

# The role of recent experience and weight on hen's agonistic behaviour during dyadic conflict resolution

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## Abstract

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Recent victory or defeat experiences and 2-hour familiarity with the meeting place were combined with size differences in order to better understand their effects on the behaviour leading to the establishment of dyadic dominance relationships between hens not previously acquainted with each other. Three kinds of encounters were videotaped: (i) a previous winner unfamiliar with the meeting place met a previous loser familiar for 2 hours with the meeting place ( $n = 12$  dyads); (ii) as in (i) but both were unfamiliar with the meeting place ( $n=12$ ); (iii) as in (i) but the previous winner was familiar with the meeting place while the previous loser was unfamiliar ( $n=13$ ). The weight asymmetry was combined with these three types of encounters by selecting hens of various weight differences: in 29 dyads the recent loser was heavier than the recent winner and in 8 dyads it was the reverse. Recent experience had a major influence upon both agonistic behaviour and dominance outcome. Hens that were familiar with the meeting site initiated attacks more frequently than their unfamiliar opponent but did not win significantly more often. Recent experience and site familiarity could be used to identify 80% of future initiators. Once the first aggressive behaviour had been initiated, it led to victory of its initiator in 92% of cases. Weight was not found to influence agonistic behaviour nor dominance outcome. However, hens with superior comb and wattles areas won significantly more initial meetings than opponents with smaller ones. In the final encounters, victory also went more frequently to the bird showing larger comb and wattles, which happened also to be the previous dominant in a majority of cases. The use of higher-order partial correlations as an *ex post facto* control for comb and wattles indicates that they were not influential upon agonistic behaviour nor on dominance outcome, but were simply co-selected with the selection of victorious and defeated birds in the first phase of the experiment designed to let hens acquire recent victory/defeat experience.

## Keywords:

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

## Introduction

This paper complements our previous work on the hen (Martin et al., 1997) by focussing on behaviour that occurred during dyadic encounters rather than focussing solely on dominance outcome. Some 37 encounters of the original study had been videotaped, and they are herein analysed for specific behavioural aspects. Firstly, we examine if weight, recent experiences of victory and defeat, and familiarity with the meeting site affect agonistic behaviour in the hen, whilst influencing or not dominance outcome. Secondly, we examine early behaviours in encounters that could serve to foretell other behaviour leading to dominance outcome in dyads of hens.

In a companion paper to the present (Martin et al., 1997), recent victory and defeat experiences were shown to affect the outcome of encounters in dyads of hens, thus confirming similar results obtained in fish (e.g., Frey and Miller, 1972; Zayan, 1975; Francis, 1983; Beaugrand and Zayan, 1985) and in chickens (Collias, 1943; Ratner, 1961; Craig et al., 1969; Zayan, 1987). However, contrary to what was expected, 2-hour familiarity with the meeting site did not significantly determine dominance outcome. Hens acquainted with the meeting site were not advantaged over 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 in fish and in the hen. In the green swordtail fish, the disadvantage of a recent defeat experience was found to greatly diminish when the encounter occurred in a place that was familiar to the recent loser but not to its opponent (Beaugrand and Zayan, 1985; Beaugrand et al., 1996). In the fowl, Zayan et al. (1983) showed that intruders were quickly dominated when residents were also handled to be reintroduced into their home area with a newcomer. In their research, residents stayed several weeks in the meeting place and were probably in a position to assess contained resources, which became defensible against intruders. Quite surprisingly, Cloutier et al. (1995) have shown in the hen that familiarity with the meeting site, when associated with recent defeat in that same site, greatly decreased the chances of victory against an opponent that had lost elsewhere. Such a site dependent effect was not obtained with hens that had received recent victory.

