

The roles of hen's weight and recent experience on dyadic conflict outcome

François Martin ^a, Jacques P. Beaugrand ^{a, *} and Paul C. Laguë ^b

^a *Département de Psychologie de l'Université du Québec à Montréal, CP 8888
Centre-Ville, Québec, Canada H3C 3P8*

^b *Department of Animal Science, Macdonald Campus of McGill University,
2111 Lakeshore Road, Sainte-Anne de Bellevue, Québec, H9X 3V9, Canada*

BP1107.wpd

30 jan 1997

The present text is a preprint and is not exactly conform to that which appeared in

MARTIN, F., BEAUGRAND, J.P. & LAGUË, P.C. (1997a).

The role of hen's weight and recent experience on dyadic conflict outcome. *Behavioural Processes*, 41, 139-150.

* Corresponding author's E-mail: beaugrand.jacques@uqam.ca

Abstract

This study simultaneously varied experiences of recent victory or defeat, 2-hour familiarity with the meeting place, and hen weight in order to understand their combined effects on the establishment of dyadic dominance relationships between hens not previously acquainted with each other. Three kinds of encounters were arranged: (i) a previous winner unfamiliar with the meeting place met a previous loser familiar with the meeting place ($n=28$ dyads); (ii) a previous winner met a previous loser, both unfamiliar with the meeting place ($n=27$); (iii) a previous winner familiar with the meeting place encountered a previous loser unfamiliar with the meeting place ($n=28$). The weight asymmetry was combined with these three types of encounters by selecting hens showing various weight differences, in favour of the recent loser in 54 dyads and of the recent winner in 29 dyads. Results indicate that recent victory or defeat experience significantly affected the outcome. Even an important weight asymmetry, or familiarity with the meeting place were not sufficient for a hen recently defeated to overcome an opponent that was previously victorious. A 2-hour period of familiarization with the meeting place did not provide any significant advantage over unfamiliarity. Although a significant relationship was found to exist between comb and wattles areas and the initial and final statuses, examination of partial correlations indicates that the influence was from initial status to final status, rather than from comb and wattles to final status. These results suggest that more importance should be attributed to recent social experience in comparison to intrinsic factors in determining dyadic dominance in the hen.

Key-words: Dominance; Agonistic conflict; Weight; Size of comb and wattles; Recent experience of victory and defeat; Site familiarity; Individual differences; Hen; *Gallus domesticus*.

Introduction

In the hen, many factors have been reported to influence dominance: the acquisition of sexual maturity (Schjelderup-Ebbe, 1935; Rushen, 1982), success in previous encounters (McBride, 1958; Zayan, 1987), prior residency (Zayan et al., 1983), presence of known individuals (Schjelderup-Ebbe, 1935), and tendency and latency in engaging in conflict (Collias, 1943; Huntington Potter, 1949; Wood-Gush, 1957; Ligon et al., 1990). These factors seem to favour a hen facing an unfamiliar rival. However, severe moulting (Collias, 1943) or defeat in a previous encounter (McBride, 1958; Ratner, 1961; Zayan, 1987) may reduce the chances of a hen being dominant. Comb size and colour attributes may also be important factors in the organization of a dominance hierarchy (Allee and Collias, 1938; Guhl and Ortman, 1953; Ligon et al., 1990; Siegel and Hurst, 1962). Within a breed, comb size and colour reflect the hens' relative blood androgen concentrations (Allee et al., 1939; Collias, 1943; Ligon et al., 1990). Hens displaying a small comb frequently find themselves at the lower end of the hierarchy even if they are heavier than their conspecifics.

Body size is most often identified as the best cue for gauging resource holding potential in animal conflicts (**RHP**; Parker, 1974; Maynard Smith, 1982). Size correlates with strength; it is presumed to be an important factor in conflict outcome. In fish, it has been shown that the larger individuals usually won (Myrberg, 1971; Jakobsson et al., 1979; Francis, 1983; Turner and Huntingford, 1986; Noble, 1939; Braddock, 1945). In hens, the importance of weight has also been studied. However, the picture which emerges is less clear. Murchison (1935) and Guhl and Allee (1944) reported that heavier subjects were more likely to adopt aggressive behaviour and to hold a higher position in the social hierarchy. These findings were later confirmed by Ligon et al. (1990). There is also evidence that body weight correlates with social rank in cocks (Graves et al., 1985). However, Huntington Potter (1949) compared dominance relations in many chicken breeds and concluded that weight differences were not a deciding factor of dominance. These results were more recently confirmed by Bradshaw (1992) who did not find any significant correlation between dominance and body weight in laying hens. The situation is sometimes further complicated by the fact that weight has a tendency to correlate with comb size (Graves et al., 1985; Bradshaw, 1992), which in turn correlates with dominance, thus confounding their respective contribution to dominance.

Once the factors which may contribute to dominance have been clearly identified, their relative contribution and possible interactions in affecting **RHP** merit further consideration. This can be achieved in experiments which seek to vary the factors suspected of affecting dominance in dyadic encounters. Varying previous experiences of victory or defeat as initial individual attributes in a dyadic situation can reasonably be assumed to approximate carry-over effects that may occur in a polyadic situation and which may be due to successive victories or defeats.

Numerous studies in fish have sought to simultaneously manipulate experimentally a number of factors. Frey and Miller (1972), Beaugrand and Zayan (1985), Beacham (1988), and Beaugrand et al. (1991, 1996) simultaneously varied many parameters to establish their combined effects. Experiments by Beaugrand and Zayan (1985) and Beaugrand et al. (1991, 1996) have investigated in *Xiphophorus helleri* the interactions of several factors in dyadic dominance encounters. Previous experiences of victory or defeat, 3-hour familiarity with the meeting place, and size differences were found to predict the dominant

subjects in unacquainted pairs. Moreover, results obtained by Beaugrand et al. (1991, 1996) clearly suggest that previous victory or defeat experience and size can either add or cancel out each other. Though *Xiphophorus* fish and *Gallus* are phylogenetically distant, it may be hypothesised that they share not only a common basic dominance mechanism, but also some determining factors as well, namely recent experience, familiarity with the surrounding, and size or weight. In contrast to studies carried out on *Xiphophorus*, most research in hens has focused on the effects of single characteristics in studies which have precluded the study of their possible interactions. Only a few researchers have investigated the relationship between several factors, mostly in a purely descriptive, non-experimental way (e.g., Collias, 1943; Bradshaw, 1992).

