About eating and not eaten. Vigilance and foraging strategies in wintering Eurasian siskins (*Carduelis spinus*)

Sobre menjar i no ser menjar: estratègies de vigilància i alimentació en lluers hivernants (*Carduelis spinus*)

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Programa de Doctorat en Biodiversitat

Memòria de tesi presentada per Jordi Pascual Sala
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El doctorand

Jordi Pascual Sala

Vist i plau del Director i Tutor de la tesi:

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Director de la tesi

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Introduction

■ Vigilance while foraging in social groups

Animals have to eat a certain amount of food every day to survive. Feeding involves different activities: searching, catching and handling food (Barnard 1980b; Beauchamp 1998). Since trophic resources are usually found in exposed locations, animals are in risk of predation while feeding (Lima & Dill 1990). Therefore, they face the well known trade-off between predation and starvation risks (McNamara & Houston 1987). Animals may reduce predation risk by scanning for predators. However, since vigilance is incompatible with feeding (see however Topic 1), an increase in the time allocated to scanning entails an increase in exposure time to predators (Newman et al. 1988; Cassini 1991). Therefore, animals may increase food intake to reduce foraging bouts at the cost of vigilance (Moreno & Carrascal 1991; Smith & Metcalfe 1994) or may do the opposite, and that they display one strategy or the other will depend on the perceived usefulness of vigilance (Lima 1987a).

Animals may reduce predation risk without reducing either energy intake rate or foraging bout length by feeding in safer patches (e.g. Caraco et al. 1980; Grubb & Greenwald 1982) and by joining groups (Beauchamp 2008). As more animals feed together, the more eyes scan ('many eyes effect', Pulliam 1973), an attacking predator may feel confused by the many targets ('confusion effect', Miller 1922), individuals hide themselves inside the group ('selfish herd', Hamilton 1971) and there is a reduction in capture probability for a given individual ('dilution effect', Bertram 1978). The way how these diverse effects apply and interact may depend on many variables (e.g. predator and prey behaviour, prey position, etc.; Bednekoff & Lima 1998), but the general pattern of a reduction in predation risk as group size increases is straightforward. Therefore and as expected, there is a general decline in vigilance with group size (Elgar 1989), although this variable explains only a small amount of the variation in vigilance (Beauchamp 2008). Maybe this is so because birds foraging in flocks still benefit from their own scanning since vigilant individuals flush to cover sooner than non-vigilant birds (Elgar et al. 1986; Hilton et al. 1999). Individual vigilance within a group will be more important with an increasing frequency of stalking predators which can assess prey vigilance before launching an attack (Cresswell et al. 2003a).

In considering group vigilance, not only group size is important but also distance to neighbours. Elgar et al. (1984) demonstrated that in house sparrows (*Passer domesticus*) group perception was related only to visible birds, and that individuals foraging more than 1.2 m apart scanned independently of each other. More recently, Fernández-Juricic et al. (2007) found a similar result in brown-headed cowbirds (*Molothrus ater*) and stressed the importance to consider as members of a group only those individuals foraging in a radius that allows the detection and dilution effects to operate.

Another important advantage of group feeding is information sharing, which highly improves food detection and exploitation (Giraldeau 2008). There are many sources of inadvertent social information available to social foraging animals, such as food quality and availability, predation risk, group composition, etc. (Giraldeau 2008). In some species, this public information can even lead to exploitation, with some individuals searching for undiscovered food (producers) and others monitoring them to scrounge their food (scroungers) (Mottley & Giraldeau 2000).

In spite of these multiple advantages of group foraging, there are some associated costs, too (Sansom et al. 2008). When the amount of food on the foraging patch is limited, an increase in the number of foraging birds reduces the amount of food available to a given individual, leading to scramble competition (Lima et al. 1999). On the other hand, if the food items are concentrated in some defendable patches, the birds will fight to access them, leading to interference/contest competition (Senar et al. 1990). As a consequence, the group size will reflect an additional trade-off between competition for food and predation risk, being increased until reaching an equilibrium flock size (Barnard 1980a; Beauchamp 1998; Fernández-Juricic et al. 2007). In this situation, animals have to be vigilant to conspecifics both to gather useful information from them (Fernández-Juricic et al. 2005; Giraldeau 2008) and to avoid their aggressions (Knight & Knight 1986; Waite 1987a). The vigilance system used to reduce predation risk may be different from that required for monitoring other group members (Slotow & Coumi 2000; Fernández-Juricic et al. 2005).

