Social environment affects correlates of dominance status in the greenfinch *Carduelis chloris*

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Abstract. Dominance status is responsible for individual variation in access to resources. The relationship between social rank and sex, age, body size, site experience, prior ownership, motivation and fat reserves has been shown to vary among species due to their different natural history. This study investigated these relationships in captive groups of greenfinches *Carduelis chloris*. Dominance status was measured as the outcome of agonistic interactions in both dyadic and group trials. Results varied according to encounter conditions due to differences in social environment. Beyond sex, asymmetries in fat score and asymmetries in body size within age were related to dominance status in dyadic trials, whereas asymmetries in body size and asymmetries in fat score within age were related to dominance status in group trials. Therefore, it seems that resource value or winner-loser effects may motivate fighting in dyads whereas fighting ability becomes more important in groups. Our results have to be considered in the design of future studies, as differences in social environment may have important implications for the outcome of trials.

Keywords: Agonistic interactions, Fighting ability, Body size, Fat score, *Carduelis chloris*.

Resumen. *Las condiciones durante los enfrentamientos afectan a las relaciones del estatus de dominancia en el verderón común* Carduelis chloris. El estatus de dominancia es responsable de la variación individual en el acceso a los recursos. Las relaciones entre el rango social y el sexo, la edad, el tamaño corporal, la experiencia en el lugar, la posesión previa, la motivación y las reservas grasas se han mostrado variables entre especies debido a su diferente historia natural. Este trabajo investiga estas relaciones en grupos cautivos de verderón común *Carduelis chloris*. El estatus de dominancia fue medido como el resultado de interacciones agonísticas en enfrentamientos dentro de diadas y grupos. Los resultados variaron en función de las condiciones de los enfrentamientos debido a diferencias en el entorno social. Más allá del sexo, las asimetrías en las reservas grasas y las asimetrías en el tamaño corporal dentro de cada grupo de edad estuvieron relacionadas con el estatus de dominancia en las diadas, mientras que las asimetrías en el tamaño corporal y las asimetrías en las reservas grasas dentro de cada grupo de edad estuvieron relacionadas con el estatus de dominancia en los grupos. Por lo tanto, parece que el valor del recurso o el efecto ganador-perdedor pudieron motivar el enfrentamiento dentro de las diadas, mientras que la capacidad de lucha adquirió más importancia en los grupos. Los resultados deben ser también considerados en el diseño de futuros estudios, ya que diferencias en el entorno social pueden tener importantes implicaciones en el resultado de los enfrentamientos.

Introduction

Social rank of an individual within a flock is assumed to lead to variations in access to resources, and consequently in body condition, mating success or winter survival (reviewed in Senar, 1994; Piper, 1997; Koivula, 1999). Due to differences in their natural history, species differ with respect to which factors affect dominance status, the most frequently mentioned for birds being sex, age, body size, previous site experience, prior ownership and motivation (Maynard Smith & Parker, 1976; Arcese & Smith, 1985; Enoksson, 1988; Komers, 1989; Cristol et al., 1990; Holberton et al., 1990; Senar et al., 1990; Andersson & Åhlund, 1991; Cristol, 1992; Lemel & Wallin, 1993; Smith & Metcalfe, 1997; Domènech & Senar, 1999). However, most studies have reported results where only some potential factors were accounted for.

In this study we investigated the relationship between dominance status and these factors in the greenfinch *Carduelis chloris*, a 25 g passerine that forms dominance-structured flocks in winter. Dominance in

greenfinches has previously been suggested to be mainly related to sex and body size (Flytström, 1985; Maynard Smith & Harper, 1988), and Hake (1996) has shown variation in the amount of fat reserves according to dominance status. To clearly deal with correlates of dominance, we assessed the social rank of captive greenfinches directly from agonistic interactions rather than from indirect measures. Furthermore, we collected data for individual dominance status by means of dyadic trials as well as group trials, given that the greenfinch is a social species (Johnstone, 2001). We analysed the relationship between the outcome of interactions and sex, age and differences in body size and fat reserves, controlling for site experience, prior ownership and motivation.