The aim of the present study was, therefore, to evaluate the effects of recent victory or defeat experience, with that of familiarity with the meeting site in hen dyads where asymmetries defined by these factors were combined or opposed.

Methods

Subjects and material

Hens

One hundred and fifty laying hens from a locally selected line of Red Rock x Light Sussex were used. Six flocks of 25 hens each were formed and kept in 2.4 m x 3.2 m pens whose floors were covered with wood shavings. Flocks were visually isolated from each other. Water and feed were provided *ad libitum*. The hens were kept under a 16:8 hour L:D photo period with lights on at 0500 hr.

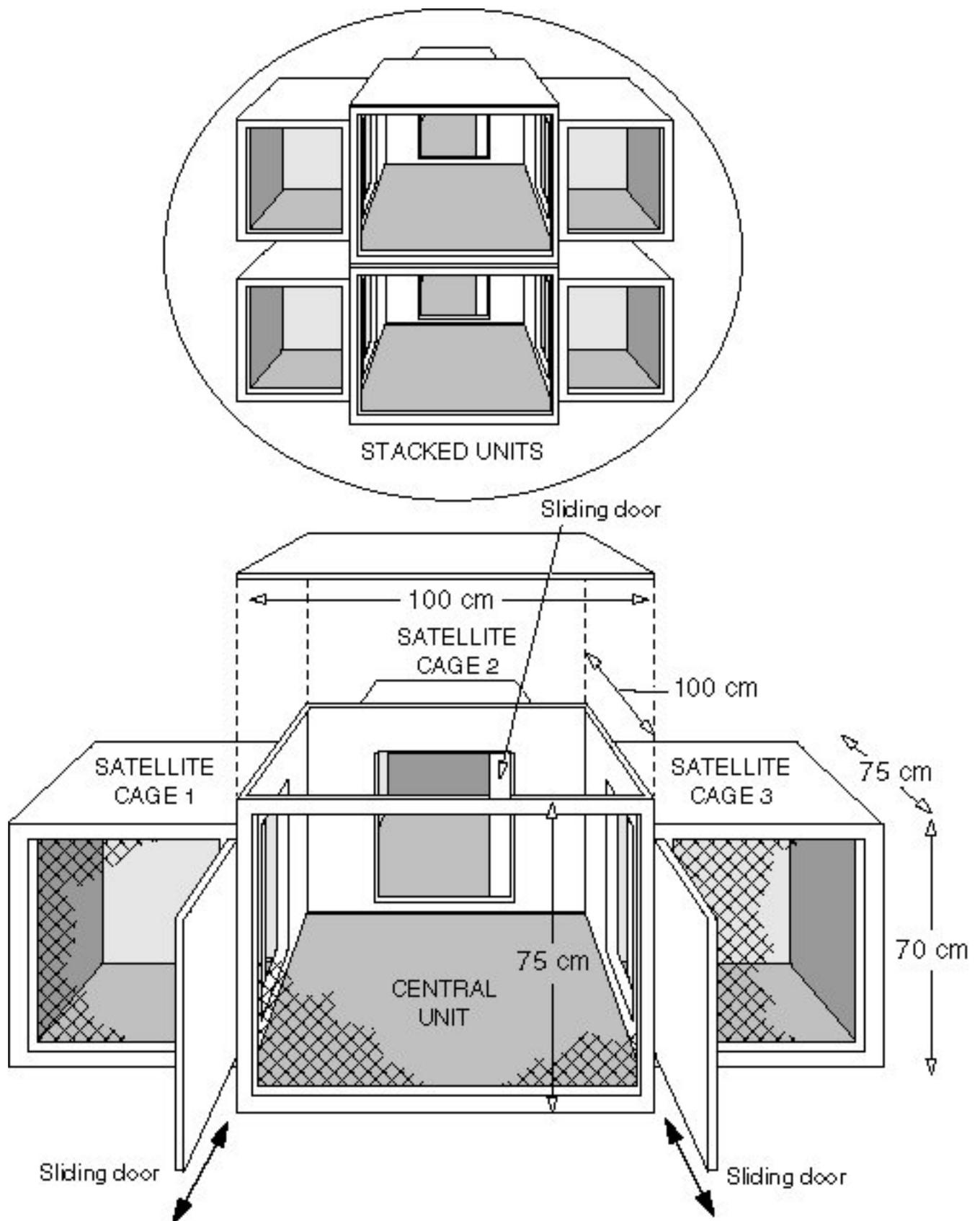


Figure 1. Central and satellite cages used to stage encounters.

Cages and apparatus

The experimental apparatus used for encounters was composed of a central cage (1 m x 1 m x 0.75 m) surrounded by three satellite cages (0.70 m x 0.75 m x 0.75 m each). Two of the experimental cage

systems were stacked one above the other (Fig. 1). The first encounter between pairs of hens served to provide victory or defeat experience and took place in the satellite cages. Final encounters took place in the central cages. Sliding doors, activated at the appropriate moment by the experimenter, allowed hens in the satellite cages to enter the central cage.

