S-29.3: Plumage coloration as a signal of social status
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In 1975 Rohwer proposed that variable plumage traits of wintering flocking birds evolved to signal individual dominance status. Evidence from more than 50 papers on the so-called status signaling hypothesis has been mixed and interpretation of the hypothesis remains controversial. Disagreement centers on whether signaling between (but not within) sex/age classes is support for status signaling: some authors claim that if the trait is only used to signal dominance between classes, it is still a badge of status since individuals use it to avoid useless and risky confrontations; however, it is also (and perhaps more convincingly) argued that a true signal of status should work both between and within age/sex classes, and that cases of signalling between classes may have evolved for reasons unrelated to status signalling. Mixed results have been obtained when introducing plumage-manipulated birds into a group to test for changes in dominance. In such studies there is confusion between demonstrating that the trait is a true signal and demonstrating the existence of mechanisms to avoid cheating so that the trait may be evolutionarily stable. There is also confusion between which is the tested bird: the manipulated one or the individual reacting to the manipulation. The reliability of the signaling system also remains controversial, although some specific hypotheses seem to fit data so far obtained. There is agreement that the system may better fit agonistic encounters between strangers, and whenever asymmetries such as prior ownership or differential hunger level are not present. However, more work is needed, and from more species, especially on heritability and fitness of individuals with different sized badges of status.

INTRODUCTION
Rohwer (1975) proposed that the variation and extent of color patches in the plumage of wintering birds could work as badges of social status. The major advantage of these signals would be that individuals of unequal status competing for limited resources would not need to risk accidental injury or waste energy assessing the relative fighting ability of potential opponents (Rohwer 1982). The so-called status signalling hypothesis has been tested in several species with variable plumage (table 1), but results so far obtained from more than 50 papers are mixed and interpretation of the hypothesis remains controversial.

In this paper I review the logic of the status signalling hypothesis and evidence in favour and against it. I assess alternative results and interpretations, try to identify areas of general agreement and suggest possible reasons for disagreement. The aim of this paper is therefore to try to clarify when there may be a true signalling of social status.
STATUS SIGNALLING OR INDIVIDUAL RECOGNITION?

An old controversy on plumage variability in flocking wintering birds, appearing just after the stimulating paper by Rohwer (1975), was whether this plumage variation had evolved for status signalling or simply for individual recognition (Shields 1977; Rohwer 1978). Whitfield (1987) reviewed the topic and concluded that in some species, especially those forming small and stable flocks, individual recognition was sufficient to explain plumage variation (Whitfield 1986; Ens & Goss-Custard 1986; Rohwer & Roskaft 1989; Watt 1986b), but in other species the correlation found between plumage badges and dominance (Table 1) or the results of several experiments (Watt 1986b; Watt 1986a) strongly suggested that a true status signalling could occur. More than a decade after the work by Whitfield, his view on the occurrence of a true status signalling still holds (Krebs & Davies 1993).

STATUS SIGNALLING OR JUST A CORRELATION?

The presence of plumage-related differences in success in agonistic encounters (Table 1) suggests the existence of a status signalling system related to plumage coloration. However, it has been widely recognized that a correlation of a plumage trait with dominance is not by itself evidence for signalling, since individuals could assess their social status by other means, and plumage could simply be a correlated trait rather than a signal (e.g. Roper 1986; Jones 1990; Slotow et al. 1993).

