ARE FORAGING SERIN *SERINUS SERINUS* FEMALES MORE VIGILANT THAN MALES?: THE EFFECT OF SEX RATIO

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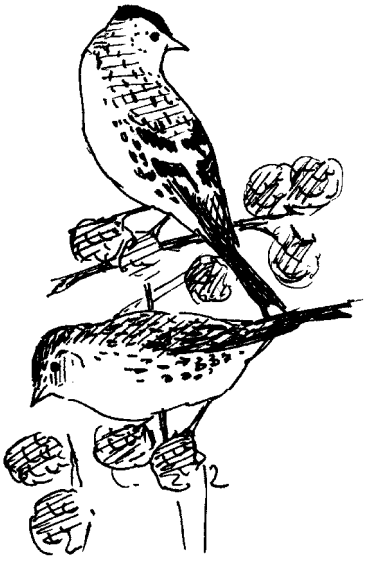

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Given that in many bird species females are subordinate to males and that, in general, subordinate individuals are more vigilant than dominants ones, we should predict foraging females to be more vigilant than males. This prediction is tested here in flocks of Serins *Serinus serinus*, where several males may forage together. We compared 41 winter foraging pairs (male versus female). Results showed that male Serins were dominant over females. Proportion of males around the focal pair had a significant effect on vigilance frequency and time spent vigilant and foraging in males, but not in females. When the percentage of males around the focal pair was lower than 50%, females displayed higher vigilance and less foraging time than males; when the percentage of males increased, males and females displayed a similar vigilance pattern. We suggest therefore that in flocks with several males (i.e. high ranking individuals) foraging together, males as well as females should keep the other flock companions as well as predators under surveillance, so that in the end the difference in vigilance rate of males and females would be diluted.

Key words: *Serinus serinus* - dominance - vigilance - flock feeding - sex-ratio

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INTRODUCTION

It is generally accepted that the vigilance rate of group foragers is lower than that of solitary individuals (Caraco 1982; Pulliam & Millikan 1982; Caraco & Pulliam 1984; Pulliam & Caraco 1984; Elgar 1989; Roberts 1996). Nevertheless, this lower vigilance rate may only be true for the average individual: subordinates may be more vigilant than dominants since vigilance may serve not only to detect predators, but also to monitor dominant flock companions, which may attempt to displace them from feeding patches (Knight & Knight 1986; Waite 1987a, 1987b; Waite & Grubb 1987; Knight & Skagen 1988; Popp 1988; Carrascal & Moreno 1992; Slotow & Rothstein 1995; see however Krams 1998).

In many bird species males are dominant over females (see Breitwisch 1989 for a review). According to the effect of dominance on vigilance rates and in order to prevent displacement aggressions, we should predict females to be more vigilant than males and to devote less time to feed. An important consequence of this may be a reduction in female survival rate and a male-biased sex ratio (Benkman 1997), which in turn may affect parental investment and sexual strategies (Breitwisch 1989; Gowaty 1996; Gowaty 1997).

The aim of this paper is to test in Serins *Serinus serinus* that males are dominant over females and to test for the higher vigilance rate of females vs males. Most tests of the hypothesis that subordinates should be more vigilant than dominants have been carried out in captivity or in experimental designs using only dyads or with very small flock sizes (Waite 1987a; Waite & Grubb 1987; Hogstad 1988; Knight & Skagen 1988; Popp 1988; Carrascal & Moreno 1992). The same appro-

ach has been used when comparing the vigilance rate of males and females (Waite 1987b). In these situations, there is only one male (i.e.: dominant individual), which may not be displaced by any other flock companion. To evict this possible confounding effect we studied free Serin flocks since in these groups several males may forage together. Our analyses show that the proportion of male birds (i.e. high-ranking individuals) around the focal pair affected the vigilance and foraging patterns of males but not that of females and that the difference in vigilance and foraging time of males vs females is dependent on the proportion of males around the focal pair.

METHODS

Field data was collected from foraging flocks of Serins during February and March 1994 in the suburban area of Barcelona (NE Spain). Serins were attracted to a bird table (110x60 cm) supplied with Rape *Brassica napus* seeds, and videotaped with a S-VHS-C movie camera Panasonic NV-S7E equipped with digital zoom x16, from a hide located four meters from the table. We videotaped 41 flocks (total time: 135 minutes, with a maximum of 25 minutes per day, during six non-consecutive days). The median size of Serin flocks (recorded as the maximum number of birds) at the feeding table was 16, and the mean (± SD) was 15.85 ± 7.42 (n = 41 flocks), with a mean foraging bout length (± SD) of 168.82 ± 103.23 s per flock, range 35-390 s.

