The role of individual differences and patterns of resolution in the formation of dominance orders in domestic hens triads

Sylvie Cloutier [*, a], Jacques P. Beaugrand [a] and Paul C. Laguë [b]

[a] *Unité d'Éthométrie, Département de Psychologie de l'Université du Québec à Montréal, CP 8888, Station Centre-Ville, Québec, H3C 3P8, Canada*

[b] *Department of Animal Science, Macdonald Campus of McGill University, 21 111 Lakeshore Road, Sainte-Anne de Bellevue, Québec, H9X 1C0, Canada*

_____

* *Corresponding author.*

Email: mailto:rana@uqam.ca

Abstract

This research compares the role of initial individual characteristics to that of patterns of resolution in which successive dominance relationships are established during the formation of triads in the domestic hen. Combining weight, prior victory or defeat in the site of encounter, and comb size, we created three levels of asymmetries on characteristics for triads of hens. The effects of these asymmetries were then examined on the resultant hierarchies and on the order of conflict resolution within triads under two different conditions of assembly. In one condition (simultaneous triad), the three hens were simultaneously introduced to each other and could thus freely choose their opponent. In the other condition (step-assembled triad), the hen predicted to occupy the highest rank was left on standby and introduced once the two other hens had settled dominance, thus disrupting the normal process of hierarchy formation by imposing the first sequence of dominance settlement. We found that the structure of triadic hierarchies can be predicted from individual characteristics existing prior to hierarchy formation. No differences in the resultant structures were found between conditions of introduction, though different paths of conflict resolution were followed indicating that individual differences had a more determining role on the resultant hierarchies than patterns of resolution. Beside showing that individual differences determine resultant triadic structures, the present results also show that the same end structures can be reached by following resolution paths that are not necessarily of the Double Dominance and Double Subordinance types as prescribed by Chase's model. It is also found that in the simultaneous condition hens select each other to form pairs. Therefore, individuals do not meet at random but choose each other as opponents. The two hens predicted from individual differences to occupy the highest ranks first settle dominance, followed by settlement between the winner of the

previous encounter and the bystander.

Key words: dominance hierarchy; prior experience of victory and defeat; size; individual differences; agonistic behaviour; hen; *Gallus domesticus*

Introduction

Previous studies attempted to explain the structural form of dominance hierarchies using differences in individual characteristics such as aggressiveness, size, hormone levels, past social experience or differences in pair-wise competitive abilities. However, analytical work by Landau (1951a) and Chase (1974), and experimental evidences (Bernstein and Gordon, 1980 and King, 1965 in Chase 1982a) indicate that individual differences cannot fully account for hierarchy structures. In order to account for the lack of correlation between initial characteristics and resultant rank in the hierarchy structure, Chase (1982a, 1982b) proposed a model, the *jigsaw puzzle*, which stipulates that hierarchy formation is a developmental process where preceding dominance interactions influence succeeding ones. Since evidences indicate that individual differences are not strong enough to explain the structure of common hierarchies they were not considered in Chase's model.

Although examination of patterns of resolution in several species has confirmed that the two patterns of resolution insuring transitivity and promoting linear structure were the most common (Chase, 1980, 1982a, 1982b, 1985; Mendoza and Barchas, 1983; Barchas and Mendoza, 1984; Eaton, 1984), Slater (1986) was not convinced by the importance given by Chase's results to patterns of resolution. He still argues that individual differences do play a more important role in hierarchy formation and that they should not be put aside. He argued that individual differences alone, on any feature that correlates with winning or losing in aggressive encounters, could lead to the form of structure obtained by Chase's model (Slater, 1986). However, Slater did not provide any empirical evidence to confirm his hypothesis.

Beaugrand (1984) and Jackson (1992) suggested that individual differences played a role at the beginning of the process of hierarchy formation but that sequences of victories and defeats introduced additional differences modifying the probability of an individual to win or lose future contests. This accounted for the poor correlation between initial characteristics and resultant ranks.

Beaugrand and Zayan (1985) showed that individual differences could be used to predict and account for dominance outcomes in dyads of *Xiphophorus* fish. They found that prior experience of victory and defeat were one of the major determinants of dyadic outcome. In encounters involving more than two individuals these experiential factors could correspond to a carry-over effect from successive encounters. Besides being tested on fish, each factor suggested by Beaugrand and Zayan's model was also found to significantly contribute to dominance hierarchies in dyads of domestic hen as well (Zayan, 1987; Cloutier et al., 1995). The evidence so far indicates that similar factors and mechanisms could account for the formation of triadic dominance structures in hens.

This study compares the role of initial individual differences to that of sequences of conflict resolution in triads of domestic laying hens. By varying the differences in characteristics between individuals in the context of hierarchy formation it could be possible to evaluate the importance of individual differences on the dynamic process of hierarchy formation. To achieve our goal, we made predictions based on initial individual differences known to determine dominance outcome in dyadic encounters. We created three levels of asymmetries of characteristics by varying weight, prior victory or defeat in the site of encounter, and comb size in three hens to form a hierarchy. We then studied those factors under a condition of «simultaneous assembly» in which the triadic hierarchy was obtained by simultaneously introducing the

three hens to each other. In order to evaluate the relative importance of individual differences compared to order of assembly, a control group, in which the individuals were assembled in step, was used. In this «step assembled» condition, the hen, which was predicted from individual differences to occupy the top ranking in the triad, was kept on standby while it watched the other two hens first encountering each other. The hen on standby was introduced to them once they had settle dominance.

The results of previous studies on dyadic encounters of hens and fish were used to derive the following postulates upon which are based our predictions:

P_1. The individual with experience of dominance, whether familiar or not with the site, should defeat an individual that experienced subordination in the site of the actual encounter (Cloutier et al., 1995).

P_2. Given an equivalent social experience, the individual with larger comb size should defeat an individual with smaller comb size (Allee et al., 1939; Collias, 1943; Guhl and Ortman, 1953; Zayan, 1987; Ligon et al., 1990).