Material and Methods

We captured 34 greenfinches (20 males and 14 females; 16 adults and 18 yearlings) with mist nets and baited feeders at two locations 100 km apart during the 2001-2002 winter (Darbo and Lestrove, NW Spain). We randomly assigned them to one of four outdoor aviaries, with groups of birds captured together being also caged together. Aviaries were visualy isolated and measured 2 x 1 x 0.8 m. We provisioned birds with a seed mixture and fresh water *ad libitum*. Capture and captive conditions were subjected to legal permissions. At the end of the study, birds were released back into the wild at the original sites of capture.

We sexed and dated greenfinches as yearlings or older birds following Svensson (1992), and we measured and marked them with leg colour bands on their capture date. Measures were collected for tarsus, keel, head and bill length with a calliper (to the nearest 0.05 mm) and for wing, 3rd primary and tail length with rulers (to the nearest 0.5 mm). We took these measures again on two different days after capture, obtaining three blind measures for repeatability purposes (Lessells & Boag, 1987; Harper, 1994; Senar, 1999). Repeatabilities were larger than 0.98, except for keel length (r=0.22, p=0.04) which is difficult to measure in live birds. Keel length is however an important measure, as a skeletal measure of size not subjected to erosion (Pascual & Senar, 1997); we therefore included the mean of the three measures of keel length in further analyses. As an index of body size, we took the first principal component of a PCA including all the above measures (eigenvalue: 3.27; explained variance: 0.47).

Social rank has been reported to be a determinant of fat storage in this species (Hake, 1996). Moreover, individuals have been shown to store fat reserves on the basis of their perceptions of future food availability, which in turn seems to be affected by dominance status (Ekman & Hake, 1990; Clark & Ekman, 1995; Gosler, 1996). Hence, in order to control for this source of asymmetry between opponents, we included the amount of fat reserves in the data analyses. Clavicular subcutaneous fat reserves were measured on an 8-point scale (Kaiser, 1993) prior to each period of observation.

We collected data for individual dominance status through two methodological approximations based on agonistic encounters. On the one hand, dyadic trials allowed us to meet the statistical requirement of independence of sample units, with each bird included only once in the analysis. However, given that the greenfinch is a social species, we subsequently performed group trials in order to obtain a more realistic scenario of what happens in the field (Johnstone, 2001). The use of the two approximations gave us a more complete understanding of dominance relationships. We assumed similar site experience for all individuals due to lack of familiarity with encounter cages. Likewise, prior ownership was controlled for, since opponents were forced to arrive at the resource at the same time. Motivation was also assumed to be the same for all individuals, since all birds were able to feed *ad libitum* during at least 15 days of captive conditions and were subjected to equal fasting times prior to encounters.

Dyads

We carried out 17 dyadic trials of randomly chosen and unfamiliar greenfinches on 15-29 January 2002. Each individual participated only once in dyadic trials. Encounters took place at 10.00 h in unfamiliar test cages (1 x 0.6 x 0.6 m), and lasted 30 minutes each. Test cages were provided with two equidistant entrances for each opponent and an individual feeder and a perch for access to which they competed. The birds chosen for each trial were removed from aviaries before dawn and were kept in individual dark cages without food until 10.00 h. Then, we simultaneously let them leave individual cages into test cages without manipulation. There were therefore no differences in time of entrance to the test cage between opponents in all trials.

We estimated the rank of each bird (dominant or subordinate) according to the rate of wins and losses during each trial. An interaction was won when the loser replied to a display, attack or supplanting with a withdrawal or a submission. As dominance status is a relative quality which depends on the opponent, the sample unit should be the dyad: in order to avoid pseudoreplication, we randomly chose only one of the two opponents of each dyad to be included in subsequent analyses.