Three different approaches have been used to test for a signalling function of plumage traits (table 2). In several experiments, the plumage trait has been manipulated and the experimental individual has been introduced into a group to test for a gain in social rank (table 2). This experimental approach has produced mixed results, probably because there are many different masking variables which should be taken into account. In the oldest experiments (Rohwer 1977; Rohwer & Rohwer 1978), for instance, manipulated birds were reintroduced into existing social groups, so that either the experimental birds were known to flockmates as subordinate (Ketterson 1979), they withdraw from recognized dominant flockmates (Shields 1977; Ketterson 1979), or, if the manipulation prevented any flock companion recognition, the experimental birds might have been in disadvantage just because of a prior residence advantage by the birds in the group (Järvi et al. 1987; Fugle et al. 1984) (see below). To avoid these problems, more recent experimental approaches have exposed manipulated birds to unfamiliar conspecifics in neutral cages (e.g. Järvi et al. 1987; Lemel & Wallin 1993), or the plumage of both dominants and subordinates has been manipulated (e.g. Grasso et al. 1996). However, the introduction of a manipulated bird into a group is not a good way to test for the signal nature of a trait because we are potentially confounding the demonstration that the trait is a true signal with the demonstration of the existence of mechanisms to avoid cheating so that the trait may be evolutionarily stable. For instance, if a bird with the dominance badge enlarged does not beat presumed dominant flock companions (e.g. Rohwer 1977; Rohwer & Rohwer 1978; Järvi et al. 1987; Moller 1987a) it does not mean that the trait is not a signal, since mechanisms to avoid cheating, as for instance that birds may be attentive not only to the trait but also to the behaviour, may be operating (see below). In this kind of experiment there is an additional confusion between which is the tested bird: the manipulated one or the individual reacting to the manipulation. Some of these experiments were designed to test whether the manipulated bird was able to rise in a dominance hierarchy, and although these experiments implicitly assume a change in the behaviour of unmanipulated birds as a result of opponent’s badge enlargement, a test of dominance recognition should test whether birds show any preference (or avoidance) between individuals differing in apparent dominance (i.e. the tested bird is not the
manipulated one, but the individual reacting to the manipulation). Another most important point for a good test of the status signalling function of a trait is that we should also record whether birds avoid probable dominants (e.g. manipulated) on the first encounter(s) (Geist 1966; Watt 1986b); otherwise other factors may mask the relationship (see below). This immediacy is not the case in several studies, especially because the recording of dominance relationships need to be based on several encounters which take place over a relatively long period of time (e.g. 30 minutes in Lemel & Wallin [1993], one month in Fugle et al. [1984]).

The problems associated with the use of manipulated live birds introduced into a group may be solved by the use of models (either stuffed or artificial). This approach has been used for several species (Table 2). Here results are more conclusive, with test birds avoiding models with enlarged badges of status, in the first encounter. This strongly suggests that these traits are recognized as signals of social rank.

The third approach used has been choice experiments (Table 2), in which it was tested whether individuals can recognise dominant competitors by plumage alone by recording active choice between feeding close to a cage containing a live dominant bird or close to another cage containing a live subordinate (Senar & Camerino 1998). The trait under study was enlarged or removed, a robust approach that has rarely been used (e.g. Rohwer [1977], but with a very small sample size of n=2 birds with trait removed, Grasso et al. [1996] with a sample size of n=7). Birds avoided large badge d individuals, either natural or enlarged, but did not avoid the individuals for which the badge had been removed, strongly suggesting that the trait under study worked as a true signal of social status.

Hence and overall, manipulative experiments confirm that in several species plumage coloration traits are not only correlated to dominance but are readily used by conspecifics as signals of social status per se.

SIGNALLING BETWEEN (BUT NOT WITHIN) SEX/AGE CLASSES
Another old controversy on status signalling refers to whether signalling between, but not within sex and age classes, should still be regarded as a true case for status signalling. The original description of the status signalling hypothesis assumed that it should work both between and within sex/age classes (Rohwer 1975) (although in fact the species under study only exhibited an inter-age/sex signalling [Watt 1986b]). The most common reasoning to support the original formulation is that plumage variability among birds of a different age and sex may have evolved for reasons completely unrelated to status signalling and that if a plumage trait is a true signal of social status it should also be used within classes (Balph et al. 1979; Whitfield 1987; Maynard Smith & Harper 1988). However, some other investigators claim that if the trait is used to signal dominance between classes, it is still a badge of status since individuals use it to avoid useless and risky confrontations (Watt 1986a; Ketterson 1979; Jones 1990). The controversy, therefore, is in fact a debate between present versus original functions. My own view is that a true badge of status should work both between and within classes and that cases in which the system only works between classes have very probably evolved under other selection pressures (e.g. crypsis or delayed plumage maturation), being in some cases secondarily used as signals of status (see Booth [1990] for a discussion between adaptation and current utility in relation to coloration). For instance, there are cases in which juvenile birds signal their lower competitive ability in order to avoid heightened aggression from adult birds (Studd & Robertson 1985b; Lyon & Montgomerie 1986; Stutchbury & Robertson 1987; McDonald 1993; Muehter et al. 1997; Senar et al.
1998) (the so called Delayed Plumage Maturation, Rohwer et al. [1980]). For these birds it is enough to signal their juvenile-subordinate status (Studd & Robertson 1985b), so that there is not too much use in a graded signal that works within in addition to between age classes (in some cases plumage coloration may be graded within age classes [e.g. Hill 1989; Senar et al. 1998], but there is still a significant difference in plumage coloration between ages). Cases such as the White-crowned sparrow (Zonotrichia leucophrys) or the Harris’ sparrow (Z. querula) (Table 3), in which badges of status only work between (but not within) juvenile and adult birds, could perhaps be better related to Delayed Plumage Maturation than to Status Signalling theory. A similar argument could be used to discuss intersexual plumage differences (see Balph et al. [1979]).

