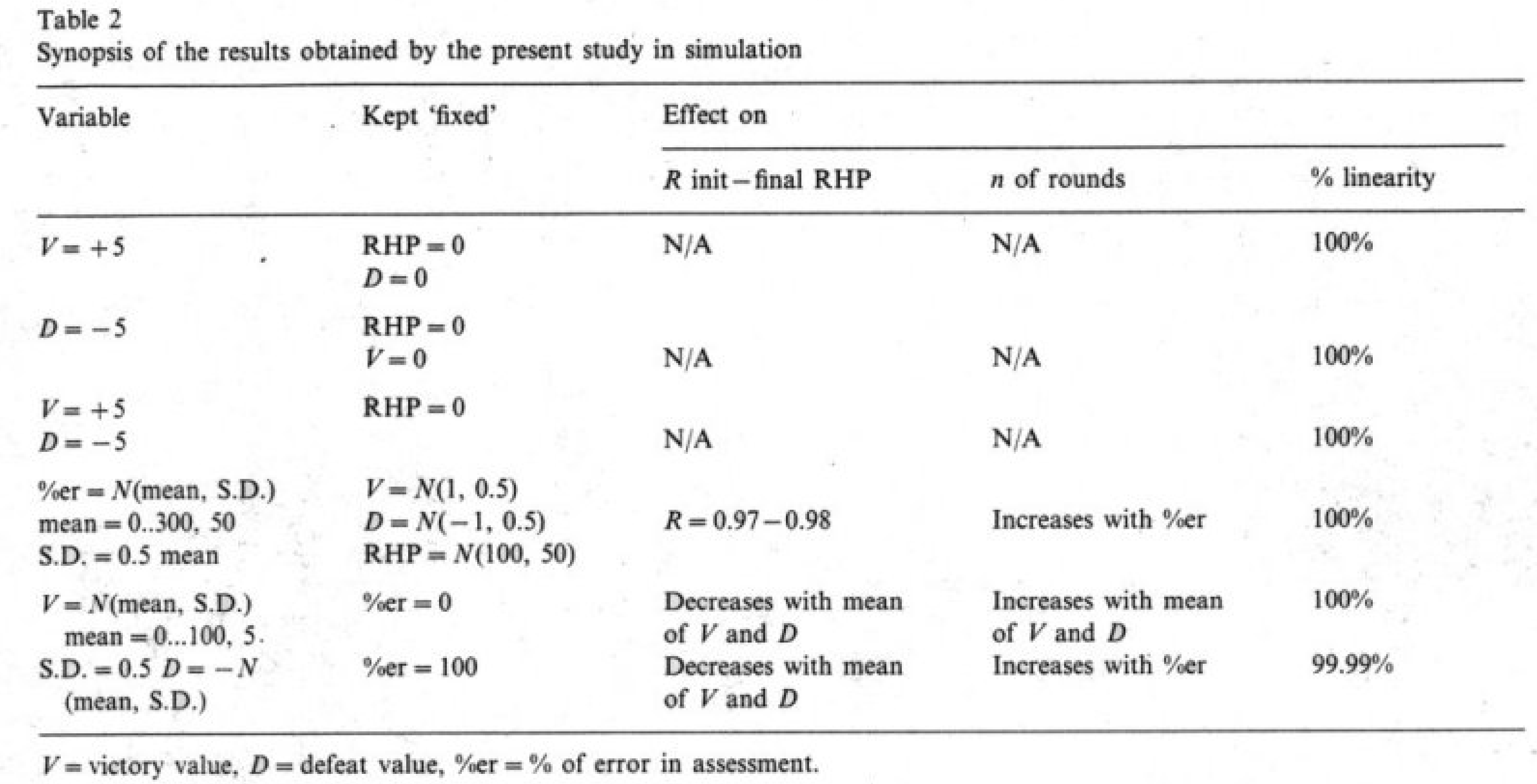

Table 2
Synopsis of the results obtained by the present study in simulation

Variable	Kept 'fixed'	Effect on		
		R init – final RHP	n of rounds	% linearity
$V = +5$	RHP $= 0$ $D = 0$	N/A	N/A	100%
$D = -5$	RHP $= 0$ $V = 0$	N/A	N/A	100%
$V = +5$ $D = -5$	RHP $= 0$	N/A	N/A	100%
%er $= N$(mean, S.D.) mean $= 0..300, 50$ S.D. $= 0.5$ mean	$V = N(1, 0.5)$ $D = N(-1, 0.5)$ RHP $= N(100, 50)$	$R = 0.97 - 0.98$	Increases with %er	100%
$V = N$(mean, S.D.) mean $= 0...100, 5$. S.D. $= 0.5$ $D = -N$ (mean, S.D.)	%er $= 0$	Decreases with mean of V and D	Increases with mean of V and D	100%
	%er $= 100$	Decreases with mean of V and D	Increases with %er	99.99%

V = victory value, D = defeat value, %er = % of error in assessment.

DISCUSSION

The present simulation shows that several aspects alone or in combination with each others can lead to the formation of perfectly linear hierarchies. Landau (1951a, 1951b) had shown that initial individual differences when they were used by animals to sort themselves out led to perfectly linear hierarchies. The present simulation confirms this: initial differences in *RHP* always lead to perfectly transitive chains in which rank order reflects the importance of initial differences. Even when simulated animals make important errors while assessing each other during round robin tournaments, emerging dominance structures are perfectly linear while ranks obtained in the structure are highly correlated with initial values in *RHP*s.

The present simulations also show that accumulated experiences of victory or defeat alone, or their combination always leads to perfectly linear hierarchies. Their combination with initial individual differences in *RHP* led to the same conclusion. Again, even when assessment was far from being accurate, not only were perfect chains obtained but initial values in *RHP*s significantly influenced rank order when the contribution of victory and defeat to *RHP* was relatively unimportant.

We consider that the modalities of assessment we have simulated were realistic. Simulated animals meeting for the first time made important errors in assessment (up to 588% in some cases). As they repeatedly met --in nature they would in addition probably learn from seeing their opponents meet other rivals-- the assessment of their rival's *RHP* gradually moved toward its true momentary value by making 50% less error on the average at each subsequent meeting. We have verified through simulations not reported herein that decreasing the slope at which estimated *RHP* moved toward the true momentary value of the rival's *RHP* did not change the end result concerning the linearity of resultant structures. Even when simulated animals continued to make on the average 25% of assessment error by the end of the tournament, perfect linearity of the hierarchies was always reached. Above 30%, some dominance relationships never reached the dominance criterion even after 100 rounds, consequently simulation had to be abandoned due to the oscillation of victories from one opponent to the other.