The great number of birds in the area and the high individual turnover in the flocks (Conroy *et al.* 1999, pers.obs) prevented us from individually colour-ringing the birds using the feeders and to ascertain their dominance relationships. Therefore, we decided to test the relationship proposed that males are dominants over females, by analysing videotaped aggressions. We only used data from those agonistic interactions in which the sex of both contestants was ascertained. In any interaction we recorded the actor, the receiver, and the individual winning the interaction (Senar *et al.* 1989). To reduce the possible dependence between the observations, only one record was made per individual.

For the analysis of intersexual variation in vigilance and aggression rates, we used 41 pairs (only one pair per flock) of focal individuals, a male (i.e. dominant) and a female (i.e. subordinate), which were feeding close together, and we followed one of them for 30 s. We then rewound the tape to the start of the focal pair and observed the other member of the dyad. We compared pairs of individuals that were foraging at the same time to standardise for the effects of flock size, sex ratio, time of day, and temperature (Elgar 1989; Lima & Dill 1990) since with this approach both members of the dyad have the same flock mates and conditions. The tapes were analysed frame by frame (25 frames per second) in a video cassette recorder 3744 SV Nokia. We considered three behaviours: interactions, scanning and foraging (defined as all time not spent vigilant or fighting). In any interaction we recorded the actor, the receiver and the time spent in each role. In relation to scanning and foraging we recorded number and duration of scans and foraging bouts while foraging at the feeder. Birds were considered to be vigilant when the tip of the beak was raised to eye level or higher (see Lendrem 1983).

When comparing scanning and foraging variables, and in order to control for number of males and females close to the focal pair, we recorded the sex of flock mates around the pair (about 15 cm around the pair) (range 2-5 birds). Those pairs for which the sex of all flock mates (within a radius of 15 cm) could not be ascertained, were excluded from analyses. This restricted analysis of vigilance variables to 35 focal pairs. We additionally computed the correlation between flock size and sex ratio within the flock from 157 flocks (with more than four birds) recorded from February to March for the years of 1992 to 1996.

The Serins were not individually colour-ringed. However, the possibility of duplication was very small. Trapping operations showed that there were several hundred birds using the feeder. Additionally, the sampling unit here is the dyad; therefore, since groups at the feeder often contained

large numbers of individuals, and sampling took place over two months, there is a negligible probability of repeating the same dyad (Popp 1988, Slotow & Rothstein 1995).

Given the lack of normality for the variables under study, we used non-parametric Wilcoxon matched pairs test (males vs females within a pair) approach for all the analyses. In order to study the effect of proportion of males around the focal pair, we used a rank transformed Repeated Measures ANCOVA (Conover 1981), which allowed for the use of covariates. This is no more than a standard ANCOVA on the rankerized data rather than on the raw data (see Conover 1981). Number and duration of scans and foraging bouts for males and females within the different focal pairs were analysed as (four) independent repeated measures (i.e. pairing the male with the female within each pair) and proportion of males around the focal pair was entered as covariate. As in standard ANCOVA, the analysis provides an overall regression statistic (Wilks' Lambda) and the different correlation coefficients (r) relating percentage of males around the focal pair to the vigilance/foraging variables of both males and females.

RESULTS

From the total number of aggressions recorded on the feeders, males won 95% of total intersexual aggressive interactions (Binomial test $P < 0.001$, $n = 76$) and initiated 87% of all intersexual confrontations (Binomial test $P < 0.001$, $n = 76$). Males initiating the intersexual interaction (actors) won on 100% of occasions, while female actors won on 40% of interactions initiated (i.e. 5% of total interactions). Therefore, female Serins were clearly subordinate to males.