Experimental design

Three conditions were used. Each corresponded to one independent sample comprising 27 or 28 pairs. In all cases, confrontations involved a hen which had recently won an encounter, called «*alpha*» (α), and a recently defeated hen, identified as «*omega*» (ω). Final encounters involved birds which had been exposed to the meeting site for 2 hr and birds which were unfamiliar with the meeting site. Three specific combinations were investigated:

- (i) Unfamiliar-Familiar (**UF**), the α hen was unfamiliar with the meeting place while its ω opponent was familiar with it;
- (ii) Familiar-Unfamiliar (**FU**), the α hen was familiar with the meeting place while the ω hen was not;
- (iii) Unfamiliar-Unfamiliar (**UU**), neither the α nor the ω hen was familiar with the meeting place.

Condition **UU** corresponded to symmetry in non-familiarity with the meeting place and was used to establish the effect of the victory/defeat experience.

Familiarity was established by allowing one hen to explore the surroundings of the future encounter site for 2 hrs (i.e., central cage) while the other bird was kept in one of the satellite cages. The hens could not establish visual contact at this point. Experience of victory or defeat was given to the hens 18 to 20 hours before their encounter. Experience of victory was established in the pre-experimental phase by introducing in a cage an unfamiliar hen weighing 10-25% less than the 2-hour "resident". In most cases, the resident became victorious over the smaller intruder. However, when the intruder became dominant over the resident hen, the members of this dyad were excluded from the sample serving that day and returned to their respective flocks. This happened in only 24.4% (60/246) of all planned cases, indicating that size superiority combined with residency provided a highly significant advantage at this step of the research ($p=q=1/2$, $x=60$, $N=246$, $P<.001$ to a binomial test). This approach ensured that social experience and statistical selection were not confounded effects (Bégin et al., 1996).

Weight asymmetry was planned as a factor to be studied *ex post facto*. The number of available hens precluded the forming of several subgroups, each corresponding to a given range of size differences within each of the three conditions. For each of the three conditions, dyads were formed so as to present weight discrepancies between pair members. In 54 of the final dyads, the α pair member was selected to be lighter than its ω opponent, while in 29 of the remaining pairs it was the reverse. Initial weighing of the 150 hens available for the experiment yielded an approximately normal weight distribution with a mean of 3.36 Kg and a standard deviation of 0.561 Kg. The within-pair asymmetries in weight obtained during the experiment were comparable to a random sample of weight differences taken from the 150-hen mother sample (anova, $F_{1,164}=2.67$, n.s.).

Other measurements

Other individual characteristics were also measured in order to study their correlation with dominance. A precision scale (A & D Co. Ltd, model *FX-6000*) was used to weigh each hen before each encounter.

Photographs were also taken of 68 of the hen's heads against cross-ruled paper used as a measuring standard. The areas of the comb and wattles were measured from these photographs with a planimeter (*Tamaya Digital Planix 5.6*). Comb colour was also measured from the photographs using Munsell's (1929) system. For each colour, this system yielded three values based on the spectral colour, the darkness or luminosity level, and the brightness or saturation with pigment.

Dominance criterion

A hen was said to be dominant when an agonistic asymmetry between the two hens was noticed on 6 consecutive occasions. This asymmetry involved the exclusive use of aggressive behaviour by one hen that was answered exclusively with defensive behaviour on the part of the other. If there was a menace or counterattack, the count was set back to zero, at which point the agonistic asymmetry had to be confirmed on 6 consecutive occasions. Furthermore, the second hen could not counterattack within a 30-min span after the sixth aggressive behaviour.

Agonistic behaviour

The agonistic behaviour patterns considered as determinants of dominance were the typical aggressive and defensive behaviour of the species as documented by Kruijt (1964), McBride et al. (1969). Aggressive behaviour units included peck, jump, claw and charge. Defensive units were escape (with or without screams and flaps), freezing or crouching on attack/approach.

Procedure

On day 1, "alpha" and "omega" experiences were given to the hens. Six to 12 hens were selected at random from the enclosures, fitted with colour plastic leg bands, weighed, and had their heads photographed. The birds were paired so that one hen of the dyad had a 10-25% weight advantage. The heavier hen was then placed into one of the satellite cages for 2 hours allowing it to become familiar with the surroundings. In the meantime, the lighter opponent remained in its enclosure and was introduced into the resident's cage only at the time of the encounter. For each conflict, the agonistic behaviour patterns were monitored continuously until one hen was declared dominant or until 3 hours had elapsed, whichever came first. In the latter case, the pair was discarded from the sample. The pairs that met the dominance criterion were left together overnight in the satellite cage with the lights off.

Day 2 served to establish hens which would be familiar or not with the future meeting site and to conduct the final encounter. Hens were first paired according to one of the three situations presented in upper part of Table 1. Dyads were assembled so that a hen that was victorious the day before encountered one that had been defeated. The pairs left together overnight were thus first separated and each hen selected for the second phase was placed alone for 2 hours in an unfamiliar cage. If both hens were to be unfamiliar with the meeting place, they were left alone in separate satellite cages and later met in the central cage. In the other two situations, the to-be familiar hen was placed in the central cage 2 hours prior to the encounter, while its opponent was left alone in one of the satellite cages. Once the 2-hour period had elapsed, the sliding door(s) opened and the intruder joined the resident hen in the central cage (**UF** and **FU** conditions) or both intruders stepped from their satellite cages into the central cage to meet (condition **UU**). At the end of the final phase, the hens were returned to their respective home pens as soon as a victor was proclaimed or after 3 hours of observation, whichever came first.

Re-use of the same hens

During the entire experiment, which lasted seven months, the same hens served on one to four occasions separated by at least one month. Hens that met always came from different pens. According to Chase (1982), hens no longer recognise penmates after two weeks of separation. Moreover, unpublished data from this research unit also indicates that in the hen, effects of victory or defeat on subsequent meetings disappear within 96 hours. Thus, a separation of at least one month spent in its home pen with usual penmates was imposed between any two meetings involving a given hen, or a given pair of hens.