The present simulation also illustrates the possible relationship between initial individual differences in *RHP* , victory, and defeat experience. We assumed that victory and/or defeat brought changes in individual *RHP*s. The greater this contribution was in comparison to that of initial *RHP* values, the smaller was the correlation between initial *RHP* values and the rank order reached by individuals in the resultant hierarchies (see Fig. 4). Moreover, as can be seen in Fig. 5, the higher the variations within individual *RHP*s, the smaller changes in *RHP* caused by successive victory and defeat affected the correlation between initial *RHP*s and rank order in the hierarchies. Inaccurate assessment further contributed to decrease the correlation between initial *RHPs* and rank order, especially when dispersion of initial *RHP* values was low and contribution of victory and defeat was high.

Such results obtained by simulation are perfectly coherent with our interpretation of the apparent contradiction between the empirical results obtained in this research unit (e.g., with hens: Cloutier et al., 1996; with fish: Beaugrand and Cotnoir, 1996) and those obtained by Chase (1982b) with hens. Cloutier et al. (1996) and Beaugrand and Cotnoir (1996) have introduced important individual differences between animals in contests leading to the formation of triads. Their conclusions was that initial individual differences not only determined the positions in the resultant hierarchies but they also influenced the order in which animals met each other. Being convinced for theoretical and empirical reasons that individual differences could not account for hierarchy formation in animals (e.g., Chase, 1974), Chase (1982a, b) did not systematically vary initial individual differences. On the contrary, he took much care to neutralize nuisance variables such as those due to previous encounters and to equalize individual differences. These rigorous controls contributed to maintain homogeneity in individual differences within the sample of hens. Even the residual individual variations that remained were not put into correlation with obtained dominance statuses. Thus it is no surprise that in the studies of Chase (1982a, 1982b) patterns of conflict resolutions remained the only salient factor to which observed transitivity could be attributed.