**BIRDS WITH THE GREATER BADGES DO NOT ALWAYS WIN**

Birds with the greater badges of status are dominant over birds with smaller badges (Table 1). However, there are cases in which the relationship may reverse. Lemel & Wallin (1993) showed in the Great tit (Parus major) that changes in motivation (e.g. hunger level) could allow hungry small badged birds to dominate larger badged ones. This is equivalent to other data on general dominance relationships not directly related to status signalling, in which hungry subordinates are able to beat otherwise dominant individuals (Andersson & Åhlund 1991; Popp 1987), and agrees with the theoretical view that when the value of the contested resource is high relative to the cost of fighting, contests should not be settled by plumage (i.e. non-costly) traits (Maynard Smith & Harper 1988).

Similarly, in territorial species, the prior ownership advantage (Hammerstein 1981; Leimar & Enquist 1984; Hughes 1986; Austad 1989) may override any badge of status advantage (Rohwer 1982; Wilson 1992). In these territorial species, badges of status may therefore only be efficiently used during the juvenile dispersal period before territory settling (Lemel & Wallin 1993; Wilson 1992) or, in migratory species, just in the phase of territory establishment (Pärt & Qvarnström 1997) (see however Studd & Robertson [1985c]). Given the similarity between prior-ownership in territorial species and prior-residency in flocking species (Oberski & Wilson 1991), we should also expect that small-badged individuals may sometimes dominate large-badged individuals when entering the flock. This has been recently found when analysing agonistic interaction between resident and transient siskins (Carduelis spinus) (Senar unpublished).

Finally, badge size seems to have no impact on the outcome of agonistic interactions between individuals with prior experience of each other (Lemel & Wallin 1993). In fact, the status signalling hypothesis was originally set out as a way of reducing agonistic confrontations between individuals unaware of the resource-holding potential of opponents (i.e. strangers) (Rohwer 1975). As a consequence, status signalling should be specially relevant in nomadic species (e.g. siskins), since an individual, even if living in a group of relatively stable membership, can interact with thousands of different individuals in a single winter (Senar et al. 1992).

**AND HOW IS THE RELIABILITY OF THE SYSTEM MAINTAINED?**

In a group of mountain sheep the males with the largest horns are dominant. This is so because during a fight large horns confer a genuine advantage on their possessor (Geist 1966). However, it is hard to see how the colour of the plumage could physically enhance
competitive ability. This is why it is said that plumage signals of status are arbitrary or conventional (Roper 1986; Maynard Smith & Harper 1988). The problem with this is that subordinates could easily pretend to be dominants simply by adopting the appropriate badge of status, so that in the end status signalling would not be evolutionarily stable. The problem is complicated by the fact that true signals of status, to be useful, should be recognized before any real fights takes place (Watt 1986b). To solve this evolutionary puzzle, several hypothesis have been proposed.