P_3. Given an equivalent social experience, the individual with a great weight advantage should defeat a lighter opponent. Although not clearly established in chicken, this regularity was repeatedly confirmed with fish and mammals (Beaugrand and Zayan, 1985; Beacham, 1988; Beaugrand et al., 1991; Locati and Lovari, 1991).

On the basis of those postulates, we defined a first hen as a prior alpha (**A**), i.e. having previously won an encounter, of large weight and large comb; a second hen as a small alpha (α), i.e. having previously won an encounter but of smaller weight and comb size than an **A**; a third hen as a small omega (ω), i.e. as being of same weight and comb size as an α but having previously lost in the site to be the meeting place of the three hens.

The first objective of this study was to demonstrate that initial individual differences determine resultant triadic structures. Based on the three postulates presented above, we predicted that the most frequently obtained structure would be of the type **A**>α>ω; the sign ">" means the agonistic dominance of the first individual over the next one(s) in the chain.

Our second objective was to show that individual differences determine which individual uses the patterns of resolution of conflicts. In order to satisfy our prediction on the resulting hierarchy, **A**>α>ω, one had to predict, for the simultaneous condition, that the large **A** should dominate the other two hens whereas the ω should submit to **A** and α. In the step condition, after the dominance of α to ω, we predict that **A** should dominate both hens or dominate ω and submit to α.

A third objective was to determine if sequences of conflict resolution affect the structure of the resulting hierarchy and if their effect outweighs that of initial individual differences. The use of two conditions of introduction will enable us to gauge the importance of the order of interaction between individuals and that of initial individual differences in the process of hierarchy formation. Dominance of two individuals by a third insures transitivity of the hierarchy, even when the third relation of the triad is not established, but it is possible only if the individual to occupy the highest rank has the possibility to interact first. Therefore, in order to disrupt the behavioural sequences under the step-assembled condition, we introduced the large **A** last once the conflict between α and ω was resolved. If individual differences are more important than sequences of assembly then similar triadic structures should be obtained under both conditions of assembly.

Methods

Subjects and material

The hens used were selected among 150 «French» hens, a local bred flock of the Red Rock x Light Sussex. Each hen was identified with a numbered coloured plastic leg band. The hens were raised in six deep litter pens (2.4 x 3.2 m), containing 25 hens each. Feed and water were available *ad libitum*. The hens were submitted to 14 hours of light dayly.

The encounters were carried out in a specially designed cage made of a central unit (75 x 100 x 100 cm) surrounded by three smaller cages (70 x 75 x 75 cm) where the hens were placed before being introduced into the central cage. The cages were made of wood and fibreglass with an aluminum door. The floor was covered with wood shavings and each cage was lighted with a fluorescent light. Two sets of those cages were used so that two triads could be done simultaneously.

During the experiment, two hens from the same pen were never used in the same triad but a hen could serve in the formation of more than one triad. Two hens used in the same triad did not meet for at least two weeks, based on previous observations showing that after two weeks hens no longer recognize penmates (Chase, 1982a). Each triad in this research can thus be considered as independent from one another.

Measurements

Each time a hen was selected to participate to form a triad, its weight was taken with an electronic scale having a sensitivity of one-hundredth of a gram. We also took a colour photograph of its head to obtain comb area and colour. Colour print photographs (35 mm Kodak film Gold, ASA: 100) were taken with a constant light source and from the same distance. Comb area was measured from each photograph with a planimeter with a precision of 0.1 cm^2. Comb colour was also obtained from the photos, applying the Munsell system. The average of two valid independent measurements was taken as an evaluation of the true value. For each triadic encounter, we recorded the order of introduction and of encounter as well as the outcome of the encounter between the three hens. The encounters were also videotaped, and the tapes were later used to confirm the results, when necessary.

Research outline

We tested and compared two situations: one in which the individuals were introduced at the same time (simultaneous) and one in which they were introduced in sequence (step-assembled). We formed 31 and 21 triads for the simultaneous and step-assembled conditions, respectively.

For each condition the experiment was divided into two phases that were performed on the same day. In the first phase, the hens acquired social experience of victory or defeat during a period lasting for a maximum of 3 h. One observer simultaneously watched six dyads. A total of 171 dyads were realized to form the triads. The dyads were completed in both the peripheral and central cages. All dyads were randomly assigned to one of the cages. Since Cloutier et al. (1995a) recently showed that experience of submission is site dependent, the encounters realized in the central cages served to obtain subordinate (ω) individuals that needed to acquire their recent subordinate experience in the same site as the future encounter. Dyads realized in peripheral cages served to obtain the two dominant individuals (**A** and α). Once the hens were accustomed to her presence, the observer simply sat quietly in front of the cages.

Secondly, the hens selected from the dyads were placed in peripheral cages in isolation for 15 minutes before being introduced by the observer into the central cage for the triad. Meanwhile, the other hens were immediately returned to their respective home pen. In the case of the simultaneous triads the hens were introduced at the same time in the central cage. In the step-assembled triads, the bystander stayed in its

peripheral cage separated from the central cage by a screened door through which it could see the other two hens interacting in the central cage. Once the dominance criterion was reached by one of the first two hens, the conflict was considered as settled and the bystander was introduced into the central cage to interact with the two others. In the simultaneous triads, when the third relation had not resolved after approximately 1h, we removed the α hen and left the other two hens together for another period of approximately 1h or until the relation concluded, whichever came first. Otherwise, we separated the hens or returned them to their respective pens either as soon as the dominance criterion had been fulfilled or after a maximum of 3h. Injuries that occurred were not lethal to the hens.

For both dyads and triads, an individual was considered as dominant when it delivered three consecutive attacks using any combinations of the following behaviours: peck, jump on or claw (Kruijt, 1964; McBride et al., 1969; Chase, 1980), followed by a 30 minute period during which the subordinate individual did not attack the initiator (Chase, 1980).