Results

Binary categories were compared using two-tail binomial (Bin) tests. Unless specified, the null hypothesis was $p=q=1/2$. The distribution free tests used and their conditions of application are described in Siegel and Castellan (1988). The maximum likelihood *G-test* or *Wald-test* can be found in Sokal and Rohlf (1995). Darlington (1990) gives a primer on the use of partial correlations, path-analysis and logistic regression.

When there was no important weight or familiarity asymmetry between hens, a hen with a previous α experience was expected to win over an opponent which had suffered a defeat. The results confirm this expectation even for large weight differences. Few ω hens were victorious even if they were larger than their α opponent.

Table 1. Frequency with which each kind of opponent won in the final test. Two-tail binomial tests were used.

<i>Conditions (n pairs)</i>	Hen that won		<i>Binomial test</i>
	α	ω	
UF (28)	21	7	$P<.024$
UU (27)	25	2	$P<.002$
FU (28)	24	4	$P<.002$
All (83)	70	13	$P<.002$
<i>Subsets</i>	<i>Familiar</i>	<i>Unfamiliar</i>	
FU & UF (56)	31	25	$P<.504$
	<i>Heavier</i>	<i>Lighter</i>	
All (83)	33	50	$P<.078$
	<i>Larger</i>	<i>Smaller comb and wattles</i>	
	<i>comb and wattles</i>		
All available (68)	53	15	$P<.002$

Table 1 shows the number of victories with respect to the characteristics of the opponents. A definite trend can be noticed: an α hen most often beats another with an ω experience. In this research, this outcome was noticed in 70 of the 83 encounters (84.3%) ($x=70$, $N=83$, Bin $P<.002$). On 54 occasions ω s were heavier than their α opponents. Nonetheless, α s defeated ω s 45 times (83%) in the final phase,

which is statistically biased towards recent experience rather than towards weight ($x=45$, $N=54$, Bin $P < .002$). This applies to all levels of familiarity with the meeting site (**FU**, $x=24$, $N=28$, Bin $P < .002$; **UU**, $x=25$, $N=27$, Bin $P < .002$) within the range of weight differentials covered by the present study (i.e., -35% to +35%), as well as when familiarity was put in opposition with recent experience asymmetry (**UF**, $x=21$, $N=28$, Bin $P < .012$).

We expected familiarity with the meeting place to favour the familiar hen over the unfamiliar one. Allowing a hen to become familiar with the encounter settings for 2 hours did not favour it over one for which the environment was unknown since victories equally went to familiar and non-familiar hens when conditions **FU** and **UF** were aligned for familiarity ($x=31$, $N=56$, Bin $P < 0.504$).

We expected that, in general, a weight advantage would favour the larger hen in encounters. Our results do not confirm this hypothesis. In general, winners on the final tests were not significantly heavier than losers (one-way Anova: $F_{1, 164} = .10$, n.s.). It was mentioned above that α s significantly defeated their heavier opponents in the final phase. Moreover, α s remained victorious in 25 of the 29 meetings in which weight differential was in their favour, which is significant to a binomial test from equiprobability ($x=25$, $N=29$, Bin $P < .012$). In general, lighter hens won equally frequently as heavier ones ($x=50$, $N=83$, Bin $P < .078$).