Groups

Encounters were staged within three groups (A, B and C) of 10 randomly chosen birds from the aviaries, on 5-21 February 2002. Each group was composed of 10 birds, some familiar and some unfamiliar mates, familiarity being included as a factor in the analyses. In order to resemble wild flocks, each group comprised individuals of both sexes and ages, with sex ratios of 1:1, 1:0.4 and 1:0.7 males:females respectively, and age ratios of 1:1.5, 1:1 and 1:1.5 adults:yearlings respectively. Each group participated in encounters on alternate days amounting to a total of 9 periods of observation, which lasted from 30 min to 3 h, with a total of more than 23 h of observation. Interactions took place in an unfamiliar test cage (2 x 0.6 x 0.6 m) which was provided with four equidistant entrances, two individual feeders, two water dispensers and four perches. We recorded bird-bird competitive interactions for these

Table 1. Logistic regression of social rank (dominant versus subordinate) on body size and fat reserves in dyadic trials with greenfinches (n=17). Body size and fat reserves were included as differences between opponents, and interactions with sex and age were included as nested interactions.

	d.f.	Log-Likelihood	Chi-square	P value
Difference in body size	1	-11.37	0.77	0.38
Difference in fat reserves	1	-9.41	3.91	<0.05
Δ body size nested in sex	1	-9.21	0.39	0.53
Δ body size nested in age	1	-7.03	4.36	<0.05
Δ fat reserves nested in sex	1	-6.90	0.27	0.60
Δ fat reserves nested in age	1	-6.58	0.65	0.42

resources similarly as in dyadic trials. Likewise, we randomly chose one of the two opponents of each dyad to avoid pseudoreplication: for each of the three groups, we alternately selected either the dominant or the subordinate bird in each dyad, thus balancing the number of dominants and subordinates in each group. Since the sample unit is the dyad, this avoids pseudoreplication because none of the dyads is repeated, although some individuals appeared several times.

Statistical analyses

We analysed correlates of dominance status by logistic reggression (Generalized Linear Model module of STATISTICA package (StatSoft, Inc) for binomial distributions) following Hardy & Field (1998). The model incorporated age and sex in dyadic analysis, and age, sex, group (A, B or C) and familiarity (familiar or unfamiliar) in group analysis as categorical factors within which the continuous factors were nested. The continuous factors were body size and fat reserves. Since social rank is a relative measure which depends on differences between opponents, each continuous factor value was taken to be the computed difference between the values for the two opponents. This provided a relative measure of the size of each individual's trait with regard to the size of its "opponent's" measure. A positive value for a given variable meant that the individual displayed a larger size for that trait than the opponent, and a negative value corresponded to a smaller size than the opponent. The accepted level of significance was 0.05. Values are shown in figures and in text as means $\pm$ SE.

Results

We observed a total of 192 interactions (11.29 $\pm$ 1.30 encounters per dyad) in 17 dyadic trials. All trials yielded a significant binomial test result (i.e. significant difference from 50% odds ratio). Fifteen dyadic trials involved opponents of the same sex (nine male-male dyads and six female-female dyads), and two dyadic trials were between a male and a female. Likewise, nine dyadic trials involved opponents of the same age (four adult-adult dyads and five yearling-yearling dyads), and eight dyadic trials were adult-yearling dyads. Our samples were not sufficient to analyse the effects of sex in dominance, but analyses of the 8 between-age classes dyadic trials resulted in yearlings
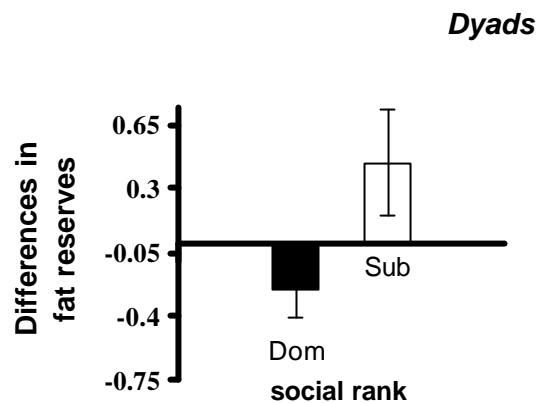
Dyads

Figure 1.- Mean asymmetry in fat score between opponents according to dominance status in dyadic trials (n=17). Dominants had significantly lower fat reserves prior to trials than subordinates. Bars show standard errors.

tending to be more dominant than adults (χ^2_1=2.86, p=0.09).