In the Martin et al. (1997) study, weight asymmetries were opposed to recent experience asymmetries in the hope of seeing one cancelling or overcoming the other as Beaugrand et al. (1991, 1996) had obtained in green swordtail fish. Martin et al. (1997) did not find that weight significantly increased chances of victory, contradicting the conclusions drawn by Murchison (1935) and by Guhl and Allee (1944), who reported that heavier subjects were more likely to adopt aggressive behaviour and to hold a higher position in the social hierarchy. However, in general, the role of weight on dominance outcome in the hen is not so clear. There is evidence that body weight correlates with social rank in cocks (Graves et al., 1985). On the contrary, Huntington Potter (1949) compared many chicken breeds and concluded that weight differences were not a deciding factor upon dominance. Such a conclusion has been more recently confirmed by Bradshaw (1992) who did not find any significant correlation between dominance and body weight in the hen. The situation gets complicated by the fact that weight often correlates with comb size (Graves et al., 1985; Bradshaw, 1992), which in turn correlates with dominance, thus confounding their respective contribution to dominance. To complicate the situation further, in the research of Martin et al. (1997), comb and wattles areas were found to significantly covary with dominance outcome, but inversely with weight.

The absence in our previous report of any significant positive influence of weight and of familiarity with the surroundings could be accounted for by the small sample of dyads that served in the experiment. Still, these factors might have influenced behaviour during contest without necessarily having a decisive nor statistically significant effect on outcome itself. There are precedents. For instance, Frey and Miller

(1972), while studying factors that could influence the establishment of dominance orders in the blue gourami (*Trichogaster trichopterus*) did not find any effects related to prior residence. Nonetheless, they noted that resident fish were the first to demonstrate fin-tugging. In the hen, residents were reported to attack first (Allee et al., 1939; Guhl and Ortman, 1953; Guhl, 1961; Banks et al., 1979; Rajecki et al., 1981; Zayan et al., 1983).

Some studies demonstrated that agonistic behaviours occurring at the onset of an encounter were often already quite asymmetric. In some cases, those behaviours could successfully foretell subsequent conflict issue. For instance, Bronstein and Brain (1991) have noted in the fish *Cichlasoma nigrofasciatum* that the future dominant always initiated the first aggressive agonistic behaviour of the meeting. Turner and Huntingford (1986), using the cichlid *Oreochromis mossambicus*, observed that circling-around and tail-beating behaviours could be used to predict, quite early in the encounter, which fish would win the fight. Ribowski and Franck (1993), in swordtails *Xiphophorus helleri*, found that certain behaviours also helped to identify the winner from the loser early in the encounter. The former would fin-grip more often, whereas the latter would have a higher biting frequency, before and after escalation. Later in the course of encounter, these same behavioural differences could not, however indicate very well the fight's outcome. In the hen, the subject showing the first agonistic behaviour has very good chances of defeating its opponent (Collias, 1943; Huntington Potter, 1949; Wood-Gush, 1957; Ligon et al., 1990; Cloutier et al., 1996).

This paper will thus complete our previous work on the hen (Martin et al., 1997) by focussing on behaviour leading to conflict outcome rather than solely on dominance outcome.

### *Subjects and material*

The hens were selected from a local bred 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 daily.

The encounters were carried out in a specially designed cage system made of a central cage (75 x 100 x 100 cm) surrounded by three smaller satellite 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 lit with a fluorescent light. Two sets of cage systems were used so that several dyads could be studied simultaneously.

### *Research outline*

The experiment creates three conditions, each corresponding to one independent sample originally comprising 28 pairs. Thirty seven of the 83 original encounters were videotaped and these results will be presented here.

In this study, all confrontations opposed a recently victorious hen, identified as "*alpha*" (♂) to a recently defeated hen, identified as "*omega*" (♀). Two-hour familiarity with the meeting site was used as a variable in these experiments as follows:

(i) Unfamiliar-Familiar (UF), the ♂ hen was unfamiliar with the meeting site while its ♀ opponent was familiar;

(ii) Familiar-Unfamiliar (FU), the ♂ hen was familiar while the ♀ was not; and

(iii) Unfamiliar-Unfamiliar (UU), neither hen was familiar. Condition UU corresponded to symmetry on unfamiliarity and was used in order to establish the effect of the recent victory-defeat asymmetry alone.

Familiarity asymmetry was given to the hens by allowing one to explore the site of the future encounter site (i.e., central cage) for 2 hours, while the intruder explored one of the satellite cages.