Results

One-tailed tests were used when a direction within differences was expected or could be predicted. Otherwise bidirectional tests were applied. When binary categories were tested we used the binomial test or its Z normal approximation when $N>25$. In some cases we indicated the nature of the null hypothesis under test, e.g. H_0: $p=\frac{1}{4}$, where $q=1-p$. Otherwise, the null is $p=q=\frac{1}{2}$. The tests used and their conditions of application are described in Siegel and Castellan (1988).
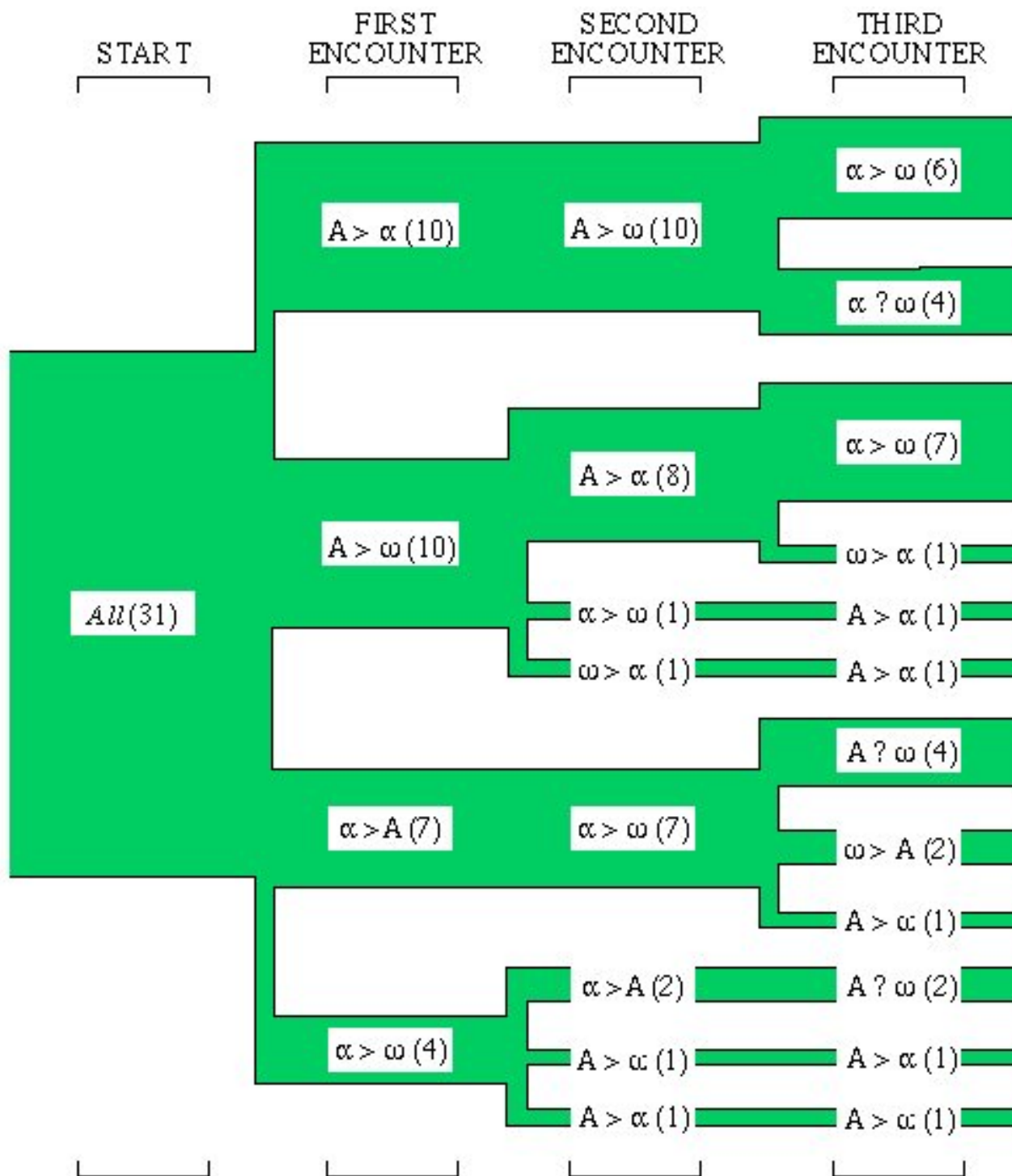
Figure 1. Successive conflict resolutions in triads simultaneously formed. Unresolved dyadic relationships are indicated by a ?
Frequencies are between parentheses.

Fig 1 and 2 depict the sequences in which successive dyads got resolved or not under each condition of assembly. Dominance structures that were noted at least once in the present research are summarized in Table 1 for triads and in Table 2 for dyads. Seventy-nine percent (41 out of 52) of all triadic structures obtained were complete and transitive. No circular structure was noted. Even the 11 structures for which one relationship remained unsettled would have necessarily led eventually to transitive triads, if no role reversal occurred in the meantime. Since transitive triad leads to linear hierarchy structure we considered