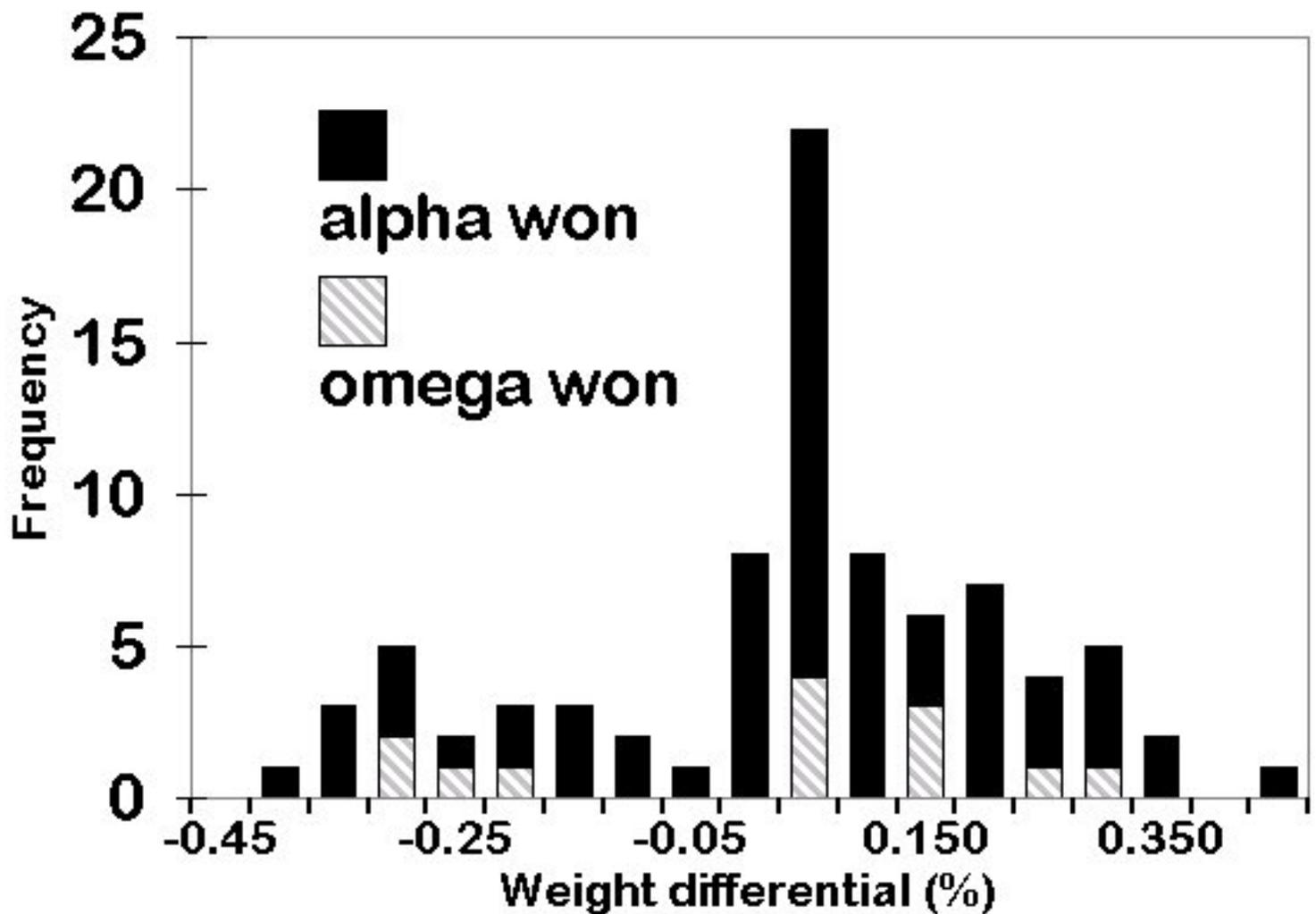


Figure 2. Relationship between the weight differential ratio of the ω hen over its α hen opponent and the corresponding victory frequencies. A positive differential indicates that the ω hen was heavier or equal in weight than the α hen; a negative indicates that the α hen was heavier than the ω . The weight differential is obtained by taking the difference between the α hen weight and that of its ω opponent, and by dividing this difference by the weight of the α hen.

Table 2 . Average area (in cm²) for comb and wattles combined

Conditions	Winner	Loser	F	<i>P</i> <
UF	15.43	11.3	6.65	.013
UU	15.29	9.07	22.86	.000
FU	18.01	13.11	6.95	.013
All	16.02	10.94	30.13	.000

Thus, the weight-differential superiority of a hen did not counteract the past social experience asymmetry (Fig. 2). Heavier hens did not defeat their opponent without in addition possessing a previous experience of victory. In some cases, even a 35% weight-differential advantage did not help a previously defeated hen to defeat a previous winner.

Table 2 presents the average of combined comb and wattles areas for each of the three types of encounters. Our hypothesis was that the hens with superior comb and wattles areas would win significantly more meetings than opponents with smaller comb and wattles. The results show that victorious hens have significantly larger combs, wattles, and comb and wattles than their opponents (one-way Anovas: smallest $F_{1,133} = 20.92$, $P < .001$). The pair member having larger comb and wattles obtained victory in 53 out of the 68 cases for which these measurements were available ($x=53$, $N=68$, Bin $P < .002$, Table 1).

We also found that, in 53 (86.8%) of the 68 available pairs, α hens had superiority in comb and wattles areas over ω s and that, in these 53 pairs, the α hens had obtained victory, which is highly significant ($x=53$, $N=68$, Bin $P < .002$).

Comb spectral colour was identical for each of the hens in our sample, and thus did not differ between winning and losing hens. The luminosity level was not statistically different ($\text{Chi}^2 = 3.36$, $\text{df} = 3$, n.s.). The same can be said about the pigment saturation level ($\text{Chi}^2 = 1.16$, $\text{df} = 3$, n.s.).

Relative importance and interaction of the various asymmetries

In order to understand the relative importance and possible interaction of the various asymmetries, data were analysed using logistic regression. The unit of analysis was the individual.

Previous experience, familiarity with the meeting place, as well as superiority in weight and comb and wattles were binary coded for their presence (1) or absence (-1) and declared as categorical variables. *Differentials* in weight and in comb and wattles areas were also calculated as a percentage of superiority or inferiority over an opponent. These dimensionless ratios were included in the analysis as continuous variables.

The reader is referred to Darlington (1990) for the proper use of logistic regression. Essentially, logistic regression properly describes the relation existing between a predicted variable and a set of predictors, i.e., the states that could take each asymmetry suspected to influence dyadic dominance outcome. The direct, as well as the stepwise entry procedures were used to introduce the various factors. By entering (or not) some factors, one can assess the relative importance of each factor in influencing the variable to be predicted, i.e., winning or losing the fight. We used this approach as a descriptive tool only, in order to isolate the specific contribution of each factor, or set of factors, to dyadic dominance outcome.

Analyses were carried out on the whole sample composed of the 83 original dyads, on a subset composed of the 54 dyads in which the ω hen was heavier to its α opponent, and on another subset composed of the 29 remaining dyads in which the ω was lighter. Since data on comb and wattles areas were not available for 15 dyads, these dyads were declared missing from the corresponding data subsets when these areas were analysed.

The results of the regression, based on the 83 original dyads, are most representative of what had been obtained from the analyses based on other subsets. Only the recent experience asymmetry reached

significance ($\text{Exp}(\beta)=.186$, $\text{Wald}=62.15$, $\text{df}=1$, $P<.001$) and was included in a model which could adequately predict dominance outcomes. Since the recent experience asymmetry was coded as a binary variable, the $\text{Exp}(\beta)$ coefficient gives its relative probabilistic contribution to the predicted variable i.e., its odd ratio. To be included in the model, a given variable had to reach the significance criterion of at least $P<.01$. The $\text{Exp}(\beta)$ coefficient indicates that being the α pair member increases chances of winning by 86% as compared to the ω pair member. The other asymmetries related to familiarity and weight did not reach the criterion of inclusion once the recent experience asymmetry had been included. A logistic equation based on this model could correctly retrodict 84% of victories, which is better than by chance alone ($Z=6.15$, $P<.001$).