Hens obtained recent experience of victory or defeat 18 to 20 hours before their encounter. Victory experience was given in the pre-experimental phase by introducing into a cage an unfamiliar hen weighing 10-25% less than the occupant. In most cases, the larger resident defeated over the smaller intruder. However, if the opposite occurred, the members of the dyad were excluded from the experiment. This happened in only 24.4% (60/246) of all planned cases, indicating that size superiority combined with familiarity and absence of handling were 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 was followed to ensure that, in the present research, recent victory/defeat experience and statistical selection would not be confounded effects (Bégin et al., 1996).

Weight asymmetry was planned as a factor to be studied *ex post facto*. For each of the three conditions above, dyads were formed so as to present various weight differences between pair members. Within the videotaped subset, in 29 of the final dyads, the ♂ pair member was selected to be lighter than its ♀ opponent; in 8 of the remaining pairs it was the reverse.

Each time a hen served in the experiment, a photograph of its head against cross-ruled paper was also taken, for use as a measuring standard. The areas of the comb and wattles were then measured from these photographs with a planimeter (*Tamaya Digital Planix 5.6*).

### *Dominance criterion*

A hen was said to be dominant when an agonistic asymmetry between it and another hen was recorded on 6 consecutive occasions. This asymmetry required exclusive demonstration of aggressive behaviour by one hen, and defensive behaviour on the part of the other. If a threat or counter-attack occurred, the count was set back to zero, following which the agonistic asymmetry had to be confirmed on 6 consecutive occasions. Furthermore, the defensive hen could not counterattack within a 30-minute period after the sixth aggression.

### *Agonistic behaviour*

The agonistic behaviour patterns considered as determinants of dominance were the species' typical aggressive and defensive acts: threat, pecking, use of claws, jump, escape and immobility (Kruijt, 1964; McBride et al., 1969).

### *Procedure*

On day 1, ♂ and ♀ experiences were given to the hens. Six to 12 hens were selected at random from the enclosures, fitted with coloured plastic leg bands, weighed, and photographed. The birds were paired so that one hen of each 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 cage. In the meantime, the

opponent remained in its home pen 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 arranged in pairs according to one of the 3 situations presented in upper part of Table 1. Dyads were selected so that a hen that had been victorious the day before encountered one that had been defeated. The pairs left together overnight were thus first separated. 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. 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 there (condition UU). At the end of the final phase, hens were returned to their respective home pens as soon as a victor was proclaimed or after 3 hours of observation, whichever came first.

In the original study by Martin et al. (1997), 37 dyadic encounters were videotaped at length until the dominance criterion was reached. The tapes were later finely analysed as follows: we identified the initiator, the type of behaviour initiated and its moment of occurrence. As well, the behavioural acts, from the onset of the encounter to the first occurrence of the first agonistic behaviour part of the dominance criterion were noted for analysis.

### *Re-use of the same hens*

During the whole experiment, which covered seven months, the same hens served on 1 to 4 occasions separated by at least one month; hens that met always came from different pens. According to Chase (1982), hens no longer recognize penmates after 2 weeks of separation. Moreover, unpublished data from this research unit also indicate that effects of victory or defeat disappear in the hen within 96 hours. Thus, a separation of at least one month spent in its home pen with usual penmates was imposed.

## **Results**

Binary categories were compared using a binomial (Bin) test. 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.

The main results concerning dominance are summarized in Table 1. In general, in the subset of videotaped encounters,  $\alpha$ s significantly defeated  $\omega$ s. Under condition UU, asymmetry in familiarity was neutralised and  $\alpha$ s defeated  $\omega$ s in 10 out of 12 occasions (83.3%), which is significant to a binomial test (Table 1, Row 2). The same is true for condition FU (Row 3). In the three conditions combined (Row 4),  $\alpha$ s won 29 times over a possibility of 37 (78.4%), thus more than explainable by chance alone. Thus, when considering the effect of recent experiences on dominance outcome, the 37 videotaped encounters

can be considered representative of the 83 encounters of the original study (largest 2-tail  $G$ -test = .721,  $P < .396$ ).