that 100% of our triads were potentially perfectly linear and that this is not due to chance since this latter probability of obtaining transitive triads is 75% (H$_0$: p=¾, 52:0, Z=4.003, P<0.001).
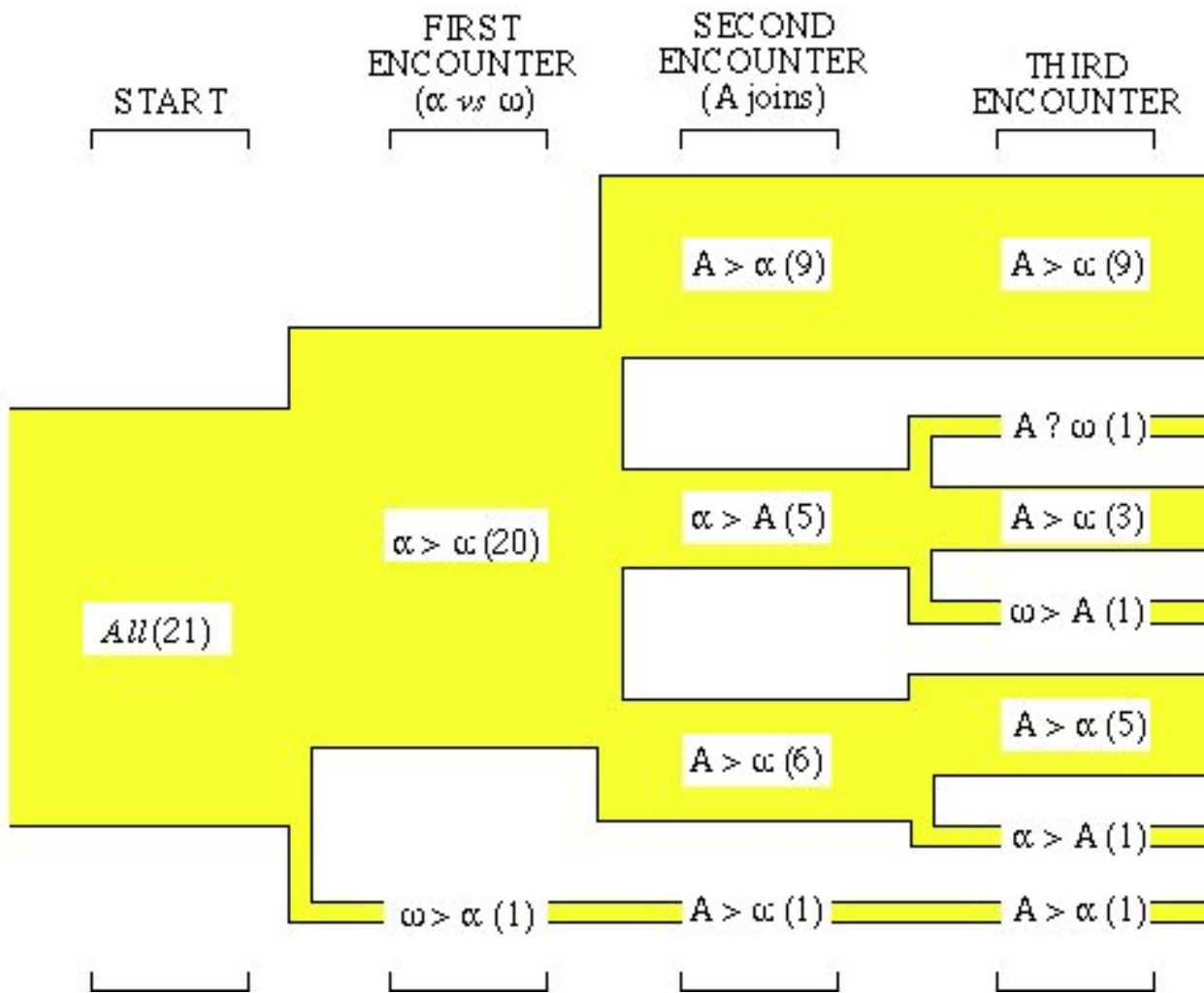

Figure 2. Successive conflict resolutions in triads formed in steps. Unresolved conflicts are indicated by a ? Frequencies are indicated between parentheses.

TABLE 1. Frequency of triadic dominance structures obtained. Undecided relationships are indicated by a **?**

TRIADIC STRUCTURE	CONDITIONS OF ASSEMBLY		
	Simultaneous	**In steps**	**Both**
A>α>ω	16(52%)	14(67%)	30(58%)
A>ω>α	2(6%)	1(5%)	3(6%)
α>A>ω	1(3%)	4(19%)	5(10%)
α>ω>A	2(6%)	1(5%)	3(6%)
A>(α?ω)	4(13%)	*Structural zero*	4(8%)
α>(A?ω)	6(19%)	1(5%)	7(13%)
	31	21	52

TABLE 2. Obtained dyadic dominance structures

DYADIC STRUCTURE	CONDITIONS OF ASSEMBLY		
	Simultaneous	In steps	Both
A>α	22(24%)	15(24%)	37(24%)
A>ω	23(25%)	19(30%)	42(27%)
α>A	9(10%)	6(10%)	15(10%)
α>ω	25(28%)	20(32%)	45(29%)
ω>A	2(2%)	1(2%)	3(2%)
ω>α	1(1%)	1(2%)	2(1%)
A?ω	6(7%)	1(2%)	7(5%)
α?ω	4(4%)	--	4(3%)
	92	63	155

Initial individual differences determine rank.

This research showed that individual differences played a major determinant role on the dyadic outcome and shaped the resulting hierarchies. This happened independently of the order of introduction of individuals (simultaneously or in steps). Indeed, we observe that for both conditions of introduction combined, more than 57% of the triads formed chain **A>α>ω** as predicted from individual differences (Table 1). There are six possible complete structures and each has an equal probability of occurrence under each condition of introduction. Structure **A>α>ω** was more frequently obtained than by chance alone (H_0: $p=1/6$, 16:5, $Z=7.02$, $P<0.001$, for simultaneous triads; and 14:6, $Z=6.1$, $P<0.001$ for in-steps triads; 30:11, $Z=9.92$, $P<0.001$, for their pool). There are also four possible incomplete structures. If both complete and incomplete structures are combined, the probability of obtaining the complete structure **A>α>ω** is 1/10 under both conditions. The fact that 16 simultaneous and 14 step **A>α>ω** triadic structure were obtained while only three and two were expected by chance is also highly significant (H_0: $p=1/10$, 16:15, $Z=7.42$, $P<0.001$, for simultaneous; 14:7, $Z=8.3$, $P<0.001$ for in-step triads).

