

Body mass regulation in resident and transient wintering siskins *Carduelis spinus*

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Abstract. Birds regulate body mass according to the trade-off between the benefits (e.g. energy insurance) and the costs (e.g. predation risk) of carrying reserves. As a consequence, several factors as ability to find food resources, dominance status, and energetic constraints related to flight, can equally determine the body mass of an individual. We test the relative contribution of these factors through the detailed monitoring of captive groups of resident and transient siskins *Carduelis spinus*, a species in which residents have previously shown to be dominant over, heavier and less mobile than transients. In the first experiment groups of residents and transients were introduced simultaneously into a cage, so removing any prior residence (and hence dominance) advantage for residents. In this situation, transients maintained a lower body mass than residents. When we removed the groups of transients and introduced them into a new empty cage, while groups of residents remained in their previous cage, both resident and transient individuals increased in body mass, albeit that the difference between them, although reduced, was still significant. Since food was provided *ad libitum*, this result suggests that the lower body mass of transients is not because of them being poorer foragers than residents. In the third experiment we introduced the group of transients into a cage where a resident group had been living for several weeks (and so were dominant due to the prior residence effect). In this situation both residents and transients again lost body mass, although transients proportionally lost slightly more mass than residents, indicating that interaction with dominant resident birds had had some effect on the decrease in transient body mass. However, since independently of body mass fluctuations among experiments, captive transients maintained a lower body mass than residents irrespectively of experimental treatment, the alternative hypothesis that transients maintain a lower body mass than residents because they are keeping their flight costs down, is fully supported.

Key words: Body mass regulation, residence, dominance, flight, Siskin, *Carduelis spinus*.

Resumen. *Regulación de la masa corporal en lúganos residentes y transeúntes.* Las aves regulan su masa corporal buscando un equilibrio entre los costes (e.g. riesgo de predación) y beneficios (e.g. asegurarse la energía necesaria) de acarrear reservas de grasa. Varios factores como la habilidad para encontrar recursos alimenticios, el estatus de dominancia, y las constricciones energéticas del vuelo, pueden afectar en el peso de un individuo. En este trabajo se analiza la contribución relativa de estos factores mediante el seguimiento detallado de grupos cautivos de lúganos *Carduelis spinus* residentes y transeúntes. Trabajos previos demostraron que los transeúntes son subordinados a los residentes, y que tienen menor peso y son más móviles. En el primer experimento se introdujeron simultáneamente en aviarios grupos de transeúntes y de residentes, eliminando así la ventaja de residencia previa de los individuos residentes, y por tanto su dominancia. En esta situación, los transeúntes mantuvieron una menor masa corporal. Posteriormente se trasladó a los transeúntes a unas jaulas nuevas y se mantuvo a los residentes en sus jaulas originales. En este caso, ambos grupos incrementaron su masa corporal, y si bien la diferencia entre ellos se redujo, ésta continuaba siendo significativa, a pesar de que el alimento se suministraba *ad libitum*. Esto sugiere que la menor masa corporal de los transeúntes no es consecuencia de que encuentren menos alimento. En el tercer experimento introdujimos los grupos de transeúntes en las jaulas donde otros grupos de residentes habían estado viviendo durante varias semanas (y por tanto éstos eran dominantes debido al efecto de residencia previa). En esta situación tanto transeúntes como residentes perdieron masa corporal, si bien los transeúntes perdieron algo más. Ello sugiere que la interacción social entre ambos grupos había acentuado la diferencia en masa corporal debido al efecto de dominancia de los residentes sobre los transeúntes. Sin embargo, el hecho de que en todos los tratamientos experimentales los transeúntes mantuvieran una menor masa corporal que los residentes apoya la hipótesis alternativa de que éstos mantienen deliberadamente su masa corporal más baja, para reducir los costes de vuelo asociados a su transumancia.