When other correlates were included, asymmetries in fat reserves were significantly related to dominance status, with birds having stored less fat reserves being more frequently dominant than birds with higher fat scores (mean difference between dominants and their opponents: -0.25 $\pm$ 0.16; mean difference between subordinates and their opponents: 0.44 $\pm$ 0.29; Table 1, Fig. 1). Within age classes, asymmetries in body size were also significantly related to dominance status in dyadic trials, dominants being larger than subordinates within each age class (mean asymmetry between opponents: adults: 0.54 $\pm$ 0.46 vs. -0.13 $\pm$ 0.68; yearlings: 0.41 $\pm$ 0.68 vs. 0.10 $\pm$ 0.39; Table 1).

Within social groups, we registered a total of 3075 interactions with 126 dyads involved. Only dyads in which the odds ratio was significantly different from 50% (binomial test) were included in the analyses (n=87). Fortyfive dyads involved opponents of the same sex (35 male-male dyads and 10 female-female dyads), and 42 dyads were between a male and a female. Likewise, 38 dyads involved opponents of the same age class (seven adult-adult dyads and 31 yearling-yearling dyads), and 49 dyads were adult-yearling dyads. With respect to familiarity, only

Table 2. Logistic regression of social rank (dominant versus subordinate) on body size, fat reserves and familiarity in greenfinch dyad interactions (n=87) recorded in group trials. Body size and fat reserves were included as differences between opponents, and interactions with sex, age, group and familiarity were included when p<0.5.

	d.f.	Log-Likelihood	Chi-square	P value
Difference in body size	1	-50.89	18.81	< 0.001
Difference in fat reserves	1	-47.84	6.11	<0.01
Δ body size nested in age	1	-47.56	0.56	0.46
Δ body size by familiarity	1	-46.82	1.47	0.23
Δ fat reserves nested in age	1	-44.42	4.80	<0.05
Δ fat reserves by group	2	-42.84	3.17	0.21

18 out of 87 dyads were between familiar opponents. In such a social environment, where we had large enough samples for between-sexes and between-ages dyads, logistic regressions of dominance status by sex and age yielded that, among adults, males always dominated females (post-hoc logistic regression: $\chi^2_1=2.97$, p=0.08, n=7), whereas among yearlings, there was no clear relationship between dominance status and sex (post-hoc logistic regression: $\chi^2_1=2.04$, p=0.15, n=31). In fact, male yearlings were more likely to be dominant than adults (post-hoc logistic regression: males: $\chi^2_1=20.35$, p<0.001, n=35; not enough data were available for females).

Additionally, dominance status was significantly related to asymmetries in body size: dominants were significantly larger than subordinates (mean difference between opponents: 0.82 ± 0.20 vs. -0.47 ± 0.20; Table 2, Fig. 2). Differences in fat reserves were also related to social rank, with a significant interaction with age: overall, dominants had higher fat scores than subordinates (mean difference between opponents: 0.04 ± 0.10 vs. -0.26 ± 0.09; Table 2). This was likely due to a larger sample size of yearling dyads, for which we have obtained this result (0.12 ± 0.10 vs. 0.02 ± 0.11), whereas, within adults, the trend was in the opposite direction (-1.11 ± 0.11 vs. -0.46 ± 0.13; Table 2, Fig. 3). In this social environment, neither the interactions between asymmetries in body size on the one hand, and age and familiarity on the other, nor the interaction between asymmetries in fat reserves and group were significantly related to dominance (Table 2). These results held once controlled for interactions with sex, group and familiarity that do not appear in the final model.

Discussion

Traditional correlates of dominance covaried with status according to social environment. Sex, which has been previously shown to be the main determinant of social rank in the greenfinch (Flytström, 1985), was related to dominance status only among adults in our study. Correlates of dominance among yearling greenfinches, which were more likely dominant than adults, appeared to fit a more complex situation, where asymmetries in body size and fat reserves seemed to play an important role. In dyadic trials, dominants had overall fewer fat reserves, and were also larger than subordinates within age classes. In groups, dominants were larger than subordinates but the
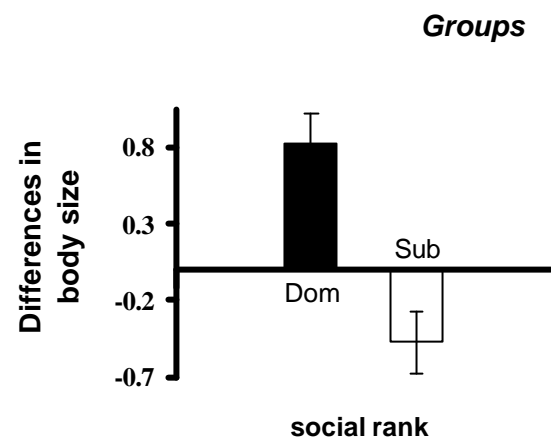

