

**A comparison of agonistic behaviour
in two Cardueline finches:
Feudal species are more tolerant than despotic ones**

J.C. Senar¹, M. Camerino¹ & N.B. Metcalfe²

¹Museu de Zoologia, Ap.Correus 593, 08080 Barcelona, Spain

²Applied Ornithol. Unit, Div. Env. & Evol. Biol., Graham Kerr Building, Univ. of Glasgow, Glasgow G12 8QQ, U.K.

ABSTRACT. *A comparison of agonistic behaviour in two Cardueline finches: Feudal species more tolerant than despotic ones.* - Patterns of agonistic behaviour between two closely related cardueline finches (*Serinus Serinus serinus* and Siskin *Carduelis spinus*), either interacting with new flock companions (socially unstable) or familiar birds (socially stable) are analysed using multivariate statistical methods. Siskins interacting with new flock companions were characterized by the use of displays and tolerance (a possessor bird allowing an intruder to stay within its individual distance), whereas serins were more likely to make supplanting attacks. When interacting with familiar birds serins used relatively more displays, whereas siskins used tolerance as their main form of agonistic interaction. Siskins therefore exhibited a more smooth social system than serins, based on tolerances (and displays) rather than on direct aggression. This supports an earlier view of the siskin as a "Feudal" species, and the serin as a "Despotic" one. It is suggested that these differences could be related to the nomadic lifestyle of the siskin, as opposed to the more resident nature of the serin; continuous movement may promote the evolution of mechanisms to maintain a high degree of cohesion between flock companions.

KEY WORDS. Agonistic interactions, Social system, Interspecific comparison, Siskin, Serin.

Introduction

There has recently been an increased interest in the causes and consequences of inter- and intraspecific variation in social behaviour (Jarman, 1982; Rubenstein & Wrangham, 1986; Ekman, 1989; Matthysen, 1990; Slobodchikoff, 1988; Lott, 1991; Matthysen, 1993; Lee, 1994). Until now, however, most of the analyses have relied on general approaches and concepts (e.g. predation risk, residence or conspecific competitive ability) (Brown, 1974; Schluter, 1984; Rubenstein & Wrangham, 1986; Marzluff & Balda, 1988; Ekman, 1989; Matthysen,

1990; Matthysen, 1993), with little emphasis on differences in interactional patterns between the individuals within the group (but see e.g. Livoreil et al., 1993). Interactions form the basis for relationships and social structure (Hinde & Stevenson-Hinde, 1976; Lee, 1994), and therefore their detailed study can lead to great insights into our understanding of the differences in social behaviour between species.

The aim of this study is to compare patterns of agonistic behaviour between to closely related species: the Serin *Serinus serinus* and the Siskin *Carduelis spinus*. Both species belong to the Carduelinae subfamily, and are non-territorial social flocking birds

Table 1. Characteristics of the different flocks used in the analysis.

Group	Species	Observation period and flock composition	Companion situation	No. observed interactions
A	Siskin	winter 1990-91 5 males	new familiar	91 293
B	Siskin	winter 1989-90 5 males	new familiar	495 1155
C	Siskin	spring 1987 4 males, 2 females	new familiar	1093 1938
D	Serin	winter 1989-90 5 males	new familiar	391 781
E	Serin	spring 1990 5 males	new familiar	416 1148
F	Serin	winter 1988-89 4 males, 5 females	new familiar	1108 2441

which form cohesive groups throughout the year (Senar, 1989). Previous work has shown some differences in their interactional patterns (Senar et al. 1989; Senar et al. 1992). Here we analyse deeper these differences, using multivariate statistical methods.

Methods

The study involved monitoring the agonistic behaviour of birds interacting with either new or familiar flock companions, and to compare these between the two species. We used three different independent flocks for each species (Table 1). Birds were colour-ringed for individual identification, and housed in outdoor cages (see Senar et al. 1990) for details of the housing procedure; birds were observed through one-way glasses). Groups A, B, D, and E (see Table 1) were created by simultaneously releasing unfamiliar birds into the cages. Flocks C and F followed a different procedure: each

flock comprised two subgroups, previously housed independently for several months. For the experiment, one subgroup was introduced into the cage occupied by the other subgroup (see Senar et al., 1990) for details on the procedure). Interactions between individuals from different subgroups could thus be regarded as being between unfamiliar birds. Siskin and serin flocks behave as socially stable units 15-20 days after the fusion of groups (Senar, 1989; Senar et al. 1990). Therefore, agonistic interactions recorded during the first 15 days since flock creation were defined as being between new flock companions, while those between 20 and 50 days since fusion were regarded as being between familiar birds. In the case of flocks C and F, only interactions between previously unfamiliar birds were used in the new companion analyses.