**Table 1.** Frequency with which each videotaped opponent won in the final test. Frequencies for the full study of Martin et al. (1997) are indicated between brackets.

	<i>Conditions (n pairs)</i>	Victory went to		<i>Binomial test</i>
		$\alpha$	$\omega$	
1	UF (12 [28])	7 [21]	5 [7]	$P < .38$ [ $P < .012$ ]
2	UU (12 [27])	10 [25]	2 [2]	$P < .019$ [ $P < .001$ ]
3	FU (13 [28])	12 [24]	1 [4]	$P < .002$ [ $P < .001$ ]
4	All (37 [83])	29 [70]	8 [13]	$P < .001$ [ $P < .001$ ]
	<i>Subsets</i>	<i>Familiar</i>	<i>Unfamiliar</i>	
5	FU & UF (25 [56])	17 [31]	8 [25]	$P < .054$ [ $P < .25$ ]
		<i>Heavier</i>	<i>Lighter</i>	
6	All (37 [83])	10 [33]	27 [50]	$P < 0.004$ [ $P < .039$ ]
		<i>Larger C+W</i>	<i>Smaller C+W</i>	
7	All (30 [68])	23 [53]	7 [15]	$P < 0.001$ [ $P < .001$ ]

In the original study, familiarity with the meeting site did not have a significant influence on dominance outcomes (Row 5). However, in the videotaped encounters, individuals familiar with the meeting site had a tendency to win more often than their unfamiliar opponent when conditions UF and FU were combined, but the effect did not reach statistical significance (Row 5).

As in the original study, winners were not significantly heavier/lighter than losers (all combined, one-way Anova  $F_{1,164} = .403$ ,  $P < .75$  and for the videotaped subset:  $F_{1,72} = 3.403$ ,  $P < .069$ ). When superiority in weight was considered, the weight advantage did not covary positively with outcome. In fact, due to the research design, the lighter hens won in 27 out of 37 the encounters, which is statistically significant (Row 6).

In Martin et al. (1997), a significant relationship between dominance outcome and areas of comb and wattles was found. In the videotaped encounters, hens displaying a larger comb plus wattles (C+W) area were also more likely to obtain victory when both were unfamiliar (UU: one-way Anova  $F_{1,20} = 5.282$ ,  $P < .032$ ) but not when one of them was familiar with the meeting site (UF: one-way Anova  $F_{1,20} = 1.170$ ,  $P < .292$ ; FU: one-way Anova  $F_{1,14} = 3.804$ ,  $P < .071$ ). However, when all videotaped data were combined, hens having larger C+W area had a definite tendency to win since they won in 23 of the 30 cases (Row 7; comparison of C+W areas by a one-way Anova:  $F_{1,58} = 8.464$ ,  $P < .005$ ).

It can thus be concluded that, except for the effects of familiarity with the meeting site upon dominance outcome, the videotaped subset appears representative of the original study by Martin et al. (1997).

### *Behavioural analyses*

The following analyses pertain to the 37 videotaped encounters.

#### *Differences between $\alpha$ and $\omega$ hens*

As mentioned above, the hens' recent experience was a deciding factor in the encounter's outcomes. Moreover, preceding experience greatly influenced agonistic behaviour. The  $\alpha$  hens initiated the encounters more often than  $\omega$ s ( $x=29$ ,  $N=37$ , Bin  $P<.001$ ). Hens with previous winning experience were the first to threaten (Mann-Whitney  $U=410$ ,  $Z=-3.618$ ,  $P<.001$ ) and to attack their opponents ( $U=530$ ,  $Z=-1.863$ ,  $P<.031$ ). They threatened more frequently (one-way Anova,  $F_{1,72}=10.469$ ,  $P<.001$ ) and demonstrated offensive behaviour more often (one-way Anova,  $F_{1,72}=4.526$ ,  $P<.037$ ). The  $\omega$  hens tried to escape (one-way Anova,  $F_{1,72}=15.00$ ,  $P<.001$ ) and were motionless more often (one-way Anova,  $F_{1,72}=5.268$ ,  $P<.025$ ).