Introduction

Several experiments have shown in birds how unpredictable food availability or reductions in temperature cause an increase in body mass (e.g. Lima, 1986; Hake, 1995; Ekman & Hake, 1990; Gosler, 1996; Lilliendahl et al., 1996; Witter et al., 1995). However, although fat stores are an insurance against periods of food shortage, it is equally recognised that they may reduce flight performance (e.g. Metcalfe & Ure, 1995; Kullberg et al., 1996; Witter et al., 1994; Veasey et al., 1998). Dominance status has also been acknowledged as an important determinant of body mass: since food is less predictable for subordinates than for dominants, which have a higher probability of acquiring enough food in the future, it has been suggested that subordinates should have a higher body mass than dominant individuals (Ekman & Lilliendahl, 1992; Haftorn, 1992; Witter & Swaddle, 1995; Clark & Ekman, 1995; Gosler, 1996; Hake, 1996; Witter & Goldsmith, 1997). Alternatively, when social status affects predation risk while foraging or access to food is restricted to dominants, the optimal level of energy reserves may be higher for dominant than for subordinate individuals (Baker & Fox, 1978; De Laet, 1985; Piper & Wiley, 1990; Verhulst & Hogstad, 1996). It is therefore widely recognised that birds are able to regulate body mass according to a trade-off between the benefits and the costs of carrying reserves (see Witter & Cuthill, 1993; Cuthill & Houston, 1997; Houston & McNamara, 1999; McNamara & Houston, 1990 for reviews).

Wintering Siskins (*Carduelis spinus*) have a social system in which there are both resident and transient individuals within the same wintering area (Senar et al., 1992). Residents are generally dominant over transients (Senar et al., 1990) and stay in wintering areas for extended periods, while transient birds move throughout the winter over long distances (Senar et al., 1992). In the wild, residents are consistently heavier than transients for a given body size (Senar et al., 1992). The species therefore provides a good opportunity to study the extent to which there is a causal proximate link between residence status, movement, dominance and body mass. Here we analyse the relationship between these variables through the detailed monitoring of captive groups of resident and transient individuals subjected to several experimental manipulations.

Material and Methods

General procedures

Transient siskins rarely stay more than a day or two in one locality during the non-breeding season, and move over long distances (Senar et al., 1992). Given the difficulty of following individual transient birds in the field, the approach we used was to experiment on captive birds in aviaries. The birds used in the experiments were captured in the suburban area of Barcelona (see Senar et al., 1992 for details of the area and capture methods), using mist nets, clap nets and traps (see Senar, 1988). An extensive capture-recapture programme allowed us to determine

which individuals were staying in the area for long periods (>3 weeks), and therefore were residents (see Senar et al., 1990; Senar et al., 1992). The use of a mist net associated with live decoy birds was used to trap transients, since transients are greatly attracted by live decoys (and therefore were trapped in the net), whereas residents are rarely caught by this method (Senar & Metcalfe, 1988). All the birds trapped with the use of decoys were unringed (i.e. were almost certainly newly arrived into the area), which further supported our assumption about their transient status. Several groups of captured residents and transients were then kept in separate aviaries (as described below) measuring 1.5 x 1 x 0.75 m.

Hypothesis, experiments and predictions

The aim of the study was to test whether transients maintain a lower body mass than residents (1) because they are less efficient at locating food sources (the food access hypothesis; see (Senar & Metcalfe, 1988)), (2) because of competitive interference interactions with dominant residents (the social interaction hypothesis), (3) because they keep their body mass down to reduce the energetic costs of being more mobile (the flight cost hypothesis), or (4) because they are just intrinsically different, due to genetic background or rearing environment, in a similar way as they maintain a difference in wing shape (Senar et al. 1994a) (the alternative phenotype hypothesis).

Under the food access hypothesis we predicted that captive conditions where food was provided *ad libitum* should result in transients increasing their body mass to that of residents, irrespective of experimental treatment. If the social interaction hypothesis was applicable, we predicted that captive transients should maintain a lower body mass than residents when interacting with them, but should increase in mass when kept isolated from residents. Under this hypothesis we additionally predicted that if we experimentally removed the prior residence advantage, and hence the dominance advantage of residents, transients should also increase their mass to reach that of residents. The flight cost hypothesis predicted that independently of body mass fluctuations among experimental treatments, captive transients should maintain a lower body mass than residents irrespective of experimental treatment. Here we assume that captivity does not affect the perception that the bird has of its own residence status; a conceptually similar example is that of birds in migratory periods which in spite of being in captivity increase body mass through migratory fuelling (e.g. Kullberg et al., 1996; Fransson & Weber, 1997). The genetic hypothesis predicted that transients should maintain a fixed lower body mass than residents in any of the experimental situations, and this should be similar to that of wild birds.