Theoretical studies suggest that honest signalling of status could be stable whenever cheaters payed a high cost against highly dominant opponents (Maynard Smith & Harper 1988). Rohwer (1977), Rohwer & Rohwer (1978) and Järvi et al. (1987) proposed that birds should be attentive to behaviour in addition to plumage cues, and that dominants would persecute any cheaters because of the perceived incongruity between their behaviour and their status signals (the incongruence hypothesis). The reason why dominants ought to act despotically would not be because cheats are cheats, but because such incongruent individuals are usually sick birds (e.g. a dominant individual which becomes ill), and thus easy to chase away from limited food resources (Rohwer & Rohwer 1978). However, in its original form, the incongruence hypothesis did not explain why behavioural cues should be disbelieved in one context and morphological cues in another. Additionally, the described tendency to punish cheats was difficult to explain in terms of advantage to the individual (Caryl 1982). The hypothesis was therefore modified and re-named the sceptical recipient hypothesis by Caryl (1982), who suggested that in agonistic encounters animals should do the following: where cues to dominance are inconsistent, it is better to believe the least impressive information that the opponent provides, basically because no one lies to devalue ones self. The hypothesis was backed by a series of experiments in which subordinate birds either were painted to look as dominants, were injected with testosterone to behave aggressively as dominants, or were both painted and injected (Rohwer 1977; Rohwer & Rohwer 1978; Järvi et al. 1987). Subordinates only were able to rise in the dominance hierarchy and to beat dominants in the last experiment, in which birds not only appeared but also behaved as dominant. It seems therefore that dominance signals must be backed up by dominant behaviour and a plumage signal. However, although these authors could be right, the experimental approach of increasing dominant behaviour by injecting testosterone may be flawed for the winter situation (Holberton et al. 1989). There is no evidence that winter aggression in flocking birds is mediated by testosterone (Belthoff et al. 1994), and by injecting it in winter we may force the birds to enter breeding condition and to behave as territorial birds rather than as dominant ones only (Holberton et al. 1989). From another point of view and because of the prediction of the incongruence hypothesis that birds should be tested/attacked when behaviour and signal are incongruent, the fact that in several species individuals are able to increase dominance just by having their plumage dyed (Table 2) clearly falsifies it.

As an alternative to the incongruence hypothesis, Rohwer (1977) and Rohwer & Rohwer (1978) proposed the social control hypothesis, which suggests that a subordinate will encounter relatively more aggression from true dominants as a cheat than as a honest signaller, simply by the fact that dominants are normally fighting each other. As the intrinsic fighting abilities of subordinates on average are lower than those of true dominants, the heightened aggression cheats receive is a cost that would outweigh any benefits arising from increased dominance status. According to the hypothesis, and in order to be evolutionarily stable, the heightened aggression should not result from the 'persecution' of cheat by true dominants in the population, but should be the result of dominant individuals interacting
more with other dominant birds than with subordinate ones (the so called “like-versus-like aggression” between dominant individuals) (Rohwer & Rohwer 1978; Moller 1987a; Slotow et al. 1993). The social control hypothesis has been tested in several species (Rohwer 1977; Rohwer & Rohwer 1978; Balph et al. 1979; Ketterson 1979; Rohwer & Ewald 1981; Moller 1987a; Slotow et al. 1993; Keys & Rothstein 1991). However, the results are highly contradictory (see Slotow et al. [1993] for a review). The social control of cheating requires the occurrence of like-versus-like aggression between dominant individuals, and this has been shown not to be always the case (see Table 4 and Slotow et al. [1993] for a critical review of the data). Similarly to the incongruence hypothesis, the social control hypothesis also predicts that birds with a dominant appearance should be tested/attacked and the fact that in several species individuals are able to increase dominance just by having their plumage dyed (Table 2) also falsifies it (Slotow et al. 1993). Additionally, theoretical analysis show that social control is not enough to maintain the evolutionarily stability of the status signalling system, since small-badged dominant individuals could invade the honest population (Owens & Hartley 1991; Johnstone & Norris 1993). Nevertheless, and as Caryl (1982) has pointed out, the presence of individuals lying to devaluate ones self is doubtful.

There is an additional problem with any test of these two hypotheses. Tests have always focused on the response of dominant birds (i.e. whether or not they attacked cheats). However different interpretations can be drawn from such data. For instance, the fact that subordinates dyed to look like dominants (cheats) do not incur increased aggression from true dominants does not necessarily mean that they have deceived their flock companions; instead they may be actively avoiding confrontations with these birds, or dominants may actually recognise them as subordinates by their behaviour but do not attack them because they are not a real threat. This makes any test of both the incongruence and the control hypothesis even harder to achieve. We have also previously mentioned how important familiarity between the birds may be to resolve agonistic encounters, so that it should be taken into account in any test of the incongruence or social control hypothesis (Grasso et al. 1996).