■ Vigilance systems and strategies in granivorous birds

Feeding in granivorous birds involves three main activities: searching for, catching (i.e. pecking) and handling food. When searching for food and pecking, birds have the head down, and when handling food birds have the head up. This lends to the widespread head-up/head-down pattern of vigilance in these birds. If vigilance could be accommodated entirely within handling intervals, so that feeding was a succession of search-peck-handle intervals, with only one peck per interval, then feeding and scanning would not be mutually exclusive tasks. Time allocation in foraging granivorous birds would be simple: head-up intervals (i.e. scan durations) would exactly reflect handling times and head-down intervals (i.e. inter-scan durations) would exactly reflect searching times (see Fig. 1b). Popp (1988) found that, as expected by this model, increasing seed manipulation time produced an increase in scan durations.

However, Baker et al. (2011) studied the feeding behaviour of four species of granivorous birds and found that the reality was far more complex. A high proportion of vigilance occurred during non-compatible components of foraging. Scanning rate was

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higher than pecking rate, so the assumption 'one scan per peck' was not met. Moreover, during handling head-down searching behaviour was frequent. This pattern of feeding-vigilance behaviour is much closer to the vigilance system we found in siskins (Fig. 1c).

Figure 1. Schematic representation of the vigilance and foraging system used by social birds feeding in foraging patches (e.g. feeders). (a) Time intervals when the bird is 'in' or 'out' of the foraging patch along the day. (b) Ideal model of vigilance and feeding behaviour with birds only searching for and handling food. When they search for food, they have the head-down and cannot scan for predators or flockmates; when they handle food, they have the head-up and can scan both for predators and flockmates. All the vigilance is accommodated in the handling time intervals. (c) More realistic model of vigilance and feeding based on the behaviour observed in wintering siskins foraging in feeders. Sometimes siskins peck but not get any food; sometimes they hear alarm calls and interrupt searching for food; sometimes they receive aggressions or attack flockmates and so they interrupt searching or handling; sometimes they catch several items of food without rising the head; and sometimes they make hops with the head-down to search for food or they make hops with the head-up to avoid aggressive individuals or to other unknown purposes. sea = searching for food intervals; han: handling food intervals; vig: vigilance without handling intervals; fight: agonistic interaction intervals. Wide bars represent pecks and double bars represent eating. Thin bars represent a change in behaviour.
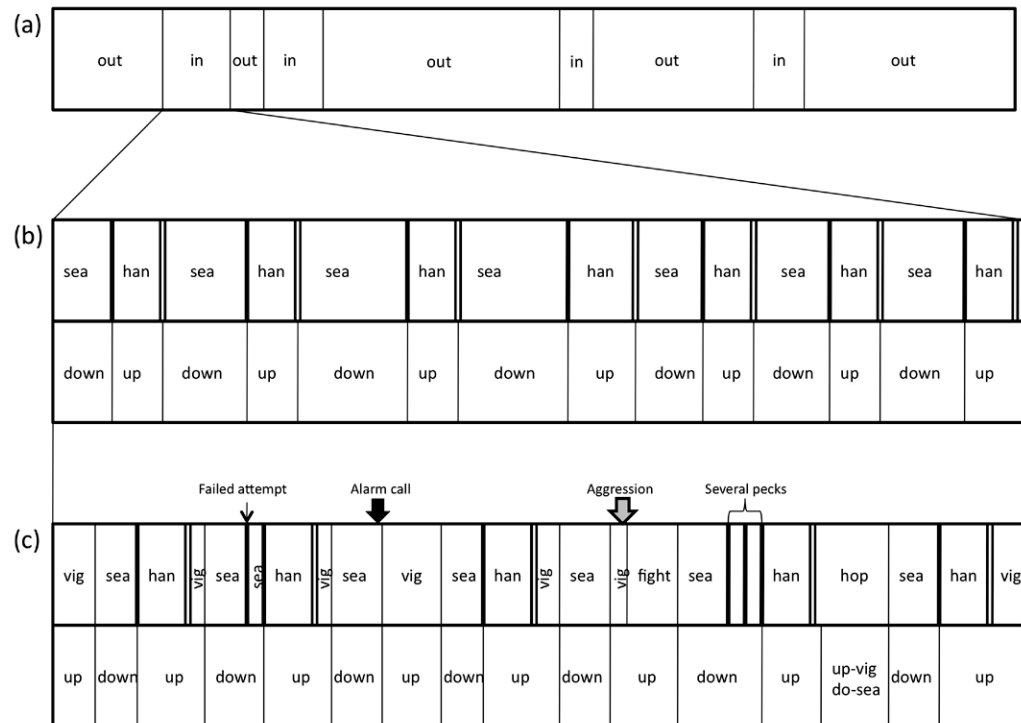
Inter-scan durations have been shown not to be regular, but instead to approximate a negative exponential distribution, although with fewer very short and very large intervals than expected by this distribution (Bednekoff & Lima 2002). Therefore, although food handling time probably sets a minimum to scan durations (Lendrem 1983) and food searching time sets a minimum to inter-scan bouts, other factors influence both variables. Hence, the vigilance system is not fixed but can be adjusted by birds to ecological factors. Constant inter-scan durations would be expected if birds' predation risk was solely associated to fast-moving predators, which could not exploit vigilance regularities of prey (Scannell et al. 2001; Bednekoff & Lima 2002). On the other hand, random initiation of scans (and therefore a negative exponential distribution of inter-scans) should be expected if birds' predation risk was mainly associated to stalking predators which observed the vigilance behaviour of prey (Scannell et al. 2001; Bednekoff & Lima 2002). In fact, some evidence for such an adjustment according to predator type has been found (Bednekoff & Lima 2002; Whittingham et al. 2004).