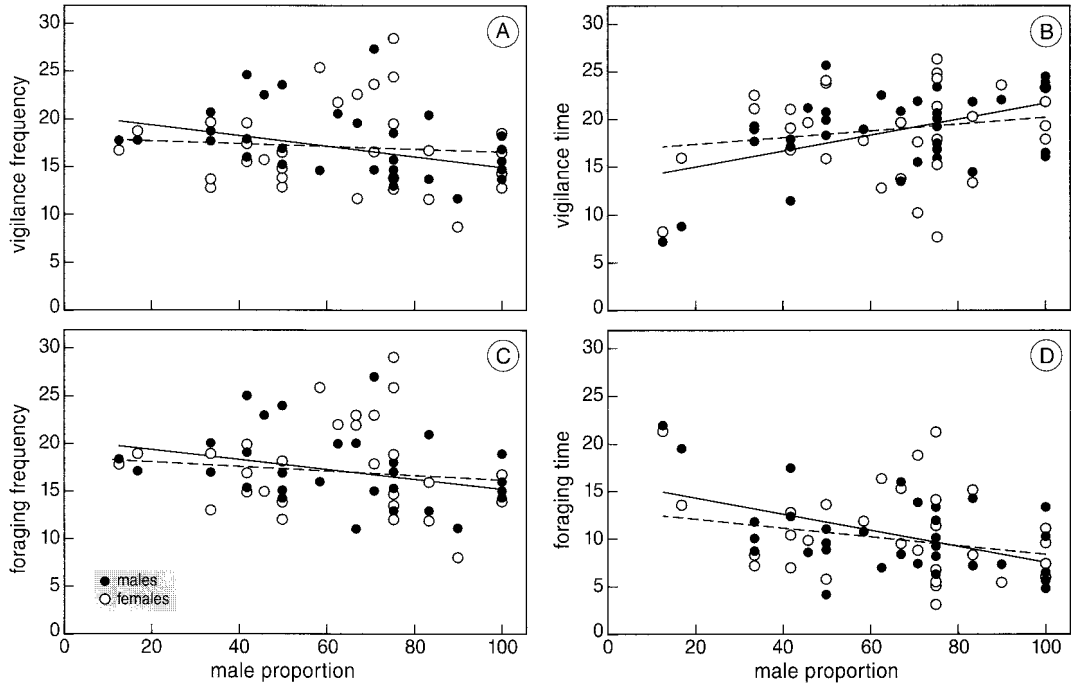

Fig. 1. Relationship between the proportion of males around the focal pair of Serins ($n = 35$) and (A) vigilance frequency, (B) vigilance time, (C) foraging frequency and (D) foraging time, of the observed focal pair. Solid lines: males, dashed lines: females.

Table 1. Mean frequency (± SE) of aggression and mean time spent in aggression per individual per 30 seconds ($n = 41$). We distinguish between actors and receivers, and between the sexes. * = $P < 0.05$, ** = $P < 0.01$.

	Frequency		Time (s)	
Sex	Actor	Receiver	Actor	Receiver
Male	0.73 ± 0.19	0.27 ± 0.11	0.12 ±0.03	0.03 ± 0.02
Female	0.12 ± 0.05	0.71 ± 0.16	0.02 ± 0.01	0.11 ± 0.03
Z	2.77**	2.27*	2.51*	2.17*

Table 2. Intersexual differences in Serin mean frequency (± SE) of vigilance and foraging bouts and mean time spent in these behaviours per individual per 30 seconds (n = 35 focal pairs). Results from rankerized Repeated Measures ANCOVA are presented. The repeated measures are the vigilance and the foraging variables which pair the male and the female within each focal pair. Percentage of males around the focal pair is entered as a covariate. For the covariate we provide the overall regression statistic Wilks' Lambda and additionally the r statistics for males and females according to the regression which relates the percentage of males around the focal pair and the vigilance and foraging variables displayed by the two sexes. The regression lines appear in Fig. 1. * = $P < 0.05$, ** = $P < 0.01$, (1) $P = 0.056$.

Sex	Frequency		Time (s)	
	Vigilance	Foraging	Vigilance	Foraging
male	17.26 ± 3.82	17.03 ± 3.84	18.78 ± 4.28	10.71 ± 4.10
female	17.46 ± 4.45	17.03 ± 4.61	19.17 ± 4.81	10.33 ± 4.80
F	0.005 n.s.	0.09 n.s.	0.69 n.s.	0.99 n.s.
Covariate (% males around focal pair)				
Wilks' Lambda	0.83*	0.84 (1)	0.81*	0.78*
male				
r	0.41	0.39	0.43	0.46
F	6.49*	6.08*	7.54**	8.74**
female				
r	0.13	0.15	0.19	0.23
F	0.54 n.s.	0.79 n.s.	1.18 n.s.	1.78 n.s.

Focal males initiated aggressive interactions (either inter and intrasexual) more often than females (Table 1: Wilcoxon matched pairs test, $Z = 2.77$, $n = 41$, $P = 0.005$). They also spent more time engaged initiating interactions (Wilcoxon matched pairs test, $Z = 2.51$, $n = 41$, $P = 0.01$; Table 1). In turn, females received a higher proportion of aggressions (Table 1: Wilcoxon matched pairs test, $Z = 2.27$, $n = 41$, $P = 0.02$) and spent more time receiving aggressions than males (Table 1: Wilcoxon matched pairs test, $Z = 2.17$, $n = 41$, $P = 0.03$).