In a natural setting, both initial individual differences and successive victories and defeats probably interact to account for the rank orders in the resultant dominance structure.

Basically, intrinsic properties would determine the victory potential of the individual. However, as soon as encounters begin there is a carry-over effect from previous encounters to following ones. This, in turn, may explain the low correlations between predicted hierarchies based on individual characteristics and observed hierarchies (Jackson and Winnegrad, 1988). When initial individual differences are significant, they may affect the resultant hierarchy in two possible manners. First, individual differences may essentially determine which animals will obtain the first victory or defeat, which in turn will affect their propensity to obtain further victory or defeat. Cloutier et al. (1996) found that when initial individual differences were important, they influenced the order in which agonistic hens resolved conflict. The two hens that possessed the greatest advantage due to initial individual differences chose each other to settle conflict in the first place. In most cases, the winner of this first settlement later encountered the bystander. Such a mechanism of opponent selection probably promotes the acquisition of a higher rank in the hierarchy. Slater (1986) had correctly foreseen such a mechanism. The second mechanism is that when the individual differences are important but fish or hens do not meet simultaneously or are prevented to do so (Cloutier et al., 1996; Beaugrand and Cotnoir, 1996), they still influence the resultant hierarchies because their effects are not sufficiently perturbed or cancelled by successive victories and defeats. A fortiori, when initial individual differences are extremely small as in Chase's experiments, successive victories and defeats essentially shape the resultant structures due to their carry-over effects. As suggested by the results of the present simulation, Chase's developmental model of hierarchy formation based on double dominance and double submissions might well be a special case applying when initial individual differences are small and opponents can freely interact.

The resemblance of Fig. 1 with structures resulting from *self-organization* (Yates, 1987) is striking. Could the emergence of social order within closed systems as those simulated here be a case of self-organization ?

Using the jargon of the domain, one notes first that there is a "forward motion" of pair comparisons among the elements which are part of a homogeneous system which at the start is unstable and disorganized. Some limitation of resource could, for instance, force competition among members and might be at the origin of such an *ordering field*. Comparisons of elements leads to *bifurcations*, i.e., establishment of dominance-subordination relationships, a situation in which homogeneity gets reduced and more structure than there was in the original system emerges. Each new bifurcation violates the symmetry of the previous configuration, and displays more regular patterns.

The idea of explaining morphogenesis as pattern formation was also developed by Kolmogorov et al. (1937) and Rashevsky (1940). The deviations from the undifferentiated state are *self-amplifying* in the sense that past deviations influence future deviations. In the case of animals forming a hierarchy, this influence takes the form of experiences of victory or defeat. A whole system of interacting deviations emerges as ordered, and differentiated states. Such a self-organizing system has an inherent tendency to move toward a stationary state. It can do so because the state of each element is only slightly modified by interactions with other elements. Once the stationary state is reached, large changes of state will need times that are much longer than the time required for a single interaction with any other element. Thus, an element can change its state drastically (i.e important raise or drop in the hierarchy) only after having interacted with a considerable part of the network, which takes much time. In addition, the state of a given element shows great remanence because its state is constantly validated and reinforced by other interactions which act coherently in the same direction. In so doing, elements which occupy a higher position in the structure than that of a given element give the appearance that they *cooperate* to keep the latter in its lower status. A particular configuration will reach stationarity only if all interactions within the network reproduce the configuration from moment to moment. This can be insured by the remanence mechanism just mentioned which corresponds in our animals, to their capacity to memorise past experiences and to associate these specific experiences with specific opponents. In other words, they are capable of "individual recognition".

The remarkable ability of animals to form true hierarchies as simulated in the present research might thus be a natural and inherent property of any self-organizing system. Since natural social structures are not *always* perfectly linear, a comparison of simulated conditions with that occurring with true animals might give some clues on the factors leading to intransitivity.

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