The examination of dyadic structures summarized in Table 2 also shows that individual differences determine rank order. The small α defeated the small ω more often than the reverse in simultaneous (H_0: $p=½$, 25:1, $Z=4.23$, $P<0.001$) and step-assembled triads (20:1, $Z=3.93$, $P<0.001$). When the two conditions of introduction were pooled, the first postulate was again globally supported (45:2, $Z=6.126$, $P<0.001$).

The comb size advantage, the weight advantage, and the prior victory advantage were confounded effects since together they defined the large **A**. Unless there were interactions between these effects, the combined action of weight and comb size are confirmed by the comparison of victories obtained by the large **A**s over that obtained by the small αs since their prior experience is the same. Comparison of the data obtained under both modes of introduction indicates that large **A**s more frequently defeated small αs than the reverse (H_0: $p=½$, 22:9, $Z=1.7961$, $P<0.02$, one-tail, for simultaneous triads; 15:6, $Z=1.7457$, $P<0.0329$ for step-assembled triads). It was again confirmed when both conditions were pooled (37:15, $Z=2.9122$, $P<0.002$). This result supports the hypothesis that weight and comb size together procure an advantage but the present experiment cannot dissociate their effects. Quite evidently large **A**, which had the triple

advantage of prior dominance experience, weight and comb size, dominated small ω in most cases (H_0: $p=\frac{1}{2}$, 23:2, $Z=4.000$, $P<0.001$ one-tail; 19:1, $Z=3.8$, $P<0.001$; 42:3, $Z=5.6647$, $P<0.001$).

For both types of triads, comb colour was also significantly associated with status (Kendall $=0.208$, $Z=2.92$, $P<0.01$ for simultaneous triads; $=0.294$, $Z=3.23$, $P<0.01$ for step-assembled triads). This implies that individuals possessing darker coloured combs had a definite tendency to defeat opponents having a paler one.

Chase's hypothesis implies that bystanders should occupy the middle position of the triadic hierarchy (Chase, 1982b). In both condition, we have found that bystanders did not end up in the middle of the hierarchy more often than expected by chance (H_0: $p=$, 31:10, $Z=0.127$, ns, for simultaneous triads; 21:4, $Z=1.16$, ns, for step triads). Its rank is more related to individual differences than to order of encounter.

These results thus clearly indicate that individual differences determined rank order, thus supporting the three postulates that allowed us to predict dyadic and triadic dominance structures. They also demonstrate that the effect of individual differences is certainly strong enough to explain hierarchy formation.

Individual differences influence orders of conflict resolution.

It was interesting to verify if individuals choose each other or meet randomly. In the simultaneous condition of this research, hens selected for a triad could choose their opponents. Each pair had an equal probability ($p=$) of getting involved in the first conflict, and each individual, a probability $p=$ of being involved in the first conflict. The large **A** participated in 27/31 (87%) of the first encounters to occur, the small α in 21/31 (68%), and the small ω in 14/31 (45%) as illustrated in Fig 1 for simultaneous triads. The participation of the large **A** hen was thus more frequent (H_0: $p=$, 27:4, $Z=2.23$, $P<0.026$, two-tail) and that of the small ω less frequent (H_0: $p=$, 14:17, $Z=2.349$, $P<0.0192$, two-tail) than explainable by chance alone. However, participation of the small α was not more frequent than by chance alone (H_0: $p=$, 21:10, $Z=0.3168$, ns). Of the 27 cases in which the large **A** was involved in the first conflict, 17 were against the small α and 10 against the small ω. This choice of the large **A** confronting first the small α rather than the small ω is not significant to a binomial test (H_0: $p=\frac{1}{2}$, 17:10, $P=0.25$, two-tail). However, if one assumes that **A**_α pairs had a $p=$ chance to form, these hens selected each other significantly more often than by chance (H_0: $p=$, 17:14, $Z=2.3664$, $P<0.02$, two-tail). Similarly, pair α_ω formed less frequently than by chance alone (H_0: $p=$, 4:27, $Z=2.2225$, $P<0.026$, two-tail).

TABLE 3. Frequency of obtained triadic assembly patterns. **DD**: Double dominance; **DS**: Double subordinance; **BDID**: Bystander dominates initial dominant; **ISDB**: Initial subordinate dominates bystander.

Conditions	Initiator	DD	DS	BDID	ISDB
	A	18	0	1	0
	α	9	0	0	0
	ω	0	2	0	1
		27	2	1	1
SIM		(87%)	(6%)	(3%)	(3%)

STEPS					
	A	0	0	10	0
	α	5	0	0	0
	ω	0	6	0	0
		5	6	10	0
		(24%)	(29%)	(48%)	(0%)
Chase (1982a)		17(74%)	4(17%)	1(4%)	1(4%)

Table 3 presents the order of resolution of conflicts transcribed in the notation developed by Chase in his *jigsaw puzzle* model. Complete as well as incomplete triads are considered in this Table 3. For a good comprehension of the results, the terminology developed by Chase (1980) is recalled here. There are four possible resolution sequences for the first two dominance relationships formed by three animals making a triad. By convention the animal becoming dominant in the first relationship is named **A**, the initial subordinate **B**, and the bystander **C**. After the initial dominance relationship of **A** over **B** (noted >), there are four possibilities: *(1)* **A>C**, the initial dominant dominates the bystander (**D**ouble **D**ominance or **DD**), *(2)* **C>B**, the bystander dominates the initial subordinate (**D**ouble **S**ubordinance or **DS**), *(3)* **C>A**, the bystander dominates the initial dominant (**BDID**), and *(4)* **B>C**, the initial subordinate dominates the bystander (**ISDB**). Of the four possible initial interaction patterns, Chase noted that the double dominance (**DD**) and double subordinance (**DS**) sequences were the most frequently used and always led to perfect transitivity within triads. The other two patterns could result either in transitive or intransitive triads (Chase, 1980). Thus according to Chase's model, linear and near linear hierarchies commonly observed in small flocks of chickens result from a predominance of **DD** and **DS** patterns in triad components of larger groups and are the only ones that guarantee transitivity.