When these behavioural differences were made to compete with one another in a logistic regression analysis (forward stepwise method), which hen initiated conflict was the only withheld factor. In the videotaped encounters, to threaten or to attack first was very characteristic of  $\alpha$  hens since they first initiated aggressive behaviour in 78.4% of encounters.

#### *Differences between site-familiar and site-unfamiliar hens*

As mentioned above, familiarity with the meeting site had a tendency to, but did not significantly determine dominance outcome. However, differences in behaviour between the familiar and unfamiliar hens appeared. Data from UU encounters were excluded from these analyses since both hens were unfamiliar with the site. Hens familiar with their environment were the first to demonstrate agonistic behaviour in 20 out of 25 occasions ( $x=20$ ,  $N=25$ , Bin  $P<.001$ ). They usually started off the encounter ( $U=134.5$ ,  $Z=-3.553$ ,  $P<.001$ ). They threatened first ( $U=222$ ,  $Z=-.0803$ ,  $P<.012$ ) and did so more often than their opponents (one-way anova,  $F_{1,48}=6.3947$ ,  $P<.01$ ). They also demonstrated offensive behaviour earlier ( $U=235$ ,  $Z=-1.698$ ,  $P<.045$ ), but however, not more often (one-way anova,  $F_{1,48}=0.264$ , ns). The hens which were unfamiliar with their environment escaped more often than their opponents (one-way anova,  $F_{1,48}=4.2$ ,  $P<.046$ ).

When these behavioural differences competed with one another in logistic regression analysis (forward stepwise method), again which hen initiated conflict was the only withheld factor. To threaten or attack first was very characteristic of hens which were familiar with the meeting site ( $\text{Exp}(\beta)=15.99$ , Wald=15.37, df=1,  $P<.001$ ) and this characteristic enabled to correctly distinguish familiar hens from unfamiliar ones in 80% of pairs.

#### *Differences between heavier and lighter opponents*

In the present research,  $\omega$  hens were heavier than their  $\alpha$  opponents in 78.4% of cases. Weight was thus experimentally made inversely correlated with previous victory experience. Therefore, there is no surprise to find that lighter  $\alpha$  hens initiated conflict in 70% of the encounters ( $x=26$ ,  $N=37$ , Bin  $P<.001$ ). They also threatened earlier in the encounter ( $U=436.5$ ,  $Z=3.269$ ,  $P<.001$ ) and threatened more often (one-way anova,  $F_{1,72}=14.31$ ,  $P<.001$ ) than their larger  $\omega$  opponents, and in general they were more

aggressive (one-way anova,  $F_{1,72}=6.88$ ,  $P<.011$ ). Eliminating the 8 encounters in which the  $\alpha$  hen was larger, the same conclusion was reached: lighter  $\alpha$  hens initiated conflict in most encounters ( $x=23$ ,  $N=29$ , Bin  $P<.001$ ).

### *Comb and wattle areas*

Comb and wattle areas, and their combination as C+W area, appeared to have a complex relationship with other variables of the present research. Firstly, total C+W area was found to be highly correlated with recent experience, with  $\alpha$ s systematically possessing larger C+W than ws. The bigger the hen's C+W, compared to its opponent, better the chances were that it might be an  $\alpha$  hen. As a matter of fact, these chances increased by 22% for each  $\text{cm}^2$  of C+W ( $\text{Exp}()=1.22$ ,  $\text{Wald}=6.48$ ,  $\text{df}=1$ ,  $P<.01$ , continuous variable). Simply knowing which hen of the pair showed the larger C+W area permitted correct identification of the  $\alpha$  hen in 87% of all cases ( $\text{Exp}(x\text{betax})=.154$ ,  $\text{Wald}=24.30$ ,  $\text{df}=1$ ,  $P<.001$ , categorical variable). Indeed, out of the 30 pairs for which C+W areas were available, in 24 cases the  $\alpha$  hen had a larger C+W area than its  $\omega$  opponent. Secondly, C+W area superiority was found to significantly predict victory in the final encounter ( $\text{Exp}(\beta)=.304$ ,  $\text{Wald}=15.19$ ,  $\text{df}=1$ ,  $P<.001$ , categorical variable). Knowing which pair member had superiority in C+W area permitted prediction of the winner in 77% of cases. Thirdly, lighter hens possessed significantly larger C+W in 25 out of 30 cases ( $x=25$ ,  $N=30$ , Bin  $P<0.001$ ). Fourthly, the correlation between C+W area superiority and "first-to-initiate" conflict was also significant ( $r=.4$ ,  $P<.002$ ); in 70% of encounters, the hen showing larger C+W area was first to initiate the encounter.