We therefore designed three experimental situations in captivity that allowed us to test between these alternative hypotheses by manipulating the social environment of the individuals. Experiments were replicated in the winters of 1997 and 2001. Once captured, the birds were kept in individual cages for three weeks before the experiments started. In the first experiment we introduced

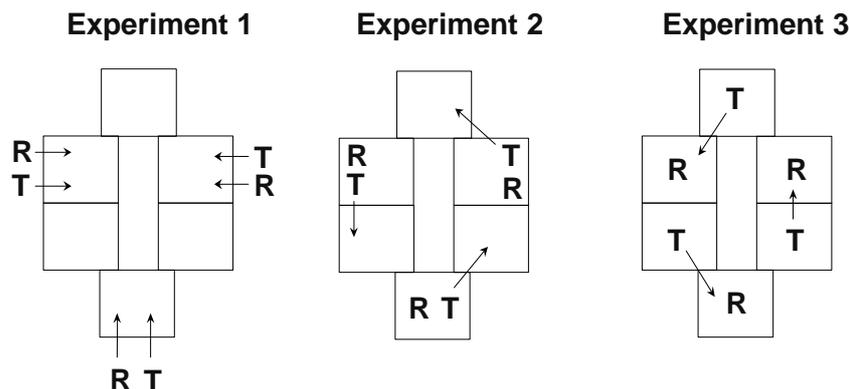


Figure 1.- Schematic description of the experimental design used in the study of the relationship between body mass and residence status in siskins. Each polygon represents a cage (six cages in total). In the first experiment (replicated nine times) a group of residents and another one of transients are simultaneously introduced into a cage. Prior to the second experiment the transient group is moved into a contiguous cage, so that the resident and the transient groups are now in separate cages. At the start of the third experiment transients are introduced into a cage with residents, which enjoy a prior residence advantage. The experiment was designed so that residents stay in the same cage for the whole experiment, whereas transients move from one cage to another.

simultaneously into a cage a group of three male resident siskins and another one of three male transients (fig. 1). In this situation we eliminate any prior residence effect so that residents are not dominant over transients (pers.obs.); by using only males we controlled for any sex effects.

In a second experiment, two weeks later, we removed the group of transients and moved them to a new identical but empty cage, while the residents remained in their previous cage (fig. 1).

After a further two weeks, the third experiment consisted of introducing the group of transients into a cage where another resident group had been living for four weeks. Under this situation, residents are dominant over transients because of a prior residence effect (pers. obs.), so this simulates the situation found in the wild.

Each experiment was replicated nine times, with birds from each residence category randomly assigned to each replicate. We designed the experiment so that the nine resident groups remained all the time in their own cages, while each transient group rotated (Fig. 1). We recorded body mass for each individual at the end of each experiment (two weeks per experiment), at the same time of day (midday) each time to control for diurnal effects. Body mass was determined to 0.1 g with an electronic balance. We did not standardize body mass by wing length (or any other size measure) because of the lack of differences in size between residents and transients, either in our experimental group ($F_{1,48} = 2.75, p = 0.10$, controlling for year) or in wild populations (Senar et al., 1992). Food was provided *ad libitum*. A resident and a transient bird escaped during the experiment and have been therefore excluded from all analyses.

We recorded contests over resources for the different groups in experiments one and three, in order to determine whether our residents increased in dominance over transients in the third experiment because of a prior residence advantage. In each interaction we recorded the actor and reactor, and the winner (see Senar et al., 1993, 1989). An individual was considered to have won an

Table 1. Effective hypothesis decomposition for GLIM multivariate test for repeated measures of the interaction between experimental treatment and residence status (see text and fig. 1), on body mass variation in siskins. The experiment was replicated in 1997 and 2001 and the Year factor tests for this difference, which is non significant.