A stepwise forward logistic regression based on the 68 dyads for which comb and wattles areas were available gave a slightly different picture, since both recent experience ($\text{Exp}(\beta)=.102$, $\text{Wald}=45.739$, $\text{df}=1$, $P<.001$) and familiarity with the meeting site ($\text{Exp}(\beta)=.482$, $\text{Wald}=4.37$, $\text{df}=1$, $P<.036$) were included in the stepwise regression. The logistic model based on these two factors predicted 88% of cases in retrospect. Superiority in comb and wattles, and weight did not satisfy the statistical criterion of inclusion by the model.

Similar logistic regressions were independently performed on dyads in which the ω hen had a larger weight than the α , or in which the ω hen was lighter. Again, only the recent experience asymmetry was included into the logistic models which best fit the data. All other factors were not included because they did not reach statistical significance. These logistic equations retained only the recent experience factor, and success in discriminating winners from losers varied in these analyses between 84 and 92% of cases, depending on the data subset considered.

Integration of factors

As mentioned above, α hens were found to have larger comb and wattles areas than ω hens; similarly, winners of the final outcome had significantly larger comb and wattles than losers. It is thus important for the present research to eliminate the rival hypothesis stipulating that it was comb and wattles areas that influenced the final dominance outcome rather than recent experience. In other words, that comb and wattles served as a precursor of recent experience and/or dominance outcome has to be discarded. Correlation coefficients were thus calculated between each pair of variables while keeping one or more variables "partialled out" of the relationship. The bivariate correlation between recent experience and dominance outcome is significant ($r=.768$, $\text{df}=136$, $P<.001$). The same applies to the correlation between comb and wattles areas and dominance outcome ($r=.574$, $\text{df}=136$, $P<.001$). When the correlation of recent experience with outcome is controlled for comb and wattles areas, it remains significant ($r=0.619$, $\text{df}=133$, $P<.001$). On the contrary when the correlation between comb and wattles areas and dominance outcome is controlled for recent experience, it loses statistical significance ($r=.05$, $\text{df}=133$, $P=.562$). Essentially the same result is obtained when higher order partial correlations are calculated: the path of influence passes from recent experience to dominance, rather than from comb and wattles areas.

Discussion

In this study, recent victory or defeat experience was found to be the major outcome determinant between two unfamiliar hens. These results on recent social experience confirm similar conclusions made by many authors. Effects of victory and defeat are amply documented in fish (e.g., Frey and Miller, 1972; Zayan, 1975; Francis, 1983; Beaugrand and Zayan, 1985) and chickens (Collias, 1943; Ratner, 1961; Craig et al., 1969). Victory has the consequence of momentarily but greatly increasing the winning

potential of the victorious animal and of greatly decreasing that of the loser. For instance, in their research, Frey and Miller (1972) found that 78% of fish having a recent victory experience defeated their opponent, whether this opponent was an intruder or a resident, bigger or smaller, and isolated for 10 days. Zayan (1987) demonstrated that dominant hens significantly dominated their opponent and that previously dominated birds were systematically defeated again when pairing hens of asymmetrical status. The present study confirms the importance of recent experience. No other factor or combination of factors including comb and wattles size, which might also have played a determining role, overcame the influence of previous victory or defeat. The effects of recent experience are powerful, as attested by our results, by the fact that in some cases even a 35% weight advantage was not sufficient for a previously defeated hen to dominate a previously victorious one. These results concur with the observations of Schjelderup-Ebbe (1935), later confirmed by Collias (1943) and Huntington Potter (1949), who suggested that weight was not a decisive factor in conflicts between hens, but they are in opposition to those made by Murchison (1935), Guhl and Allee (1944), and Ligon et al. (1990). Using the same line of birds as in the present experiment, Cloutier et al. (1996) found that previous α hens, 20-30% heavier than other α opponents, systematically defeated and dominated the smaller ones in triads. However, in their study, the large α hens had also been chosen for their larger combs than their smaller α opponents. One can thus presume that the effects of these two factors combined and were confounded.

We were expecting that the hen greatly advantaged by weight would have defeated the lighter opponent, a regularity repeatedly confirmed with fish and mammals (Beaugrand and Zayan, 1985; Beacham, 1988; Beaugrand et al., 1991, 1996; Locati and Lovari, 1991). For example, Beacham (1988) with *Lepomis*, and Beaugrand et al. (1991, 1996) with *Xiphophorus*, found that a 30% to 40% weight or size superiority allowed subjects with a recent ω experience to win over an α subject. However, the present results suggest that weight is not as important in overcoming α - ω asymmetry in the line of hens we studied as in these fish.

In this study, hens acquainted with the surroundings of the encounter for only 2 hours were not advantaged in respect to hens unfamiliar with the same environment. This contrasts with studies reporting that prior residency or familiarity with the meeting place is an advantage in agonistic encounters, especially in fish (Zayan, 1975; Beaugrand and Zayan, 1985; Beaugrand and Beaugrand, 1991; Beaugrand et al., 1996). In green swordtail fish, the disadvantage of a recent defeat experience is greatly diminished when the encounter occurs in a place that is familiar to the loser but not to its opponent (Beaugrand et al. 1996). In the fowl, Zayan et al. (1983) showed that intruders are quickly dominated even when residents are also simultaneously introduced into their home area with a newcomer. In their research, resident hens stayed several weeks in the meeting place and were probably in a position to value contained resources, which became defensible against intruders. These two forms of «residency» are surely not equivalent, since in the present research prior residency only consisted of being familiar with the encounter area for 2 hours. The mere fact of being familiar with a site probably advantages an individual because that individual is not subjected to the stress of adapting to a new environment and is therefore less susceptible to experience fear of the surroundings than the newcomer (Thinès and Heuts, 1968; Beaugrand and Zayan, 1985). It can then concentrate more rapidly on the new situation (Rowell, 1974). Differences between the two forms of residency may come from the fact that positive or negative experiences are more prone to become associated with the site of residence as the period of residency gets longer (Bronstein, 1987). Cloutier et al. (1995) have shown that recent defeat in the meeting site becomes a great disadvantage for a hen against an opponent also familiar with the meeting site but which had experienced defeat elsewhere. It remains that the present results clearly

suggest that a 2-hour period of familiarity with the meeting site was not sufficient to give any prior residency advantage in the line of hens herein studied. Longer periods of residency should be systematically tested, together with various kinds of imposed experiences, to determine the conditions under which «prior residency» becomes a distinct entity from «familiarity» *per se*.