Figure 2.- Mean asymmetry in body size between opponents according to dominance status within group trials (n=87). Dominants were significantly larger than their opponents in the three experimental groups, which were pooled. Bars show standard errors.

relationship between dominance and fat reserves depended on age.

Greenfinch feeding flocks may reach more than a thousand birds, with small groups joining as they find the feeding site (Newton, 1972). Thus, greenfinches should often check dominance relationships. We have observed interactions first between two unfamiliar and hungry birds in a new environment, and, then, between hungry members of social groups. Given that there were no asymmetries in prior ownership, we may expect fighting when costs of injury were low relative to the value of the resource. However, several asymmetries, such as differences in 'resource holding power' due to size, sex and fighting ability, would prevent the birds from fighting if the asymmetries were clear and the costs of fighting were high (reviewed in Pusey & Packer, 1997). In dyadic trials, where we had insufficient sample sizes to analyze the effects of sex because most trials were within-sex dyadic trials, yearlings were more likely to be dominant than adults. Also, in these trials two other sources of asymmetries were related to dominance status. On the one hand, asymmetries in fat reserves may imply asymmetries in motivation if greenfinches with fewer fat reserves valued more the scarce
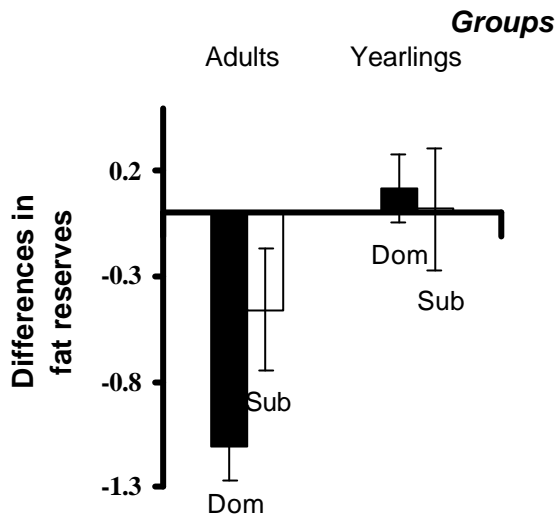
Groups

Adults   Yearlings

Figure 3.- Mean asymmetry in fat score between opponents according to dominance status within ages in group trials (n=87). Within adults, dominants showed lower mean fat scores than subordinates whereas, within yearlings, dominants tended to show higher mean fat scores than subordinates. Groups A, B and C were pooled. Bars show standard errors.

resource regarding to the costs of fighting, whereas the value of the resource was lower for fatter greenfinches and it paid them to be subordinates. However, we had previously assumed a similar motivation for opponents due to *ad libitum* conditions in aviaries and same fasting times prior to trials. Thus, 1) if this is a mistaken assumption, motivations, reflected by fat scores, varied between opponents and the asymmetry in resource value was related to dominance status in this simple social environment; and 2) if motivations were actually the same between opponents and not related to fat scores, differences in fat reserves between opponents prior to trials might be the consequence of previous experience in aviaries, where subordinates stored larger reserves than dominants (Hake, 1996). In such a case, the main basis of dominance relationships might not be the resource value but the winner-loser effect, that is, those greenfinches that were dominants in original aviaries, were dominants also in dyadic trials, and the same for subordinates (Dugatkin, 1997; Hsu & Wolf, 1999).