Alternatively predation risk has been suggested as the selective force controlling cheating (Balph et al. 1979; Fugle & Rothstein 1987; Fugle et al. 1984; Slotow et al. 1993). The hypothesis assumes that individuals displaying large badges of status are more easily detected by predators, but that true dominant individuals may compensate the handicap of higher conspicuousness with higher experience and ability to escape predators. A higher predation risk associated to larger badges of status has been suggested for the House sparrow (Passer domesticus) (the tendency was far from clear since it was only significant for a part of the population and only in autumn) (Moller 1989). However, since badges of status are normally small and black, it is hard for me to believe that one centimetre more of black in the breast will make that bird more easily detected by a predator. Additionally, highly conspicuous colours as for instance black-and-white, may be disruptively cryptic in contrasting backgrounds (Götmark & Hohlfält 1995). It could be alternatively, and as Veiga (1993) has suggested, that dominant birds (with the larger badges) are more active (Moller 1990) or exposed than subordinates and hence are more easily located and predated (Götmark et al. 1997). It is also doubtful that dominants are more experienced than subordinates (e.g. Wiley 1991), unless dominance is for instance correlated to age (Enoksson 1988; Desrochers 1992); so predation risk could perhaps select for small badges of status within the context of Delayed Plumage Maturation (see before). Empirical data to support (or reject) the differential predation hypothesis does hardly existent, but perhaps experiments with mounts may be useful (Götmark & Unger 1994).
As outlined before, the main evolutionary problem with badges of status is their arbitrary nature. However, the identification of a production cost for these badges would solve part of the problem (Owens & Hartley 1991; Johnstone & Norris 1993). It has been suggested that if testosterone plays a role in badge production, its immunodepressive effects (Zuk et al. 1990; Folstad & Karter 1992; Saino et al. 1995; Moller et al. 1996; Saino & Moller 1996; Silver et al. 1996) would determine that large badges of status would be maintained only by individuals that survive despite this indicator. However, badges are produced during the annual moult, in late summer or early autumn, when gonadal activity is low, thus casting doubt on the suggested relationship between testosterone and badge size (Veiga 1993). Other handicaps (Grafen 1990) of bearing large badges of status, not related to social behaviour or predation risk, have also been suggested. For instance, House sparrows experimentally manipulated to be cheaters by increasing their bib area, had reduced survival, probably because of their increased breeding effort (Veiga 1995). Nevertheless, it is still unclear how processes related to breeding strategies may be relevant to social strategies during the wintering season. A higher metabolic rate has been suggested as a cost to dominance (Roskaft et al. 1986; Hogstad 1987; Bryant & Newton 1994; Reinertsen & Hogstad 1994; Cristol 1995a) and hence has also been suggested as a cost to large badges of status (Johnstone & Norris 1993). In status signalling species, however, we should predict just the reverse, a higher metabolic rate for subordinate individuals than for dominants, since subordinates have to be continuously attentive to and actively avoiding large badged flock companions meanwhile dominants enjoy preferential access to resources just by signalling their higher fighting ability (Senar & Camerino 1998). Data on Siskins support this prediction (Senar et al. in preparation).

A totally different view to account for the control of deception, is to suggest that social hierarchies are examples of a mixed evolutionarily stable strategy (mixed ESS) (Maynard Smith 1982). Here individuals of different status are presumed to pursue different but equally fit strategies, so that the existence of a social hierarchy is to the direct advantage of each individual (Rohwer 1982; Maynard Smith 1982; Roper 1986). By abandoning the assumption that dominants are at advantage and that subordinates are willing to become dominants (“hopeful dominants”, West Eberhard 1975; Ekman 1989; Hogstad 1989), the evolutionary puzzle about deception is solved (Rohwer 1982). Species displaying a feudal social system (Rohwer & Ewald 1981; Senar et al. 1990a; Wiley 1990; Cristol 1995b; Senar et al. 1997) conform nicely to this view. A prediction from this hypothesis is that the distribution of badges of status should be bimodal, but this has only been found for the Siskin (Fig. 1) (Senar et al. 1993); the Harris’ sparrow, for instance, displays a normal distribution (Rohwer 1982). Data on reproductive success in Yellow warblers (Dendroica petechia) suggests that dominant and subordinate birds may follow different equally successful strategies (Studd & Robertson 1985a) (but see Yezerinac & Weatherhead 1997). However, there are many other reports which suggests that dominants are at a clear advantage in many different respects (for a review see Senar 1994), so that an idea of a mixed ESS for dominance hierarchies may not be general.