We recorded all the interactions observed. All the interactions were recorded by only one of us (MC) to reduce any bias. Observations were done on

Table 2. Results of the CA analysis on the contingency table relating each individual (either siskin or serin) to the behaviour patterns it used when interacting with new or familiar flock companions. C1 to C4 indicate the different components of CA.

	C1	C2	C3	C4
New flock companions				
Singular value	0.43	0.31	0.23	0.21
% inertia explained	41%	21%	12%	10%
Familiar flock companions				
Singular value	0.53	0.34	0.30	0.21
% inertia explained	46%	19%	15%	7%

a nearly daily basis, recording periods lasting for about 45 minutes (normally after introducing new food into the cage). In any interaction, the first bird to display or attack was defined as the Actor, and the bird receiving the display the Reactor. The behaviours used by serins and siskins in agonistic interactions were defined as follows: Physical Attack, in which the actor pecks directly at the head, body or wings of the other bird; Supplanting Attack, in which one bird flies at another, who abandons its perch, the attacker perching in its place; note that while there is no physical aggression (eg. pecking), the reactor has to move in order to avoid contact with the incoming bird; Display, in which the bird faces the opponent with a threatening posture; and Tolerance, in which a possessor bird allows another one to be within a radius of 10 cm. The major responses by the reactor were Flying and Hopping withdrawals, Physical and Supplanting attacks, Display and Submission. If the reactor showed no clear response, continuing with its previous behaviour, it was defined as No-response. Due to the low frequency with which Submission and No-response appeared, these two behaviours have been excluded from subsequent analyses.

We compared the two species interacting with new and familiar companions by carrying out Correspondence Analyses (CA, Heijden et al. 1990) on the matrix relating each individual (both species entered in the same analysis) to the frequency dis-

tribution of behaviour patterns it tended to use or receive. This allowed us to generate a "social space", and to establish the main components of behavioural variation, so that different birds could be classified according to the behaviours that characterized them (Senar et al. 1990). Each bird had therefore a score for each one of the behavioural CA components detected. Since serins and siskins were entered simultaneously into the same CA, the analysis could detect differences between the two species. The statistical significance of the species differences were tested using a nested MANOVA on the scores for the first four CA components. Factor group was nested within factor species. This was preceded by a one-way ANOVA on the CA scores to test for behavioural consistency between the different groups of each species. Since the correlation between the agonistic behaviour used by an individual and the response it receives from the reactor is not perfect (e.g. the response to a single behaviour such as a display can be either a hopping or a flight withdrawal, depending on the situation and individuals), and since the response that the actor receives is as important in characterizing that bird as the behaviours that it displays, we have used both "given" and "received" behaviours in the analysis (e.g. a flight is given by the reactor in response to an agonistic behaviour, but it can also be described as having been received by the actor bird) (see Senar et al., 1994).