On the other hand, asymmetries in body size were significantly related to dominance within ages. Thus, when a greenfinch was interacting with a same-age opponent, the larger one was more likely to win. This result cannot be due to effects of sex on dominance status, since most trials were within-sex trials. Conversely, this may imply that when age effects were not operating and, independently of if the resource value or the winner-loser effect were more important, asymmetries in body size were also related to the outcome of agonistic interactions, presumably affecting the relative costs of fighting (Garnett, 1981; Rohwer et al., 1981; Maynard Smith & Harper, 1988).

The social environment was complex and more

realistic in group trials. Some birds of each group were familiar as they came from the same original aviary. Thus, we may expect fighting to be not so frequent among them. In fact, most dyads included in the analyses were between unfamiliar opponents. On the other hand, other birds were unfamiliar and we may expect dominance rank to be checked repeatedly among them. Furthermore, in groups there were more unfamiliar birds checking dominance relationships than familiar birds behaving according to previous experience. However, since groups were observed several days, as birds were becoming familiar with each other, we may also expect asymmetries to become more important for solving dominance relationships. Our results may be explained in accordance with these expectations, as we obtained that dominance in groups was mainly related to asymmetries in body size, and thus fighting ability, between opponents. This result is also consistent with the suggested enhanced importance of fighting ability when social instability increased (Maynard Smith & Harper, 1988).

Asymmetries in fat reserves were overall positively related to dominance in groups, but this result appears to resemble the relationship among yearlings, which were more abundant and more likely to be dominant than adults. Within yearlings, dominants had stored larger fat reserves than subordinates. Conversely, within adults, dominants had lower fat scores than subordinates. Since age has not been previously suggested as a correlate of dominance in the Greenfinch (Flyström, 1985), yearlings had no reason to dominate over adults, unless some subyacent mechanism has been operating within yearlings but not within adults. We have, however, no convincing explanation for this mechanism. Differential modulation among age classes of hormone titres, specifically testosterone and corticosterone, which may be enhanced due to fasting, social instability and the approach of spring (Siegel, 1980; Wikelski et al., 1999; Creel, 2001; Deviche et al., 2001) could explain this result, as differential modulation among individuals has been previously suggested (Scott & Fredericson, 1951; Barnard et al., 1998; Peters et al., 2000; Deviche et al., 2000). Nevertheless, to our knowledge, there is no published literature about differences in corticosterone titres or in aggressiveness, which could be related to enhanced testosterone and corticosterone titres (Wingfield et al., 1990; Silverin, 1998; Briganti et al., 1999), between first-year and older birds in captivity or in the wild. Only Love et al. (2003) have found that American kestrel *Falco sparverius* fledglings had higher stress-induced corticosterone titres than one-year-old individuals, and Stoinski et al. (2002) have shown that young gorillas *Gorilla g. gorilla* also had higher corticosterone titres than adults in captivity. Alternatively, differential motivation due to asymmetries in foraging efficiency has been suggested to operate in a few species (House sparrow *Passer domesticus*, Simmons, 1954; Watson, 1970; Black-billed magpie *Pica pica*, Reese, 1982; Komers, 1989; Snow bunting *Plectrophenax nivalis*, Smith & Metcalfe, 1997). However, given that there are no previous data about wild yearling greenfinches being dominant to adults, what we can deduce

is that, whatever the mechanism, this result seems to be the consequence of stressful circumstances and captivity.

When social environments became more complex, familiarity with opponents might also affect the outcome of trials. We may expect individual recognition and previous experience to help in solving interactions rather than in fighting (Barnard & Burk, 1979; Pusey & Packer, 1997). In accordance with this expectation, the importance of asymmetries in body size tended to be diluted among familiar opponents, although this result was non-significant.

In sum, it may be concluded that the main motivation for agonistic interactions, and therefore the correlates of dominance status, was affected by social environment in the greenfinch. Interactions in a simple social environment seemed to be resolved mainly by the value of the resource with respect to the costs of fighting, or by the previous experience, whereas social instability provided a scenario where interactions were resolved mainly by asymmetries in fighting ability between opponents. Furthermore, fighting ability appeared to be related to aggressiveness, body size and sex in the greenfinch. Additionally, we can extract practical conclusions such as that the method of agonistic data recording (from dyads or from groups) highly influences results due to variation in social environment, and that a stressful methodology may influence correlates of dominance. This should be taken into account in the design of future experiments.

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