### *Differences between ultimate winners and losers*

In our research, aggressive behaviour was rare. During the 37 encounters, only 5 jumps were observed (3 by future winners, 2 by future losers). Counter-attacks were also very rare. These occurred only 7 times. The future loser submitted to the other hen in 30 out of 37 cases (81.1%) without showing any aggressive behaviour.

Counter-attacks, if and when they occurred, were also very brief. In 6 out of 7 cases when counterattacks occurred, the future loser showed less than 4 aggressive behaviours before submitting. In 19 out of 37 cases (51.4%), the future winner made only one aggressive act before its opponent accepted defeat. After the future winner's third agonistic act, 83.3% of all dyad outcomes were already decided. In only one case, the winner acted aggressively more than 6 times before its opponent submitted. In 11 cases, submission came without any physical contact; the eventual loser hen submitted after a single threat from its opponent.

Reversal of status was not observed. Once a hen showed submissive behaviour, it would inevitably lose. Thus, the encounters ended quickly. In 43% (16/37) of all encounters the winner could be identified after only one minute. After 2 minutes, the percentage was of 64.7%.

Future winners more often (92%) initiated conflicts ( $x=34$ ,  $N=37$ , Bin  $P<.001$ ). They threatened earlier ( $U=411$ ,  $Z=-3.605$ ,  $P<.001$ ) and showed more offensive behaviours (one-way anova,  $F_{1,72}=10.026$ ,  $P<.002$ ). Future winners showed, as first agonistic act, either threats or pecks ( $x=17$ ,  $N=37$ , Bin n.s.). The future losers obviously escaped (one-way anova,  $F_{1,72}=130.5$ ,  $P<.001$ ) or kept still more often (one-way



anova,  $F_{1,72}=9.931$ ,  $P<.002$ ).

We used the forward stepwise method of logistic regression to study the relative importance of certain behaviours and variables to predict, in retrospect, the encounters' outcome. When all behavioural independent variables were let to compete with one another, initiating conflict ( $\text{Exp}(\beta)=94.49$ ,  $\text{Wald}=24.63$ ,  $\text{df}=1$ ,  $P<.001$ , dichotomic variable) could be used to correctly identify the winner in 34 out of 37 (92%) of the observed cases, which is quite exceptional.

### *Integration of factors*

Since comb and wattles area, recent experience, first to attack and dominance outcome were highly inter-correlated, it seemed imperative to examine the possible paths of influence leading to victory. Our main hypothesis was that previous experience (together with familiarity) influenced which hen initiated encounter, which in turn determined dominance outcome. One rival hypothesis was that C+W areas, rather than recent experience (combined with familiarity), influenced first-to-initiate, which in turn influenced dominance outcome. In other words, the rival hypothesis stated that C+W area served as a precursor of recent experience and/or of first-to-initiate. Indications of the respective roles of these factors can be obtained by the use of higher-order partial correlations as *ex post facto* control (Darlington, 1990).