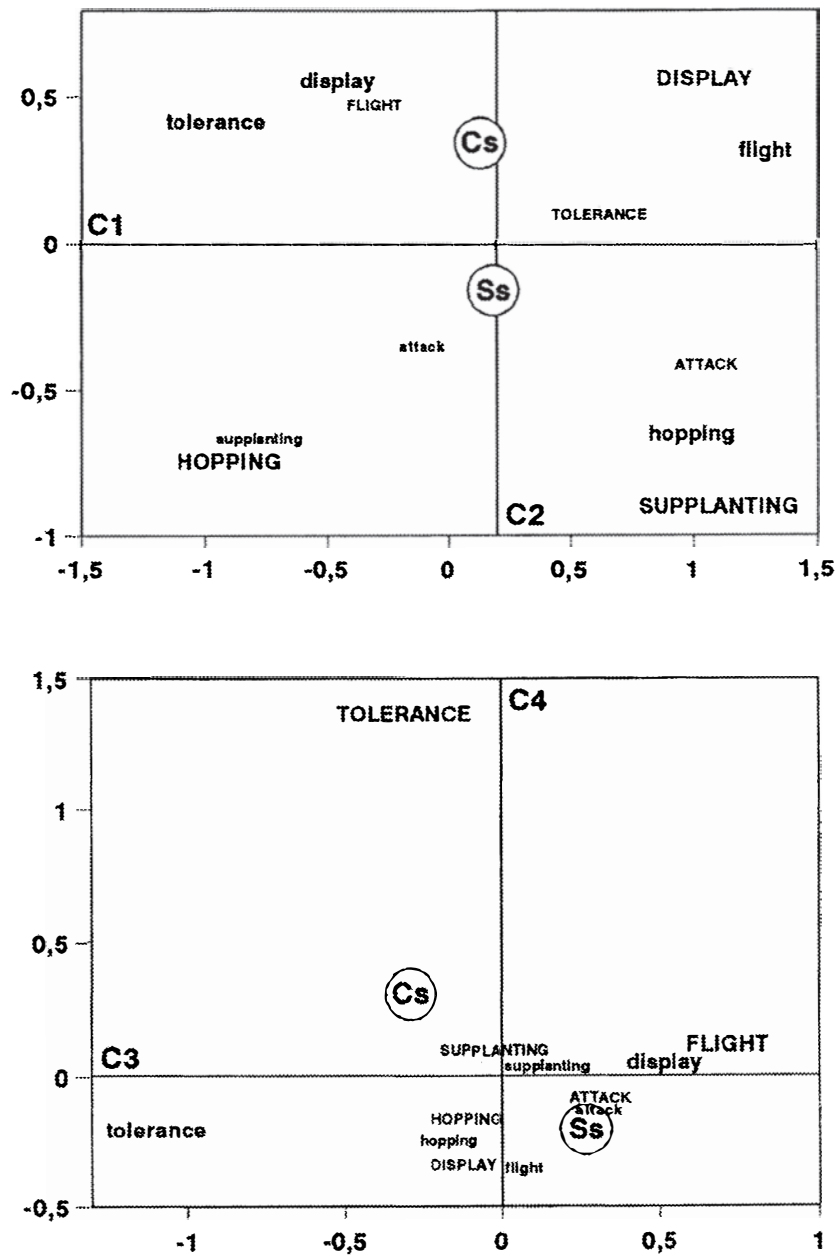


Fig. 1. Plot of the first four axes generated by CA of the different agonistic behaviours used by different individual serins and siskins in intraspecific encounters between new flock companions. Behaviours given are shown in capitals, while those received are in lower case. Behaviours which contributed more than 10% to the inertia of each dimension are in a larger font size. Cs= mean score for siskins, Ss= mean score for serins.

Table 3. Oneway ANOVAs testing for homogeneity between the 3 groups of each species. ANOVAs based on the scores of each individual for the first four components of CA (C1-C4)(see table 2).

	C1	C2	C3	C4
New companions				
Siskin				
F _{2,15}	0.03	0.21	0.05	2.34
p	0.97	0.81	0.95	0.14
Serin				
F _{2,15}	0.02	55.09	0.03	0.75
p	0.98	<0.001	0.96	0.49
Familiar companions				
Siskin				
F _{2,15}	0.00	4.56	1.51	0.70
p	1.00	0.03	0.26	0.51
Serin				
F _{2,15}	0.55	191.27	2.73	1.36
p	0.59	<0.001	0.10	0.28

Results

Interactional patterns among new flock companions

The first axis from the CA on the matrix relating each individual (either serin or siskin) to the behaviour patterns it used or received when interacting with new flock companions explained 41% of the variability in this contingency table (Table 2). Certain behaviour patterns were negatively correlated with the axis: actors that made supplanting and physical attacks, tolerances and displays, and, in return, received flight and hopping withdrawals (Fig.1). All of these behaviours are typical of dominant birds. In contrast, receiving supplanting and physical attacks, tolerances and displays, and giving in response flight and hopping withdrawals (all typical of subordinates) had significant positive scores. This axis (component 1, C1) was therefore related to dominance, and the dominance status of an individual was indicated by its position on the axis (Senar et al. 1994). As expected, each flock

contained both dominant and subordinate individuals in each species, so that flocks behaved consistently within each species (Table 3), and the two species showed no difference in mean C1 scores (Table 4).