	F	d.f.	p
Experiment	25.90	2,47	<0.001
Experiment x Year	1.14	2,47	0.33
Experiment x Residence	3.47	2,47	0.04
Experiment x Residence x Year	0.90	2,47	0.41

encounter if its opponent gave a submissive posture or withdrew. Within each dyad, we considered a bird to be dominant over the other one if it had won significantly more than 50% of the encounters (according to χ^2 test; $p < 0.05$) (Senar et al. 1993; Senar et al., 1994b). We only considered for analyses those dyads where more than 10 interactions were recorded.

Analysis

The same individual birds were used for the three different experiments, allowing us to test for treatment effects while standardising for individual effects. Therefore, body mass was analysed by mixed-model repeated measures analysis of variance. Residence status (residents vs. transients) was treated as a between-subjects effect and the within-subjects effect was defined by the experimental treatment (one to three). The *a priori* parameter of interest in these analyses is the Residence*Experiment interaction, that is, do the different experimental treatments cause differential changes in body mass and fat score between residents and transients?. Values are shown as means ($\pm SE$), and two-tailed tests of significance have been used throughout.

Results

As expected, the residents used in the experiments had a higher body mass than transients on capture (Residents:

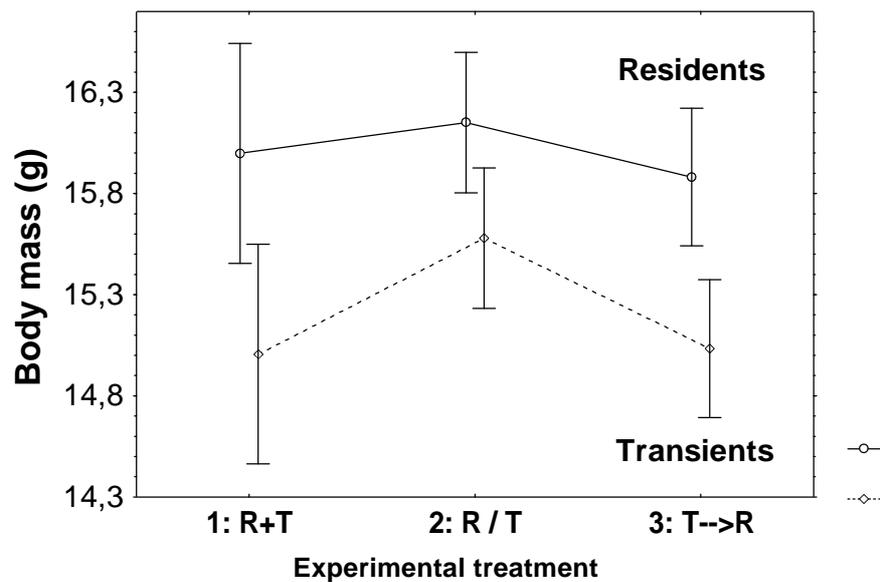


Figure 2.- Body mass (s.e.) variation in siskins according to residence status and experimental treatment. 1: residents and transients simultaneously introduced into the same cage; 2: residents and transients are in separate cages; 3: transients have been introduced into the cage of residents (see fig. 1 for details).

13.7±0.15 g, transients: 12.5±0.13 g; $F_{1,50}=33.16$, $p<0.001$). Both residents and transient birds increased body mass upon being taken into captivity, (average increase for Residents 18%, for Transients 21%; Residents: $F_{1,50}=4400.9$, $p<0.001$; Transients: $F_{1,50}=4050.0$, $p<0.001$; see also Fig. 1). The difference in the percentage of increase between the two classes was however not significant (Planned comparison testing the interaction between residence status and body mass increase during captivity: $F_{1,48}=3.34$, $p=0.07$).

Residents significantly increased in dominance in relation to transients from the first to the third experiment (first experiment, dyads dominated by residents: 22, by transients: 30; third experiment, dyads dominated by residents: 24, by transients: 15; Fisher 2x2 test $p=0.05$), supporting the dominance advantage of residents through prior residence in the third experiment.