No significant differences between males and females appeared in either vigilance or foraging rates (Table 2). However, proportion of males around the focal pair had a significant effect on vigilance and foraging of males, but not of females. The higher the proportion of males around,

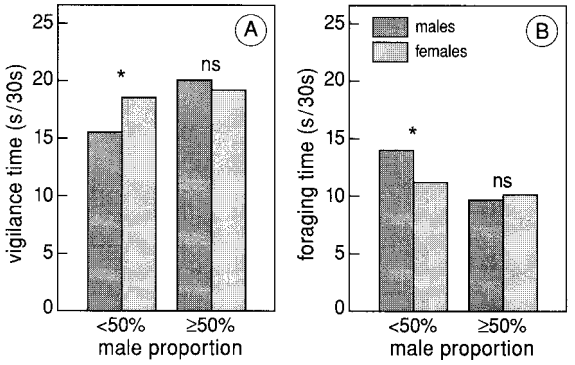

Fig. 2. Comparison of (A) mean vigilance time and (B) mean foraging time (± S.D.) between the male and female of the focal pair according to the proportion of males around that focal pair (lower than 50% [n = 9] and equal or higher than 50%[n = 26]).

the higher was the time spent vigilant by the focal male and the lower its vigilance frequency and time spent foraging (Table 2, Fig. 1). Additionally and although marginally non-significant, the higher the proportion of males around the lower was the foraging frequency of the focal male (Table 2, Fig. 1).

In order to test whether the increase in male but not female vigilance, associated to the increase in the proportion of males around the focal pair, caused a variation in the difference between the sexes in vigilance and foraging variables, we divided the data set into flocks with percentage of males less than 50% and flocks with a percentage equal or larger than 50%. In focal pairs with a proportion of males lower that 50% (i.e.: low inter-male competence) (n = 9), females devoted more time to vigilance and less to foraging than males (Wilcoxon Matched pair test; vigilance time: Z = 2.24, n = 9, $P < 0.05$; foraging time: Z = 2.19, n = 9, $P < 0.05$). No differences were found in vigilance or foraging frequencies between sexes (Wilcoxon Matched pair test; vigilance frequency: Z = 1.36, n = 9, P = 0.17; foraging frequency: Z = 1.33, n = 9, P = 0.18). However, focal pairs with a proportion of males around them equal or higher than 50% (n=26) did not show differences in vigilance or foraging variables (time and frequency) between sexes (Wilcoxon Matched pair test. Vigilance: time, Z = 0.37, n = 26, P = 0.71; frequency, Z = 0.58, n = 26, P = 0.56. Foraging: time, Z = 0.23, n = 26, P = 0.82; frequency, Z = 0.33, n = 26, P = 0.74) (Fig. 2).

No correlation was found between the size and the sex ratio of the flock (Spearman Rank Order Correlation; r_S = -0.17, n = 157, P = 0.84). For the groups used in the vigilance analyses, no difference was found in flock size between groups with higher and with lower (or equal) than 50% of males around the focal pairs (U Mann Whitney; Z = 0.24, n = 35, P = 0.81).

DISCUSSION

It is generally stated that vigilance may serve not only to detect predators, but also to monitor flock companions (Knight & Knight 1986; Waite 1987a, 1987b, Waite & Grubb 1987; Knight & Skagen 1988; Popp 1988; Carrascal & Moreno 1992; Slotow & Rothstein 1995; see however Krams 1998). Given that in many bird species males are dominant over females (Breitwisch 1989), we should predict females to be more vigilant than males. Results show that, according to this prediction, females devote more time to vigilance and less to foraging than males, but only when the proportion of males around the focal pair was lower than 50% (i.e. low inter-male competence). Nevertheless, and contrary to the prediction, when the proportion of males around the focal pair was equal or higher than 50% (i.e. high inter-male competence) we found that vigilance and foraging rates did not vary between the sexes, in spite that females received many more aggressions than males.