The second axis explained 19% of the total variability (Table 2). Displays, either given or received, had positive scores. Supplanting attacks and hopping withdrawals had negative scores (Fig. 1). Significant differences appeared between the two species in relation to this component (Table 4). Serins, however, were not homogeneous (Table 3), with one group displaying lower scores for C2 than the other two (mean C2 values for each group: D=0.21, E=0.25, F=-0.78). Nevertheless, the difference between siskins and serins was maintained even excluding group F from the analysis (t-test comparing groups A-C vs. D-E: $t=3.18$, $df=24$, $p=0.004$). Siskins could therefore be characterized by being associated with the use of displays, whereas serins tended to use more supplanting attacks (and attacks) as their usual form of agonistic interaction (Fig. 1).

Table 4. Mean scores \pm standard error obtained by siskin and serin groups in relation to the first four components of CA (C1-C4) (see table 2). F-test from nested MANOVA is provided. In all the cases, N is 3 groups for siskins (16 birds), and 3 groups for serins (19 birds). Overall test for species effect, new companion situation, Rao R4,26= 18.71, $p < 0.001$; F.

	C1	C2	C3	C4
New companions				
Siskin	-0.01 \pm 0.03	+0.44 \pm 0.02	-0.04 \pm 0.03	+0.28 \pm 0.14
Serin	-0.01 \pm 0.03	-0.11 \pm 0.34	-0.04 \pm 0.02	-0.10 \pm 0.10
F _{1,29}	0.000	69.710	0.002	6.304
p	0.995	<0.001	0.969	0.018
Familiar companions				
Siskin	-0.06 \pm 0.00	+0.34 \pm 0.13	-0.29 \pm 0.13	+0.30 \pm 0.11
Serin	-0.00 \pm 0.13	-0.16 \pm 0.41	+0.26 \pm 0.17	-0.20 \pm 0.11
F _{1,29}	0.068	6.877	14.326	11.175
p	0.796	0.014	0.001	0.002

No differences appeared between the two species in relation to the third axis (Fig. 1, Table 4). The fourth axis was again important in discriminating between siskins and serins. This component was highly associated with tolerance, which had a large positive score (Fig. 1). Siskins could therefore be characterized by showing more tolerance than serins (Table 4), the difference being consistent across groups (Table 3).

Interactional patterns among familiar flock companions

The first axis from the CA based on birds interacting with familiar flock companions was also associated with dominance, and explained 46% of the total variance (Table 2). No differences appeared between siskins and serins (Tables 3 and 4). The second axis (Table 2, Fig. 2) was also similar to that found in the new flock companion situation. This time, however, flocks did not behaved consistently within either species (Table 3), and most of the difference found between siskins and serins (Table 3) was because of serin group F (C2= -0.67).

The third component was characterized by birds receiving displays and giving flight withdra-

wals (positive part), as opposed to birds receiving tolerances (negative part) (Fig. 2). Groups behaved consistently within species (Table 3), with siskins receiving tolerances whereas serins received displays, prompting them to take flight (Table 4, Fig. 2). The fourth axis was also similar to that found in the new flock companion situation (Table 1, Fig. 2). This component was again highly correlated with the use of tolerance (Fig. 2), and again, siskins were characterized by being far more ready to show tolerance than serins (Table 4), there being no variation within species (Table 3).

Discussion

The joint Correspondence Analysis, in which both siskins and serins were simultaneously analyzed, allowed a comparative examination of relative differences between the two species (e.g.: an unstable siskin can use less tolerances than when in the stable situation, but even in that way it is using proportionally more tolerances than unstable serins). This is important since allows to characterize to each species in relation to their agonistic mechanisms, irrespective of the number