Correlations were thus calculated between each pair of variables while keeping one or more variables "partialled out" of the relationship. The bivariate correlation between previous experience and first-to-initiate reached significance ( $r=.533$ ,  $\text{df}=59$ ,  $P<.001$ ). The same applied to the correlation between C+W area *superiority* and first-to-initiate ( $r=.4$ ,  $\text{df}=59$ ,  $P<.002$ ). When the correlation of recent experience with first-to-initiate was controlled for C+W superiority, it remained significant ( $r=0.48$ ,  $\text{df}=59$ ,  $P<.001$ ). On the contrary, when the correlation between C+W superiority and first-to-initiate was controlled for recent experience, it lost all statistical significance ( $r=.016$ ,  $\text{df}=59$ ,  $P=.9$ ). This supports the hypothesis that it is recent experience rather than C+W superiority which influences first-to-initiate. A similar conclusion was reached when partial correlations between these variables and dominance outcome were examined: previous experience remained significant while C+W superiority lost all statistical significance, indicating that the path of influence passed from previous experience to dominance outcome rather than from C+W superiority to dominance outcome. Moreover, the significance of the correlation between familiarity and first-to-initiate remained unaffected by the control of C+W superiority (and of previous experience). As for the correlation between first-to-initiate and dominance outcome, it remained significant when recent experience, familiarity, and C+W superiority were kept out ( $r=.784$ ,  $\text{df}=59$ ,  $P<.001$ ). These analyses thus support the hypothesis that previous recent experience and familiarity with the site --- and not C+W superiority --- were the principal factors determining which hen would initiate conflict; together, these two variables could be used to retrospectively identify 80% of initiators. Once the first aggressive behaviour had been initiated, it further led to the victory of its initiator in 92% of cases.

### **Discussion**

The present results confirm that previous dominance or submissive experience influences not only the dominance outcome but also the hens' behaviour during the encounter. Hence,  $\text{O}_2$  hens win significantly

more encounters than their opponents. They are also the first to show aggressive behaviour and, as reported by Zayan (1987), they are more aggressive. They threat and peck more often than do their opponents.

Familiarity with the meeting site shows less clear effects. In the original study by Martin et al. (1997) hens that have been familiarized for 2 hours with their meeting site did not win significantly more often than their unfamiliar opponents. In the present videotaped subset, effects of site familiarity on dominance outcome almost reached significance. Moreover, familiarity with the encounter site had, most definitely, an impact on the hens' behaviour. As a matter of fact, hens that were familiar with the meeting place initiated the encounter more frequently than their unfamiliar opponents. This happens to be the most distinguishable factor between familiar and unfamiliar hens. Though familiar hens did not demonstrate offensive behaviours more frequently, their latency period was shorter. These results on behaviour confirm those obtained by Zayan (1987).

One might think that familiarity with the environment can alleviate a hen's stress resulting from the presence of an unknown adversary. Can it induce the hen to attack first? Being familiar with a site probably advantages an individual because it is not subjected to the stress of adapting to a new environment and is therefore less likely to experience fear than the newcomer (Thinès and Heuts, 1968; Beaugrand and Zayan, 1985). It can then concentrate more rapidly on the new situation (Rowell, 1974).

In our research, we have to emphasize the minimal and conciseness of agonistic behaviour needed to establish a dominant order within the hen dyads. As in the Huntingford and Turner's study (1987) on fish, exchanges are in most cases unidirectional. The latency of conflict resolution was very short: after two minutes, two-thirds of the mutual relation is established. In more than 80% of all cases, the future dominated hen submitted to the other hen without displaying any aggressive behaviour.

This study did not obtain the expected sequence of assessment at a distance-threat-attack-decision which is typical in some animal conflicts. Future winners were the first to initiate the attack by a threat or a peck. It is possible that the future loser adopted a posture, which remained unidentifiable to the human observer, but which would have indicated to the opponent a willingness to submit. It is possible that future winners could have identified these signs, which were unnoticed by the human observer. This could be a reason for the short length of the interactions and the absence of the observation and threat phases in our experiment.

From a behavioural point of view, hens that won usually initiated the encounters. They showed more aggressive behaviours and were the first to do so. The animal that started the interaction, in most cases, became victorious. This result confirms those obtained in hens by Bronstein and Brain (1991), Collias (1943), Hogue et al. (1997), Huntington Potter (1949), and Ligon et al. (1990).