On the other hand, it had traditionally been assumed that head-down birds could not be vigilant to predators (Barnard 1980b; Pulliam et al. 1982; Bednekoff & Lima 2002). Therefore, the percentage of time spent in vigilance was assumed to be equal to the percentage of time with the head-up. However, Lima & Bednekoff (1999) found this assumption not to be correct: head-down birds could still detect approaching predators, although less efficiently. More recently, Fernández-Juricic et al. (2004) have shown that the usefulness of head-down vigilance highly depends on the visual perception of birds, which are classified in three main groups according to the extent of their visual fields. Large visual field species can gather much information about their environment with the head-down, although attention to peripheral vision also entails a cost in terms of food intake rate. Visual acuity and coverage also influence the vigilance system of birds (Tisdale & Fernández-Juricic 2009).

Finally, birds do not only make up-down head movements, but also move the head in the horizontal axis (lateral head-turning; Jones et al. 2007) and even can make head cocking (i.e. "rotation of the head about the longitudinal axis of the body so that one eye looks up and the other down"; Barnard 1980b). Jones et al. (2007) found that chaffinches (*Fringilla coelebs*) increased head-turning after seeing a domestic cat model, but not a sparrowhawk (*Accipiter nisus*) model, as compared with exposition to control (i.e. non-predator) ground and aerial models. Moreover, they did not find any difference in the traditional vigilance variables (scan duration, inter-scan duration and scan rate) before and after the exposure to the models, stressing the importance to take into account all the head movements.

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The study of vigilance in birds is far from simple. According to their large visual fields (Fernández-Juricic et al. 2004), it is difficult to know what they are watching at any time, and we can only deduce indirectly their vigilance to predators or flockmates through their response to experimental manipulations. Hence, much of

Photo 1. Couple of male siskins moving their wings in an aggressive interaction while foraging at the inner small (IS) bird feeder table of the study area, with a female on the left not involved in the fight and husking a turnip seed.

the work on vigilance has been based upon the modification of distance to cover (either protective cover (e.g. Caraco et al. 1980) or cover from which an attack may come (e.g. Lima et al. 1987)), amount and density of food (e.g. Barnard 1980a; Elgar 1987; Baker et al. 2010), visual obstructions (e.g. Lima 1987a), etc. to birds either feeding at wild or in enclosed aviaries (e.g. Cresswell et al. 2003b; Fernández-Juricic et al. 2005). Many studies have tested explicit theoretical models relating environmental factors to vigilance behaviour (e.g. Pulliam 1973; Lima 1987b; Bednekoff & Lima 1998). However, in most of the experimental manipulations in the wild the decrease in predation risk was associated to an increase in group size

and therefore in competition (e.g. Caraco et al. 1980; Barnard 1980a; Saino 1994), so that they failed to discriminate the effects of predation risk and competition on vigilance. Probably because of this most of recent studies on vigilance have been carried out with captive birds in enclosures under controlled environmental conditions (e.g. Fernández-Juricic et al. 2007; Baker et al. 2010). However, the way how captivity may alter the vigilance behaviour of birds both for the stress of captivity and for the artificiality of the environment is difficult to know, and could have an important influence on the results.

When predation risk increases, animals generally increase the proportion of time allocated to vigilance by increasing mean scan durations (beyond handling time) at the cost of reducing food intake rate (e.g. Fritz et al. 2002; Barta et al. 2004; Baker et al. 2011). Another reported reaction to the increase in predation risk in socially foraging birds is the increase in scan rate by reducing mean inter-scan durations (Cresswell et al. 2003b). This vigilance strategy has the advantage that is not costly in terms of food intake rate, since scan rate and feeding rate are positively correlated. However, inter-scan durations are limited by the time needed to find a food item (i.e. searching time, see Fig. 1), so they not always can be reduced. Effective and fast detection of an approaching avian predator precise of short inter-scan durations (Hart & Lendrem 1984; Whittingham et al. 2004). When the space from which an attack may come increases (e.g. close to cover vs. open areas), birds have to increase mean scan durations as they must scan a broader area (Carrascal & Moreno 1992). When decreasing the perceived group size, and therefore the many eyes and dilution effects, birds can increase mean scan durations to scan a broader area (Carrascal et al. 1990; Carrascal & Moreno 1992) or reduce inter-scan durations to detect sooner a possible attack (Knight & Knight 1986; Elgar 1989; Saino 1994; Roberts 1995). Otherwise, birds facing an increase in predation risk can increase their lateral head movements (or head turning) without altering the head-up/head-down pattern (Jones et al. 2007) or, if they perceive vigilance as few useful (Lima 1987a), they can reduce foraging bouts by increasing food intake rate at the cost of reducing vigilance (Moreno & Carrascal 1991; Smith & Metcalfe 1994).