Nonetheless, the present data do not rule out that when opponents have equivalent recent experiences (e.g. the two are α , ω , isolated, or "neutral" hens), weight or even prior residency would become for them the decisive factor in the absence of any other preponderant asymmetry. The case is clear for a 3-hour residency in *Xiphophorus*: Beaugrand and Zayan (1985), and Beaugrand et al. (1996) have shown that when opponents were of equivalent size and were both previously isolated, or ω hens, residency essentially determined the outcome of dyadic conflicts. However, within up to 30% size differences, as soon as an asymmetry in recent experience existed in addition to a prior residency asymmetry, conflict resolved according to prior experience, not to prior residency, nor to size. In the first phase of the present experiment, size superiority combined with familiarity together with non manipulation of the resident was a significant advantage to the resident, and highly effective in creating dominants and subordinates. However, one cannot conclude unambiguously that familiarity was the operant factor since its effects may have been confounded or combined with that of other factors.

In this research, comb spectral colour, luminosity level, and pigment saturation level did not differ between winning and losing hens. However, we found *ex post facto* that hens with superior comb and wattles areas won significantly more meetings than opponents with smaller combs and wattles. These results support those obtained by Allee and Collias (1938), Guhl and Ortman (1953), and Ligon et al. (1990). Comb size is probably used by the hens as a salient cue in assessing the potential of an opponent as suggested by Rushen (1984). Moreover, the size of comb and wattles is controlled by testosterone in the fowl, which is also the hormone controlling basic aggressiveness in this species (Allee et al., 1939; Ligon et al., 1990). The use of partial correlation in the present research indicates that comb and wattles areas were not causal upon dominance outcome but rather acted as a collinear factor of previous experience. Future works should more carefully control for comb and wattles size, e.g. by experimentally making that aspect vary independently of recent experience. Hormonal levels should also be monitored. The influence of the size of comb and wattles upon dominance outcome was probably overshadowed in the present results by that of recent experience, whose effects had been made "in coherence", consecutive to the experimental procedure used. Under more natural and "noisy" conditions, when many and partly opposed factors are simultaneously playing, comb and wattles size and colour are most probably very significant social indicators of the internal state (hormonal) of their possessors, of their motivation and possibly of their previous general status (high or low in the peck-order) in their flocks of origin. Their mutual assessment in a conflict between two unfamiliar hens is surely influential upon which bird will decide to attack first and eventually win.

The importance of comb and wattles areas in the present research casts ambiguity upon the present results. Bégin et al. (1996) have demonstrated that in experiments allowing winners and losers to self-select, what appears to be the result of recent experience may actually be caused by uncontrolled differences between individuals on attributes associated with dominance ability. They suggest that by imposing victory or defeat (by retaining only winners and losers that were predicted to win or lose in experimentally rigged contests), such a confounding is most probably reduced. In the present experiment, victory or defeat was "imposed" in order to avoid "self-selection" of spurious and confounding factors. This was done by retaining only pair members in which the outcome had been correctly forecasted. Nonetheless, comb and wattles areas were most probably, but involuntarily, co-selected by the

researcher: in general, the victorious hen had a tendency to possess larger comb and wattles than its losing opponent, an effect which showed up to be statistically significant when the group of winners was compared to that of losers.

The present results suggest that some intrinsic factors (e.g., the hormonal state as indicated by comb plus wattles area) influence dominance, but that experiential factors, especially those related to recent victory or defeat are also of preponderant importance. In some fish, experiential factors were shown to override partially intrinsic factors. For instance, Beacham (1988) and Beaugrand et al. (1991, 1996) noted in fish that the influence of weight or surface area of the body was overridden by recent experience of dominance or subordination.

A precise demonstration of the preponderance of experiential factors over intrinsic ones is available from the study of Goulet and Beaugrand (in prep.) who were successful in reversing the social hierarchy status in a majority of dyads of male *Xiphophorus helleri* fish showing minimal size differences. This was achieved by having 2-hour residents defeat intruders and by making both members of a pair forget their initial relationship by a separation of 7 days. The loser of the initial encounter was then given a 2-hour prior residency advantage while the winner was used as the intruder. When the two were rematched, the initial dominance relationship was reversed in over 80% of the cases.

It thus becomes evident that the outcome of agonistic encounters is not determined by a single intrinsic factor but rather by a combination of factors including experiential ones; they add to one another, cancel one another, or intertwine. Dominance appears as the result of more or less significant asymmetries in a set of individual characteristics to which is added the influence of recent social experience.

Acknowledgements

We thank Sylvie Cloutier and Michèle E. Hogue for their assistance in collecting data. We are grateful to Randolph Stephenson and Darwin Veroba for many valuable comments on the manuscript. The Macdonald Campus of McGill University kindly provided the animals and poultry research facilities. This work was funded by a Canadian NSERC grant to J.P. Beaugrand.