Knowledge of some animals' physical attributes or past dominance history enables the human observer to predict the direction of the dominance relation when those animals are put together (Beaugrand et al., 1991, 1996). Behavioural acts evident at the onset of an encounter can also help to predict, with a high success rate, which subject will dominate. During an aggressive agonistic encounter, the animal offers the observer, in first-to-initiate or "first-to-attack" behaviour, valuable information concerning the subsequent agonistic behaviour (Bronstein and Brain, 1991). Of all the different factors observed in the present research, initiation of the encounter and the prior status of the adversaries were the best indicators of the hens' future dominance status.

We have mentioned that 92% of all encounters were initiated by future winners; in the 25 encounters between familiar and unfamiliar opponents, 80% were initiated by the familiar pair members but the tendency of residents to obtain victory did not reach statistical significance ( $x=17$ ,  $N=25$ , 1-tail Bin  $P<.054$ ). Since the significance is borderline, future research should replicate the present study while increasing sample size.

The relationship obtained in the present research between comb and wattles areas with recent experience as well as with ultimate victory has to be further examined. In the present research, comb and wattles size was not under experimental control. These measures were not obtained in order to equalize opponents in these aspects, nor to create levels in the corresponding independent variables to study their effect on behaviour and dominance outcome. They were simply measured, to be correlated *ex post facto* with other variables. We found that hens with superior comb and wattles areas won significantly more initial meetings than opponents with smaller combs and wattles. This means that, when hens were divided into two sub-samples, one of winners and one of losers, comb and wattle areas were also co-selected. The result was that birds of the ♀ sample had in general larger comb and wattles than birds of the ♂ sample. The same occurred in the final contest. Victory went more frequently to the bird showing larger comb and wattles, which happened also to be the ♀ hen in a majority of cases, as well as the lighter individual of the pair.

These results on the importance of comb and wattles upon dominance outcome in the hen support those obtained by Allee and Collias (1938), Guhl and Ortman (1953), Ligon et al. (1990), and Cloutier et al. (1996). As suggested by Rushen (1984), comb size is probably used by the hens as a salient cue in assessing the potential of an opponent. 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). Future research should measure/monitor hormonal levels, and make comb and wattles size independent of recent experience.

Our hypothesis to account for the present data is that recent experience and familiarity together determined which pair member first initiated attack, which in turn determined which animal obtained victory. The size of comb and wattles were accidental collinears of having won. A rival hypothesis is that basic aggressiveness, of which the comb and wattles size serve as an index for the human observer and as a salient cue for the opponent, rather than recent experience (combined with familiarity), influenced aggressive behaviour and dominance outcome. In other words, the rival hypothesis states that comb and wattles served as a precursor of recent experience and/or of first-to-initiate. Clearly, further experimental work is required to eliminate one of these alternatives. However, the rudimentary path-analysis that we did relying on higher-order partial correlations supports the hypothesis that recent experience and familiarity with the site --- and not comb and wattles --- were the principal factors determining which hen would first initiate encounter. Together, these two variables could be used to retrospectively identify 80% of future initiators. Once the first aggressive behaviour had been initiated, it led to the victory of its initiator in 92% of cases. The difference between the two percentages will have to be accounted for by factors other than recent experience and familiarity, which together with these two last factors would determine which hen will first initiate aggressive behaviour. Paradoxically, comb and wattles could play that role. The influence of comb and wattles upon first-to-initiate (or upon dominance outcome) was overshadowed in the present results by that of recent experience and site familiarity, whose effects were experimentally made in coherence, i.e. artificially aligned. Under more natural and "noisy" conditions, when many factors are simultaneously playing partly in opposition, comb and wattles size is most

probably a very powerful social indicator of internal state (hormonal), motivation and possibly of the prior general status (high or low in the peck-order) in the flock of origin. Its mutual assessment when there is a conflict between two unfamiliar hens is surely influential upon which bird will first attack the other.

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. Nonetheless, comb and wattles size was co-selected with the repartition of the birds into victorious and defeated ones at the issue of rigged contests in which victory and defeat had been correctly forecast. This raises serious questions either about the effectiveness of the control procedure suggested by Bégin et al. (1996), or about the generality of co/self-selection in the present domain.

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