Body mass changed according to experimental treatment (Fig. 2, table 1), birds having a higher mass when residents and transients were in separate cages than when they were together (planned comparison comparing periods 1 and 3 vs. 2; $F_{1,48}=5899.78$, $p<0.001$). A significant interaction appeared between residence status*experimental treatment when all three experiments were considered together (table 1), stressing that variations in body mass between experiments was more pronounced for transient than for resident birds (Fig. 2). Although transients reduced their difference in body mass with residents when they were in separate cages, the difference between residents and transients was still significant (Planned comparison, $F_{1,48}=5.48$, $p=0.02$). A planned comparison analysing the interaction between residence*experiment, from the first to the second experiment, was not significant ($F_{1,48}=2.18$, $p=0.15$). However the interaction was significant when we compared

body masses of residents vs. transients in the situation in which both classes stayed in separated cages (exp. 2) with the situation in which transients were introduced into the cage of residents (exp. 3) ($F_{1,48}=5.88$, $p=0.02$), indicating that although birds in both classes lost body mass when transients were introduced into the residents cage, the reduction was greater for the transient class (Fig. 2). The difference in significance between the two interactions, however, was probably caused in part by the large overlapping standard errors in the first experiment compared to the third one.

Discussion

Wild transient siskins maintain a lower body mass than resident birds (Senar et al., 1992). Several hypothesis could account for this variation. The lower body mass could be a result of transients not being as efficient as residents at locating food (see Senar & Metcalfe, 1988). Under this situation, captivity conditions, with food provided *ad libitum*, should have caused an increase in the body mass of transients to reach that of residents for all three experiments. This was not the case, which rules out this explanation.

Alternatively the lower mass of transients could be due to intrinsic differences resulting from a morphological adaptation to continuous movement (Witter & Cuthill, 1993), similar to the more pointed wings already detected for transient siskins (Senar et al., 1994a). Under this situation transients should have maintained a lower body mass than residents in all three captivity experiments. This has partially been the case, since transients tended to have a lower mass than residents throughout the experiments; however, since the weight gain upon being taken into captivity was substantially greater in both

categories of birds than the difference between them, some other factors are likely to be operating.

Since resident siskins are dominant over transients in the wild (Senar et al., 1990), the difference in body mass between them could be a consequence of social interaction (Witter & Goldsmith, 1997). The differential reduction in the body mass of transients when introduced into a cage with residents, which enjoyed a prior residence effect and therefore were dominant over transients, supports this view. However, the difference between the body mass of transients and residents also appeared when transients cohabited with residents that had been simultaneously introduced into the same cage, so that the prior residence (and hence dominance advantage) of residents had been eliminated. This stresses that although the lower body mass of transients in the wild may be partially causally related to social interaction with dominant residents (Ekman & Lilliendahl, 1992; Witter & Swaddle, 1995; Witter & Goldsmith, 1997), the difference is also related to another factor.

The fourth possibility is that in the wild, transients are deliberately keeping their weight down to reduce the energetic flight costs associated to their more mobile life style (Metcalf & Ure, 1995; Senar et al., 2002; Kullberg et al., 1996; Witter et al., 1994; Veasey et al., 1998). Since birds are not conscious of how long captivity may last (in fact captivity is a totally abnormal condition for birds), this strategic adjustment may also operate; in this sense, a conceptually similar example is that of birds in migratory periods which in spite of being in captivity increase body mass through migratory fuelling (e.g. Kullberg et al., 1996; Fransson & Weber, 1997). This hypothesis predicted that independently of body mass fluctuations among experimental treatments, captive transients should maintain a lower body mass than residents irrespective of experimental treatment. This is what we found.

Summarising, although wild transient siskins are poorer foragers than residents (Senar et al., 1992), this is not the cause of their lower body mass. Our results agree with the hypothesis that transients may have a lower mass than residents because they are keeping their flight costs down, and to a lesser extent, because of interactions with residents, which are normally dominant over them (Senar et al., 1990). This flight adaptation parallels that found in their wing shape, with transients having more pointed wings than residents (Senar et al., 1994a), but allows for some more flexibility and variation than that of morphological characters, probably because of the several additional constraints that shape body mass (Lima, 1986; Gosler, 1996). Nevertheless, a confirmation of transients keeping a lower body mass as a flight adaptation would need to measure or manipulate flight costs.

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