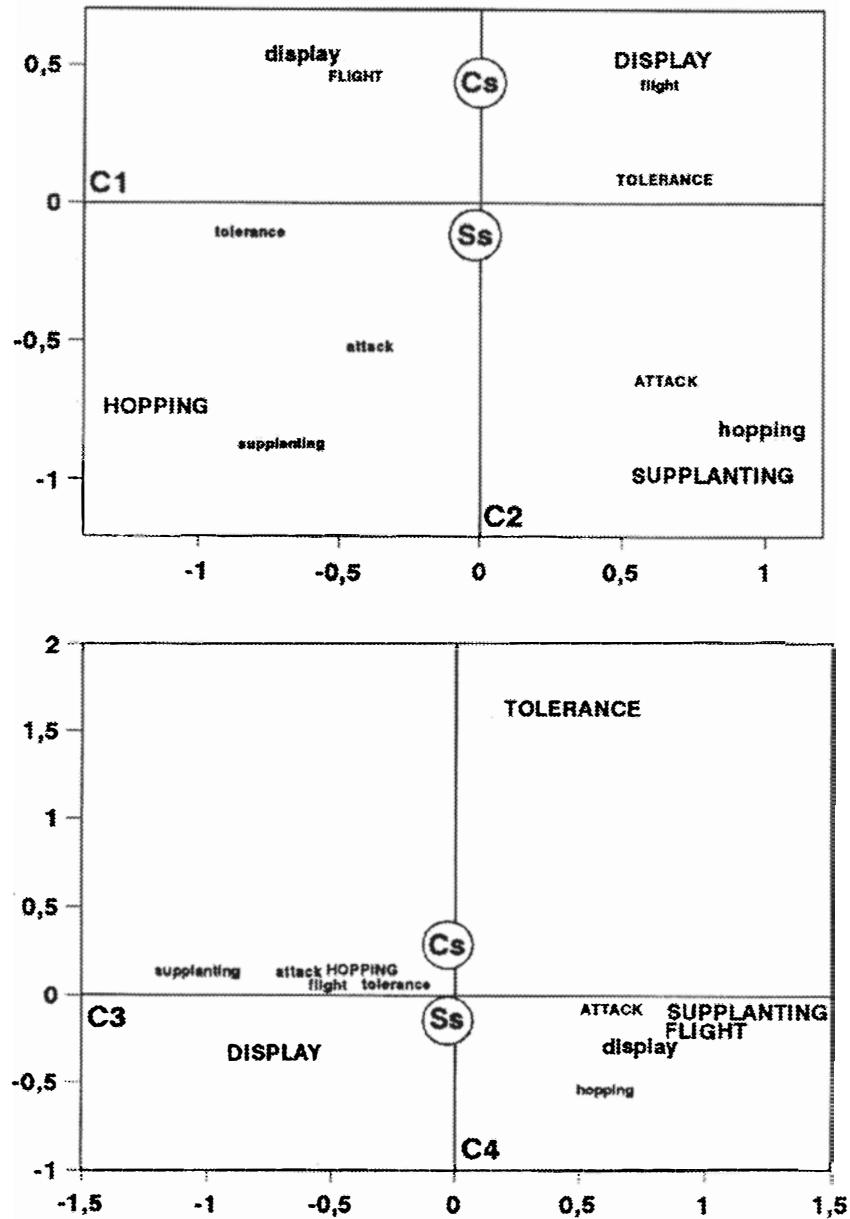


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of interactions in which birds are involved (or the observer recorded). Analysis showed that, when interacting with new flock companions, siskins tended to use displays and tolerances, whereas serins were more likely to make supplanting attacks. In the familiar situation serins used relatively more displays, whereas siskins showed tolerance as their main form of agonistic interaction. Tolerance is therefore a behaviour characteristic of siskins, especially amongst familiar birds (see also Senar et al., 1990; 1990), whereas serins generally behaved more aggressively (Figs. 1 and 2). This difference appears robust given the general intraspecific consistency between flocks: the few intraspecific inconsistencies were due to groups C and F, which differed from the others by the presence of females and because they were formed by the fusion of two subgroups.