Summarising, there are several hypotheses that try to explain how the reliability of the status signalling system is maintained, but none of them is fully supported by the data. Hypotheses that fit one species are falsified in others. Perhaps there is no single route to badges of status and therefore there is no unique mechanism to maintain the honesty of the signals. The kind of social organization displayed by the species (e.g. feudal versus despotic [Senar et al. 1997]) may be highly relevant. In a feudal social system both dominants and subordinates may be equally fit (mixed ESS, see before) allowing for the stability of the
system; meanwhile, in a despotic social system, in which only dominants are at advantage, other mechanisms should be at work. For some species sexual selection may well explain the evolution of some armaments (Berglund et al. 1996), while in other species, the traits may only have evolved by social selection (Tanaka 1996). For instance, displaying a trait that developed by social selection may favour both dominants and subordinates and this may be enough to explain the stability of the signal (see before), but if the trait is additionally selected by females in mate choice, subordinates may be at disadvantage and the stability of the trait should be explained in another way. Therefore, the present overview of hypotheses clearly shows that honest signals are possible (Maynard Smith & Harper 1988; Grafen 1990) (see tables 1 & 2), that there are different ways of controlling of cheating, but there is no obvious reason for one way to be the unique one.

**CONCLUDING REMARKS**

More than two decades after its original description, the status signalling hypothesis remains controversial. More data and from more species are still needed, so that we can find a logic for interspecific variability so far presented. More data are also needed on the heritability of the different traits. We know for instance that the black bib of the House sparrow (Moller 1989), the black tie of the Great tit (Norris 1993) or the white forehead patch of the Collared flycatcher (*Ficedula albicollis*) (Sheldon et al. 1997) are heritable, but these traits are also highly related to sexual selection (Moller 1989; Moller 1990; Norris 1990b; Norris 1990a; Gustafsson et al. 1995; Sheldon et al. 1997; Qvarnström 1997) which might affect heritability. To which point signals of social status may be related to sexual selection is an additional issue that needs further research. Although an evolutionary explanation for armaments that become ornaments has been proposed (i.e. traits of dual utility) (Berglund et al. 1996), this is not (nor needs to be) always the case (Jones 1990). For instance, some traits may just evolve under social selection, and females may not use the trait for mate choice (e.g. the black bib of the Siskin, Senar unpublished). Finally it could be very useful to have data on fitness of individuals with different sized badges of status, and to know how fixed are these traits within individuals. Until we get more data on all of these different topics we can at least safely say that badges of status exist, that they are true signals of dominance ability and that they may be evolutionarily stable, which in reality is as saying that Rohwer’s hypothesis is supported, at least during certain circumstances.

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Table 1. Overview of the different species for which a relationship between plumage colour and dominance is available. The body area related to dominance is provided. In all the cases the relationship between the two variables is positive. Under the correlation heading, $r^2$ refers to percentage of dominance explained by the size of the plumage trait (according to a regression); when only a percentage is provided it refers to the proportion of contests in which the bird with the larger badge won agonistic encounters. In some cases neither of these two values is provided in the literature. Data on the Pine Siskin (Balph & Balph 1979) is not included because results are doubtful (Jones 1990) and never were published.

<table>
<thead>
<tr>
<th>Species</th>
<th>Nature of plumage variability</th>
<th>correlation</th>
<th>Author(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spheniscus demersus</td>
<td>black &amp; white contrast on head</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Aethia pusilla</td>
<td>white underpart</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Cinclus cinctus</td>
<td>area of the chesnut lower breast</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Agelaius phoeniceus</td>
<td>red epaulets</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Nectarinia johnstoni</td>
<td>scarlet pectoral tuft</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Dendroica petechia</td>
<td>brown streaking in breast</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Ficedula albicollis</td>
<td>frontal white patch</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Parus major</td>
<td>black breast stripe</td>
<td>$r^2= 74%$</td>
<td>8-11</td>
</tr>
<tr>
<td>Parus montanus</td>
<td>black breast stripe</td>
<td>$r^2= 92-96%$</td>
<td>12</td>
</tr>
<tr>
<td>Fringilla coelebs</td>
<td>red breast</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Carduelis chloris</td>
<td>plumage yellowness</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Carduelis spinus</td>
<td>black bib</td>
<td>$r^2= 50-70%$</td>
<td>14</td>
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<tr>
<td>Passer domesticus</td>
<td>black bib</td>
<td>$r^2_s = 27-79%$</td>
<td>9,15</td>
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<td>Emberiza calandra</td>
<td>black bib</td>
<td>9</td>
<td></td>
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<tr>
<td>Junco hyemalis</td>
<td>head and bib blackness</td>
<td>69%</td>
<td>16,17</td>
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<td>Zonotrichia querula</td>
<td>head and bib blackness</td>
<td>75%</td>
<td>18</td>
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<td>Zonotrichia leucophrys</td>
<td>black and white in head</td>
<td>87-96%</td>
<td>19,20</td>
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Authors:
Table 2. Overview of the different experiments carried out to test for the dominance signal nature of plumage traits. In all the experiments the stimulus birds were manipulated enlarging the badge of status.