In the present study, the simultaneous condition was characterized by **DD** (27) in accord with Chase's hypothesis. The large **A** initiated 66% of **DD** (H_0: $p=$, 18:9, $Z=3.47$, $P<0.001$), more than its part by chance, followed by the small α (33%). Pattern **DD** occurred more frequently than by chance, as the distribution of the 4 patterns departed highly from a uniform ($p=\frac{1}{4}$) distribution ($Chi^2=70.5$, $df=3$, $P<0.0001$). The present distribution was not statistically different from that obtained in a similar simultaneous condition by Chase (1982a) in chickens ($Chi^2=3.38$, $df=3$, ns).

In the step-assembled triads, as predicted by our second hypothesis, **BDID** and **DS** were the most frequently observed patterns. They were respectively initiated by the large **A** and the small ω. The only **DD**s noted were initiated by the small α. This distribution is statistically different from a uniform one ($Chi^2=8.14$, $df=3$, $P<0.05$) and also from that obtained by Chase (1982a) ($Chi^2=14.26$, $df=3$, $P<0.01$). Evidently, the four types of sequences were not equally realized under the two conditions of assembly ($Chi^2=27$, $df=3$, $P<0.001$).

Considering that essentially similar triadic dominance structures (e.g. **A>**α**>**ω) were generated by both conditions of assembly ($Chi^2=0.84$, $df=3$, ns) but through significantly different paths of conflict resolution, the hypothesis that conflict resolution sequences *per se* or alone produce the resultant structures is untenable.

Discussion

The present results showed that individual differences determine resultant triadic structures. The importance of individual differences is revealed by our ability to use them to predict triadic hierarchies in

the domestic fowl. Prediction was made possible by using individual differences that had been found to be determinants of dominance encounters in pairs of hens. Thus asymmetries in prior experience of dominance/ submission, in weight and comb size were experimentally combined to create hens having various propensities to dominate others in triads. We also found *ex post facto* that darkness of the comb was significantly associated with resultant higher status.

Our results agree with the study of Cloutier et al. (1995) in showing the importance of familiarity combined to past social experience of subordination. They also are in agreement with several studies (Allee et al., 1939; Collias, 1943; Guhl and Ortman, 1953; Ligon et al., 1990) in showing the importance of comb size and colour. This is not surprising if, as suggested by Rushen (1985), comb size is used by hens as a salient cue in assessing the potential of an opponent. However, our results on weight contrast with the observations of Schjelderup-Ebbe (1922), later confirmed by the work of Collias (1943) and Potter (1949), which suggest that weight is not a decisive factor in encounter. Nonetheless, they concur with studies on various species of fish that found out that weight (or body size) effect can add to other factors, or is effective only when the effect of more important factors is inhibited (Beacham, 1988, on *Lepomis gibbosus*; Beaugrand et al., 1991, on *Xiphophorus helleri*).

By showing that some combinations of factors are advantageous for one individual over opponents having a different combinations, our results confirm the model proposed by Slater (1986) as an alternative to Chase's *jigsaw puzzle* model. In Slater's model the dominant of an encounter would be the individual scoring the highest on individual differences, that is the one which gains most advantage by individual differences and so on to the last individual which scores lowest.

Individuals do not meet at random but choose each other as opponents. We found that initial individual differences when they are important, influence the order in which opponents resolve conflict. The two hens that possess the greatest advantage due to initial individual differences choose each other to settle conflict in the first place. In most cases, the winner of this first settlement later encounters the bystander. Such a mechanism of opponent selection probably promotes the acquisition of a higher rank in the hierarchy. Slater (1986) had correctly foreseen that such a mechanism of choice could explain the **DD** process described by Chase (1982a, 1982b).

The present results show that the same end structures can be reached through different paths of resolution that are not necessarily of the **DD** and **DS** types as predicted by Chase's model. They clearly show that under certain circumstances the effects of initial individual differences outweigh those of the order of resolution of conflict. Under the simultaneous condition of the present study, $A>\alpha>\omega$ and $\alpha>A>\omega$ structures have been reached in 90% of cases by **DD**s. These results confirm those obtained by Chase (1980, 1982a, 1982b, 1985) under similar conditions in chickens. However, in our results the same structures were reached under the step condition of resolution through a mixture of 48% of **BDID**s, 29% **DS**s, and 24% **DD**s. That similar triadic social structures can be reached through alternative paths of conflict resolutions while the resultant dominance structure remains invariant clearly indicates the preponderant role of initial individual differences over resolution paths under the present conditions. This casts doubt on the relative importance of patterns of conflict resolution compared to individual differences in the determination of hierarchy. The demonstration is particularly clear since Chase's model logically implies, as a corollary, that bystanders should invariably end up in the middle of the hierarchy due to the necessity to satisfy the **DD** and **DS** patterns. In both condition of the present research, bystanders did not end up in the middle of the hierarchy more often then expected by chance.

One word of caution is in order about a methodological limit in the present research that may preclude

drawing inference on the effect of winning or losing, since winner and loser of the first phase were self-selected. Indeed, this procedure of self-selection potentially confounds a difference in aggressive experience with other differences in characteristics because an individual winning against an ostensibly equally matched opponent would be expected to be better than average on other attributes associated with dominance. Although our hens were carefully matched for weight and comb size, it is possible that other characteristic such as aggressiveness or other, still unknown or unmeasurable factors, may have been confounded with winner or loser effect.

The discrepancy between our results and those obtained by Chase, concerning the patterns of resolutions, can be due to the importance given by each study to individual differences. Chase's model did not take into account the effect of individual differences although there is nothing in his model that assumes that individual differences are without importance in hierarchy formation. Chase considers that while differences in individual characteristics do play a part in hierarchy formation, these characteristics, often do not adequately account for the presence of highly linear hierarchies. Consequently, in his model, he puts all emphasis on the order in which conflicts get resolved during hierarchy development, minimizing individual differences. Rigorous controls most probably contributed to homogeneity in individual differences within the sample of hens that served in Chase's experiments. Even the residual individual variations that remained were apparently not put into correlation with the obtained dominance statuses. Therefore, it is not surprising that patterns of conflict resolutions remained the only salient factor to which Chase could attribute observed transitivity.