References

- Allee, W.C. and Collias, N.E., 1938. Influence of injected male hormone on the social hierarchy in small flocks of hens. *Anat. Record*, 72: 119.
- 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: 412-441.
- 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. and Beaugrand, M., 1991. Prior residency and the stability of dominance relationships in pairs of green swordtail fish *Xiphophorus helleri* (Pisces, Poeciliidae). *Behav. Proc.*, 24: 169-175.
- 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.
- Beaugrand, J.P., Payette, D. and Goulet, C., 1996. Conflict outcome in male green swordtail fish dyads

- (*Xiphophorus helleri*): interaction of body size, prior dominance/subordination experience, and prior residency. *Behaviour*, 133: 303-319.
- Beaugrand, J.P. and Zayan, R., 1985. An experimental model of aggressive dominance in green swordtail male fish (*Xiphophorus helleri*, *Pisces: Poeciliidae*). *Behav. Proc.*, 10: 1-52.
- Bégin, J., Beaugrand, J.P. and Zayan, R., 1996. Selecting dominants and subordinates at conflict outcome can confound the effects of prior dominance or subordination experience. *Behav. Proc.*, 36: 219-226.
- Braddock, J.C., 1945. Some aspects of the dominance-subordination relationship in the fish *Platypoecilus maculatus*. *Physiol. Zool.*, 18: 176-195.
- Bradshaw, R.H., 1992. Individual attributes as predictors of social status in small groups of laying hens. *App. Anim. Behav. Sc.*, 34: 359-363.
- Bronstein, P.M., 1987. *Betta splendens*: Familiarity with visual cues fails to produce a prior-residence effect. *Bull. Psychonomic Soc.*, 25: 296-298.
- Chase, I.D. 1982. Dynamics of hierarchy formation: the sequential development of dominance relationships. *Behaviour*, 80: 218-240.
- Cloutier, S., Beaugrand, J.P. and Laguë, P.C., 1995. The effect of prior victory or defeat in the same site as subsequent encounters on dominance in domestic hens. *Behav. Proc.*, 34: 293-298.
- Cloutier, S., Beaugrand, J.P. and Laguë, P.C., 1996. The role of individual differences and of patterns of resolution in the formation of dominance orders in triads of domestic hens. *Behav. Proc.*, (in press).
- Collias, N.E., 1943. Statistical analysis of factors which make for success in initial encounters between hens. *Am. 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.
- Darlington, R.B., 1990. *Regression and linear models*. McGraw-Hill, New York, 542 pp.
- 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.
- Goulet, C. and Beaugrand, J.P., ms. Reversal of dominance/subordination relationships in *Xiphophorus helleri* using 2-hour prior residency. (in prep.)
- Graves, H.B., Hable, C.P. and Jenkins, T.H., 1985. Sexual selection in *Gallus*: Effects of morphology and dominance on female spatial behavior. *Behav. Proc.*, 11: 189-197.
- Guhl, A.M. and Allee, W.C., 1944. Some measurable effects of social organization in flocks of hens. *Physiol. Zool.*, 27: 320-347.
- Guhl, A.M. and Ortman, L.L., 1953. Visual patterns in the recognition of individuals among chickens. *Condor*, 55: 287-298.

- Huntington Potter, J., 1949. Dominance relations between different breeds of domestic hens. *Physiol. Zool.*, 22: 261-280.
- Jakobsson, S., Radesater, T. and Jarvi, T., 1979. On the fighting behavior of *Nannacara anomala* males. *Z. Tierpsychol.*, 49: 210-220.
- Kruijt, J.P., 1964. Ontogeny of social behaviour in Burmese Red Jungle fowl (*Gallus gallus spadiceus*). *Behaviour suppl.*, 12: 1-201.
- Ligon, J.D., Thornill, 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.
- 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. Monogr.* 2: 127-181.
- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. New York: Cambridge University Press.
- Munsell, A.H., 1929. Munsell book of color: defining, explaining and illustrating the fundamental characteristics of color. Standard ed., 2 vol. Baltimore, Md.
- Murchison, C., 1935. The experimental measurement of a social hierarchy in *Gallus domesticus*: IV. Loss of body weight under condition of mild starvation as a function of social dominance. *J. Gen. Psychol.*, 12: 296-312.
- Myrberg, A.A., 1971. Social dominance and territoriality in the bicolor damselfish, *Eupomacentrus partitus* (Poey) (*Pisces: Pomacentridae*). *Behaviour*, 41: 207-231.
- Noble, G.K., 1939. The experimental animal from the naturalist's point of view. *Am. Nat.*, 73: 113-126.
- Parker, G.A., 1974. Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.*, 47: 223-243.
- Ratner, S., 1961. Effect of learning to be submissive on status in the peck order of domestic fowl. *Anim. Behav.*, 9: 34-37.
- Rowell, T.E., 1974. The concept of social dominance. *Behav. Biol.*, 11: 131-154.
- Rushen, J., 1982. The peck orders of chickens: How do they develop and why are they linear? *Anim. Behav.*, 30: 1129-1137.
- Rushen, J., 1984. How peck orders of chickens are measured: a critical review. *App. Anim. Ethol.*, 11: 255-264.
- Schjelderup-Ebbe, T., 1935. Social behavior in birds. In: Murchison's Handbook of Social Psychology. Clark University Press, Worcester, pp. 947-972.

- Siegel, P.B. and Hurst, D.C., 1962. Social interactions among females in dubbed and undubbed flocks. *Poul. Sci.*, 41: 141-145.
- 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.
- Turner, G.F. and Huntingford, F.A., 1986. A problem for game theory analysis: assessment and intention in male mouthbrooder contests. *Anim. Behav.*, 34: 961-970.
- Wood-Gush, D.G.M., 1957. Aggression and sexual activity in the Brown Leghorn cock. *Br. J. Anim. Behav.*, 5: 1-6.
- 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. *Rev. Comp. Anim.*, 8: 296-311.
- Zayan, R., 1987. Analysis of dominance and subordination experiences in sequences of paired encounters between hens. In: R. Zayan and I.J.H. Duncan (Editors), *Cognitive aspect of social behaviour in the domestic fowl*. Elsevier, Amsterdam, pp. 182-320.
- Zayan, R., Doyen, J. and Duncan, I.J.H., 1983. Social and space requirements for hens in battery cages. In: S.H. Baxter, M.R. Baxter and G.A.C. Mac Cormack (Editors), *Farm animal housing and welfare*. The Hague: Martinus Nijhoff Pub., p. 67-90.