Siskins show therefore a more smooth social system than serins, based on communication (e.g. displays) and associative signals (e.g. tolerances) rather than on direct aggression (see Balph, 1977). Additionally, siskins distinguish between familiar and unfamiliar flock companions, and display different behaviours according to the group affiliation of the opponent (Senar et al. 1990), meanwhile serins use the same agonistic behaviours against any bird (Senar, 1989). Possession of the resource is also of importance for siskins (Senar et al. 1989), subordinate possessors being allowed to win encounters, meanwhile for serins this is not the case (Senar et al. 1992). All of this makes us to suggest that the social system of the serin is very different from that of the siskin, and should be classified as "Despotic": dominants attack to any individual in conflict with them, using more high intensity aggressions than probably needed. This would oppose to the "Feudal" social system already defined for the siskin (Senar et al. 1990; Senar, 1989), in which dominants allow their subordinates to feed in close proximity, offering in this way, a profitable fee-

ding area, at the same time that defend them against other dominants. In return, they use their subordinates as food-finders, supplanting them to obtain food.

The lower intraspecific aggression of siskins should perhaps be seen as a characteristic of their social system rather than as a characteristic of the species. Siskins are highly aggressive to other species (Glue, 1982; Popp, 1989), but for an intraspecific feudal social system to work birds must be highly tolerant of those more subordinate (from their own species and group) (Rohwer & Ewald, 1981; Senar et al. 1990). This is not the case for despotic species (e.g. serin).

Hence, the question arises as to why such closely related species show so different a pattern of social organization. At present we do not have enough comparative data on other species to be able to generalize, but the difference could be explained by the nomadic lifestyle of the siskin, as opposed to the more resident nature of the serin (Senar, 1989; Senar et al. 1992). The high mobility of a nomadic species should lead either to no flock cohesion at all, as is the case with sanderlings (*Calidris alba*) (Myers, 1983), or to a high degree of cohesion, as in siskins (Senar et al. 1989; Senar, 1989; Senar et al. 1990; Payevsky, 1994). Otherwise familiar flock members would become separated by movement, with high costs for those individuals switching from one flock to another (Balph, 1979; Senar et al. 1990). This problem would not arise for a resident species (Matthysen, 1993) such as the serin. The greater integration of siskin flocks may therefore have evolved in parallel with behavioural mechanisms that promote a smooth social system (Senar, 1994), which fits with the results found in this paper.

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Resumen

Las interacciones forman la base sobre la que se asientan las relaciones entre individuos y la organización social de una especie. Existen sin embargo, pocos trabajos que analicen en detalle los flujos de interacción entre los distintos individuos de un grupo, y los comparen entre especies. En el presente trabajo, se analizan, utilizando técnicas estadísticas multivariantes, los patrones relativos de interacción agonística de dos especies de fringílicos Carduelinos: el lúgano (*Carduelis spinus*) y el verdecillo (*Serinus serinus*). El análisis analizó separadamente las interacciones con compañeros de bando nuevos (situación socialmente inestable), y con individuos con los que ya estaban familiarizados (situación socialmente estable). Los lúganos que interactuaban con nuevos compañeros se caracterizaban por utilizar despliegues agonísticos y tolerancias (un poseedor que le permite a un intruso permanecer dentro de su distancia individual), mientras que los verdecillos utilizaban mayoritariamente los ataques suplantadores. En la situación de interacción con individuos familiares, los verdecillos tendieron a utilizar, y de forma relativa, más despliegues, mientras que los lúganos continuaron utilizando la tolerancia como su principal forma de interacción agonística. Los lúganos, por tanto, parecen exhibir un sistema social más fluido que el de los verdecillos, basado en las tolerancias (y despliegues) en vez de la agresión directa. Estos resultados apoyan por tanto la visión del lúgano como especie con un sistema social tipo "Feudal", y al verdecillo como especie "Despótica". Se sugiere que estas diferencias podrían estar relacionadas con el carácter nómada del lúgano, en oposición a la naturaleza más residente del verdecillo. La alta movilidad de las especies nómadas necesariamente conduce, o bien a una falta de integración total del bando, como en el caso de los correlimos tridáctilos (*Calidris alba*), o a un alto grado de cohesión, como en el caso de los lúganos. De otro modo, el grupo social como tal se iría desmembrando como

consecuencia del constante movimiento, con unos altos costes para aquellos individuos que pasasen de un bando a otro. De este modo se propone que el movimiento continuado de los individuos de lúgano podría promover la evolución de mecanismos que mantuvieran un alto grado de cohesión entre los compañeros del bando, lo que permitiría el continuado movimiento sin la desmembración del grupo.

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