This research assumed on the contrary that individual differences played a determining role during hierarchy formation. This preconception guided the experiment as we varied relevant individual characteristics.

When initial individual differences are not extreme, victory and defeat experience acquired during the formative period could add to or cancel out initial individual differences, thus essentially determining future victories or defeats. Especially when initial intrinsic differences are small, victories and defeats are prone to shape progressively the hierarchy and gradually camouflage the effects of initial attributes on dominance outcomes. The camouflage reaches the point where a correlation that is calculated *ex post facto* between resultant statuses in the social structure and initial, but not necessarily relevant characteristics, reveals itself quite modest. In such a case, sequences of victories and defeats (e.g. **DD**, **DS**) may appear causative whereas in reality it is the experience that each victory or defeat procures an individual that is accountable for future events. In other words, in the simultaneous triadic situation created by Chase (1982a), experience of victory and defeat acquired during hierarchy formation could account for **DD** and **DS** patterns because individual differences were initially very small. Effects of victory and defeat are amply documented in fish (Braddock, 1945; Gibson, 1968; McDonald et al., 1968; Thinès and Heuts, 1968; Muckensturm, 1969; Rasa, 1969, 1971; Frey and Miller, 1972; Zayan, 1975; Beaugrand and Zayan, 1985; Francis, 1983), and in rodents and chickens (Collias 1943; Craig et al., 1969; Ratner, 1961). That effects of recent victory or defeat are powerful has been established by Beacham (1988) and Beaugrand et al. (1991). They demonstrated that an advantage of 30-40% in weight/size was required in a prior looser to defeat a prior winner.

Victory would have the consequence to increase momentarily but greatly the winning potential of the victorious animal **A**, and defeat, to decrease greatly that of the animal **B**, which lost. During that time **C**, which remained in standby is not affected by victory nor by defeat; when it joins, its winning potential is located between that of **A** to which it most probably readily submits, and that of **B**, which it most probably defeats. In such a case, proportions prescribed by Chase (1982a, 1982b) are realized: a majority of **DD**

(animal **A** will also dominates **C**), and **DS** (**B** is also defeated by **C**).

Basically, intrinsic properties determine the potential of victory of the individual. However, as soon as encounters begin there is a carry-over effect from previous encounters to following ones, a «social» factor was cleverly identified by Landau (1951b) in his «second model». A similar suggestion was made by McBride (1958) when he wrote that chickens, in his study, were influenced by memories of their previous successes or failures. Jackson (1988) also suggested that past social experience of an individual can affect its behaviour in initiating the attacks in subsequent encounters. This, in turn, may explain the low correlations between predicted hierarchies based on individual characteristics and observed hierarchies (Jackson, 1988).

Our working hypothesis is that during the course of hierarchy formation, successive victories and defeats add up to the already complex interactions between initial individual differences and together determine future outcomes. However, there are two exceptions to this hypothesis. When initial individual differences are extremely important as in the present experiment, initial individual differences essentially determine resultant hierarchies because their effects are not sufficiently perturbed or cancelled by successive victories and defeats. 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. Chase's developmental model of hierarchy formation based on successive victories and defeats would thus be a special case applying when initial individual differences are small.

Acknowledgments

References

Allee, W.C., Collias, N. E. and Lutherman, C.Z. 1939. Modification of the social order in flocks of hens by the injection of testosterone propionate. Physiol. Zool., 12: 412-440.

Barchas, P.R. and Mendoza, S.D. 1984. Emergent hierarchical relationships in rhesus macaques: an application of Chase's model. In: P.R. Barchas (Editor), Social hierarchies: Essays toward a sociophysiological perspective. Greenwood Press, Westport, Connecticut, pp. 23-44.

Beacham, J.L. 1988. The relative importance of body size and aggressive experience as determinants of dominance in pumpkinseed sunfish, *Lepomis gibbosus*. Anim. Behav., 36: 621-623.

Beaugrand, J.P. 1984. Modèles de dominance et théorie de l'évolution. -- In: J.J. Lévy and H.H. Cohen (Editors), Darwin après Darwin . P.U.Q., Québec, pp. 111-137.

Beaugrand, J.P. and Zayan, R.C. 1985. An experimental model of aggressive dominance in *Xiphophorus helleri* (*Pisces, Poeciliidae*). Behav. Processes, 10: 1-52.

Beaugrand, J.P. and Zayan, R.C. 1986. Outline of a model on aggressive dominance in green swordtail male fish (*Xiphophorus helleri*, *Pisces*, *Poeciliidae*). In: P.W. Colgan and R.C. Zayan (Editors), Quantitative models in ethology. Privat, Toulouse, pp. 9-23.

Beaugrand, J.P., Goulet, C. and Payette, D. 1991. Outcome of dyadic conflict in male green swordtail fish,

Xiphophorus helleri: effects of body size and prior dominance. Anim. Behav., 41: 417-424.

Bernstein, I.S. and Gordon, T.P. 1980. The social component of dominance relationships in rhesus monkeys (*Macaca mulatta*). Anim. Behav., 28: 1033-1039.

Braddock, J.C. 1945. Some aspects of the dominance-subordination relationship in the fish *Platypoecilus maculatus*. Physiol. Zool., 18: 176-195.

Chase, I.D. 1974. Models of hierarchy formation in animal societies. Behav. Sci., 19: 374-382.

Chase, I.D. 1980. Social process and hierarchy formation in small groups: a comparative perspective. Amer. Soc. Rev., 45: 905-924.

Chase, I.D. 1982a. Dynamics of hierarchy formation: the sequential development of dominance relationships. Behaviour, 80: 218-240.