<table>
<thead>
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<th>Experiment</th>
<th>Species</th>
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<td>Parus major</td>
<td>raising dominance</td>
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<td>subordinates</td>
<td></td>
<td>no effect</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Zonotrichia querula</td>
<td>raising dominance</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>no effect</td>
<td>4,5</td>
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<tr>
<td></td>
<td>Zonotrichia leucophrys</td>
<td>raising dominance</td>
<td>6-8</td>
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<td></td>
<td>Junco hyemalis</td>
<td>raising dominance</td>
<td>9,10</td>
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<td></td>
<td>Fringilla coelebs</td>
<td>raising dominance</td>
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<tr>
<td>model presentation</td>
<td>Aethia pusilla</td>
<td>model avoidance</td>
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<td></td>
<td>Dendroica petechia</td>
<td>heightened aggress.</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>Setophaga ruticilla</td>
<td>no effect</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Parus major</td>
<td>model avoidance</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Parus montanus</td>
<td>model avoidance</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Passer domesticus</td>
<td>model avoidance</td>
<td>17</td>
</tr>
<tr>
<td>choice tests</td>
<td>Carduelis spinus</td>
<td>large badges avoided</td>
<td>18</td>
</tr>
</tbody>
</table>

Authors:
Table 3. Circumstances in which a relationship between plumage variability and dominance appears. The relationship may appear between sexes, ages or individuals (i.e. within ages and sexes).

<table>
<thead>
<tr>
<th>Species</th>
<th>sexes</th>
<th>ages</th>
<th>individuals</th>
<th>author</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aethia pusilla</em></td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>1</td>
</tr>
<tr>
<td><em>Parus major</em></td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>2, but see 3,4</td>
</tr>
<tr>
<td><em>Parus montanus</em></td>
<td>--</td>
<td>--</td>
<td>Y</td>
<td>5</td>
</tr>
<tr>
<td><em>Junco hyemalis</em></td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>6</td>
</tr>
<tr>
<td><em>Zonotrichia leucophrys</em></td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>7,8</td>
</tr>
<tr>
<td><em>Zonotrichia querula</em></td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>9-11</td>
</tr>
<tr>
<td><em>Fringilla coelebs</em></td>
<td>Y</td>
<td>--</td>
<td>--</td>
<td>12</td>
</tr>
<tr>
<td><em>Carduelis spinus</em></td>
<td>--</td>
<td>Y</td>
<td>Y</td>
<td>13</td>
</tr>
<tr>
<td><em>Passer domesticus</em></td>
<td>--</td>
<td>Y</td>
<td>Y</td>
<td>14, but see 15</td>
</tr>
</tbody>
</table>

Authors:
Table 4. Overview, for different species, of the direction in which most agonistic aggressions take place. In some cases the dominance is not a true individual dominance, but the sex and/or age of the individuals has been taken as an estimation of dominance.

<table>
<thead>
<tr>
<th>Direction of aggressions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Like-vs-like</td>
</tr>
<tr>
<td>Parus major</td>
</tr>
<tr>
<td>Parus atricapillus</td>
</tr>
<tr>
<td>Zonotrichia querula</td>
</tr>
<tr>
<td>Junco hyemalis</td>
</tr>
<tr>
<td>Hesperiphona vespertina</td>
</tr>
<tr>
<td>Carpodacus mexicanus</td>
</tr>
<tr>
<td>Carduelis sinica</td>
</tr>
<tr>
<td>Carduelis chloris</td>
</tr>
<tr>
<td>Carduelis tristis</td>
</tr>
<tr>
<td>Carduelis spinus</td>
</tr>
<tr>
<td>Carduelis flammea</td>
</tr>
<tr>
<td>Passer domesticus</td>
</tr>
</tbody>
</table>

Authors:
Figure 1. Frequency distribution of male Eurasian Siskin bib-size classes in relation to age (n = 638 yearling and 311 adult males). Values recalculated from Senar et al. (1993), according to regression: badge size = 0.594 length x breadth (Senar & Camerino 1998).