A low proportion of males around the focal

pair may lead to a low competition between males (including the focal male), and then these males could devote more time to foraging and less time to vigilance than females. Differences between sexes in vigilance and foraging rates have been found previously by Waite (1987a) working with pairs of birds (i.e. there was only one high-ranking individual, the male). Similarly other authors (Waite & Grubb 1987; Hogstad 1988; Knight & Skagen 1988; Popp 1988; Carrascal & Moreno 1992) working with dyads or small groups, with only one or very few high-ranking individuals (i.e. dominants) found differences in vigilance and foraging rates between dominants and subordinates.

When the proportion of males around the focal pair increases and becomes equal or higher that 50%, several males forage together in close proximity. In this case both the male as well as the female should keep the other males (i.e. highly competitive birds) around under surveillance to avoid aggressive interactions, so that no difference would appear in the vigilance and foraging rates of the two sexes. This explanation is suggested by the fact that the proportion of male birds around affected the vigilance and foraging patterns of focal males but not that of focal females: the higher the proportion of males around, the higher was the time spent vigilant by the focal male and the lower its vigilance frequency and time spent foraging. Our results can not be due to a collateral effect caused by a variation in sex ratio related to flock size, since no correlation was found between these two variables. In contrast to our study and many other studies Slotow & Rothstein (1995) and Catterall *et al.* (1992) did not find differences in vigilance rate between dominant and subordinate birds. Unfortunately neither of them computed the proportion of dominant birds around the studied individuals. Since Slotow & Rothstein (1995) worked with large flocks of White-crowned Sparrows *Zonotrichia leucophrys* and three simultaneous feeding spots, they interpreted their results as meaning that dominants also paid attention to conspecifics to assess the relative richness of other feeding spots. In our experimental design this possible confounding effect is excluded because we only used a single feeding table (i.e. there were no other feeding spots to assess). Catterall *et al.* (1992), interpreted their results in relation to the lack of predators in their study area, which was clearly not the case in our study (several cats and a Sparrowhawk *Accipiter nisus* routinely captured birds in our study area). The fact that these both studies were carried out studying flocks that contained several dominants could explain, according to our results, their lack of differences between the vigilance rate of dominant and subordinate birds.

Our data additionally show that although subordinate females receive much aggression, taking time from foraging, males also invest considerable time in these agonistic displays, so that in the end their feeding time is equal.

If our explanation of the effect of a simultaneous presence of several males (i.e. high ranking individuals) on vigilance rate of males and females is right, we could predict that a similar effect should be detectable when analysing vigilance rates between dominant and subordinate individuals within birds of the same sex. Hence, we suggest that hypothesis on differential vigilance rate of dominants vs subordinates (Waite 1987a, 1987b; Knight & Skagen 1988; Popp 1988; Slotow & Rothstein 1995; Carrascal & Moreno 1992) should take into account the possible simultaneous presence of several dominants individuals within a flock.

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SAMENVATTING

Vogels die in een groep naar voedsel zoeken, kijken geregeld op. Dergelijk opkijkgedrag heeft een aantal mogelijk functies, zoals (1) het op tijd ontdekken van een roofvogel of andere predator en (2) het in de gaten houden van soortgenoten die voedsel of goede voedselplekken willen stelen. Vooral subdominante dieren lopen het risico bestolen te worden, en de auteurs voorspellen daarom dat subdominante dieren in een groep vaker zullen opkijken en minder tijd zullen hebben om naar voedsel te zoeken dan dominante dieren. Om dit idee te toetsen, bestudeerden de auteurs vrijlevende, ongeringde Europese Kanaries *Serinus serinus* op een voedertafel in een buitenwijk van Barcelona. De groepen met een gemiddelde grootte van 16 vogels foerageerden gemiddeld een minuut of drie op de tafel en van 41 groepen werden videobeelden verzameld. Per

groep werd één vrouwtje en één mannetje bestudeerd die zich dicht in elkaars buurt bevonden. Ook werd het geslacht bepaald van alle andere vogels die rond dit tweetal naar voedsel zochten. Uit alles blijkt dat de vrouwtjes ondergeschikt zijn aan de mannetjes. Zoals voorspeld, kijken vrouwtjes vaker op en besteden minder tijd aan voedsel zoeken dan mannetjes, maar de verschillen zijn klein en treden alleen op als er weinig mannetjes in de buurt foerageren. Het lijkt erop dat vrouwtjes hun gedrag niet veranderen afhankelijk van wie er in de buurt naar voedsel zoekt, maar dat mannetjes oplettender worden naarmate er meer mannetjes in de buurt zijn. Op basis van deze gegevens suggereren de auteurs dat alle individuen beter moeten opletten naarmate er meer dominante dieren in hun omgeving naar voedsel zoeken. (BJE)

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