Chase, I.D. 1982b. Behavioral sequences during dominance hierarchy formation in chickens. Science, 216: 439-440.

Chase, I.D. 1985. The sequential analysis of aggressive acts during hierarchy formation: an application of the 'jigsaw puzzle' approach. Anim. Behav., 33: 86-100.

Cloutier, S., Beaugrand, J.P. and Laguë, P.C. 1995. The effect of prior victory or defeat in the same site as that of subsequent encounter on the determination of dyadic dominance in the domestic hen. Behav. Processes, 34 293-298.

Collias, N.E. 1943. Statistical analysis of factors which make for success in initial encounters between hens. Amer. Nat., 77: 519-538.

Craig, J.V., Bismas, D.K. and Guhl, A.M. 1969. Agonistic behavior influenced by strangeness, crowding and heredity in female domestic fowl (*Gallus gallus*). Anim. Behav., 17: 498-506.

Eaton, G.G. 1984. Aggression in adult male primates: a comparison of confined Japanese macaques and free-ranging olive baboons. Int. J. Primatol., 5: 145-160.

Francis, R.C. 1983. Experiential effects on agonistic behavior in the paradise fish, *Macropodus opercularis*. Behaviour, 85: 292-313.

Frey, D.F. and Miller, R.J. 1972. The establishment of dominance relationships in the blue gourami, *Trichogaster trichopterus* (Pallas). Behaviour, 42: 8-62.

Gibson, R.N. 1968. The agonistic behaviour of juvenile *Blennus pholis* L. (Teleosti). Behaviour, 30: 192-217.

Guhl A.M. and Ortman, L.L. 1953. Visual patterns in the recognition of individuals among chickens. Condor, 55: 287-298.

Jackson, W.M. 1988. Can individual differences in history of dominance explain the development of linear dominance hierarchies ? Ethology, 79: 71-77.

Jackson, W.M. 1992. Further examination and testing of individual attributes models are needed. Anim. Behav., 43: 687.

King, M.G. 1965. The effect of social context on dominance capacity of domestic hens. Anim. Behav., 13: 132-133.

Kruijt, J.P. 1964. Ontogeny of social behaviour in Burmese red junglefowl (*Gallus gallus spadiceus*). Behaviour, suppl. 12: 1-201.

Landau, H.G. 1951a. On dominance relations and the structure of animal societies: I. Effect of inherent characteristics. Bull. Math. Biophysics, 13: 1-19.

Landau, H.G. 1951b. On dominance relations and the structure of animal societies: II. Some effects of possible social factors. Bull. Math. Biophysics, 13: 245-262.

Ligon, J.D., Thornhill, R., Zuk, M. and Johnson, K. 1990. Male-male competition, ornamentation and the role of testosterone in sexual selection in red jungle fowl. Anim. Behav., 40: 367-373.

Locati, M. and Lovari, S. 1991. Clues for dominance in female chamois: Age, weight, or horn size ? Agg. Behav., 17: 11-15.

McDonald, A.L., Heimstra, N.W. and Damkot, D.K. 1968. Social modification of agonistic behaviour in fish. Anim. Behav., 16: 437-441.

McBride, G. 1958. The measurement of aggressiveness in the domestic hen. Anim. Behav., 6: 87-91.

McBride, G., Parer, I.P. and Foenander, F. 1969. The social organization and behaviour of the feral domestic fowl. Anim. Behav., Mono. 2: 127-181.

Mendoza, S.D. and Barchas, P.R. 1983. Behavioural processes leading to linear status hierarchies following group formation in rhesus macaques. J. Hum. Evol., 12: 185-192.

Muckensturm, B. 1969. La signification de la livrée nuptiale de l'épinoche. Rev. Comp. Anim., 3: 39-64.

Murchison, C. 1935. The experimental measurement of a social hierarchy in *Gallus domesticus*. II. The identification and inferential measurements of a social reflex no. 1 and social reflex no. 2 by means of social discrimination. J. Soc. Psychol., 6: 3-29.

Potter, J.H. 1949. Dominance relations between different breeds of domestic hens. Physiol. Zool., 22: 261-280.

Rasa, A.O. 1969. Territoriality and the establishment of dominance by means of visual cues in *Pomacentrus jenkinsi* (*Pisces, Pomacentridae*). Z. Tierpsychol., 26: 825-845.

Rasa, A.O. 1971. Appetence for aggression in juvenile Damsel fish. Z. Tierpsychol., suppl. 7.

Ratner, S.C. 1961. Effect of learning to be submissive on status in the peck order of domestic fowl. Anim. Behav., 9: 34-37.

Rushen, J. 1985. Explaining peck order in domestic chickens. Bird Behav., 6: 1-9.

Schjelderup-Ebbe, T. 1922. Beiträge zur sozialpsychologie des haushunhs. Z. Psychol., 88: 224-252.

Siegel, S. and Castellan, jr. N.J. 1988. Nonparametric statistics for the behavioral sciences. 2nd edition, (Book), McGraw-Hill, Montreal, 399pp.

Slater, P. 1986. Individual differences and dominance hierarchies. Anim. Behav., 34: 1264-1265.

Thinès, G. and Heuts, B.A. 1968. The effects of submissive experiences on dominance and aggressive behaviour of *Xiphophorus* (*Pisces, Poeciliidae*). Z. Tierpsychol., 25: 139-154.

Zayan, R. 1975. Modification des effets liés à la priorité de résidence chez *Xiphophorus* (*Pisces, Poeciliidae*): le rôle de l'expérience immédiate de dominance et de soumission. Revue du Comportement Animal, 8: 296-311.

Zayan, R. 1987. Analysis of dominance and subordination experiences in sequences of paired encounters between hens. In: R.C. Zayan and I.J.H. Duncan (Editors), Cognitive aspects of social behaviour in the domestic fowl. Elsevier, Amsterdam, pp. 182-320.