When interference competition increases, animals generally increase mean scan durations (and as a consequence increase % of time scanning) in order to keep flockmates as well as predators under surveillance. For instance, Knight & Knight (1986) found that when the rate of attempted kleptoparasitism amongst bald eagles (*Haliaeetus leucocephalus*) increased (due to an increase in group size), the eagles increased their mean scan durations while keeping inter-scans constant. Knight & Skagen (1988) subsequently found that the eagles probability to keep an item of food was positively correlated with the duration of the head-up interval prior to an attack.

The increase in vigilance due to competition implies a correlated reduction in food intake rate (Cresswell 1997; Beauchamp 1998; Gauvin & Giraldeau 2004; Sansom et al. 2008). On the other hand, the 'competition hypothesis' (Lima et al. 1999) states that when increasing the number of birds competing for a limited food supply (i.e. scramble competition), their feeding rate could increase (and their vigilance decrease) in order to obtain a higher portion of the food supply. This would be achieved because of a reduction of the search and handling food times (Beauchamp & Livoreil 1997). However, this hypothesis lacks of empirical support (Lima 1987a).

Photo 2. Male siskin in an agonistic display showing the yellow wing and tail stripes which signal the parental quality of the individual and that increase its conspicuousness in flight.

■ TOPIC 2: VIGILANCE, PREDATION RISK AND CONSPICUOUSNESS

Charles Darwin, in his famous book "The descent of man and selection in relation to sex" (Darwin 1871), suggested that plumage sexual dichromatism in birds could have evolved through mate selection, with females selecting as mates the most ornamented (e.g. conspicuous) males. Alternatively, Wallace (1889) suggested the possibility of conspicuous plumage coloration being the ancestral state. Recent studies have revealed that sexual dichromatism is often an ancestral rather than a derived state, that dichromatism sometimes results from changes in female coloration, that selection can favour lesser ornamentation as well as higher conspicuousness and that sexual ornaments can have high evolutionary lability (Badyaev & Hill 2003).

Whatever the forces that have shaped dichromatism in the past, it has been generally assumed that plumage conspicuousness increases the predation risk of the most ornamented sex through increasing its detectability to predators (Huhta et al. 1998; Zuk & Kolluru 1998; Huhta et al. 2003). This is the reason why the most conspicuous sex is usually the less involved in incubation, with females being more conspicuous than males when they are not involved in parental care (Andersson 1994; Götmark et al. 1997). Therefore, the most conspicuous sex is expected to face a higher predation risk and hence to compensate for it by increasing its vigilance. On the other hand, Baker & Parker (1979) suggested that plumage conspicuousness could be an aposematic signal of unprofitability. The so called 'unprofitable prey hypothesis' (UPH) assumes that conspicuous birds are less edible (Cott 1947; Götmark 1994a) or more difficult to catch because of its "good vision and escape potential" (Baker & Parker 1979, p.70). According to this hypothesis, the conspicuous sex would be avoided as prey, and therefore we should expect that it allocated less time to scan for predators.

The unprofitable prey hypothesis was experimentally tested by Frank Götmark and collaborators by the use of stuffed pied flycatcher (*Ficedula hypoleuca)* mounts differing in brightness. Birds of prey more often attacked dull coloured than brightly coloured birds, showing that conspicuous birds were avoided as prey (Götmark 1992; Götmark 1995). This was explained by male flycatchers having a higher ability to escape, as calculated from wing loading data (Götmark & Unger 1994).

However, as pointed out by Slagsvold et.al. (1995), in the stuffed bird mount experiments the detectability of conspicuous (e.g. males) and non-conspicuous (e.g. females) birds was very similar due to the experimental design, while an increased detectability is the suggested cost of increasing conspicuousness by the sexual selection theory (Darwin 1871; Butcher & Rohwer 1989). The sex bias in prey capture not only depends on the ability to escape from the predator, but it also depends on

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the difference between sexes in the probability of encounter and the probability of detection (Endler 1991). This could explain why Slagsvold et.al. (1995), working with the pied flycatcher as Götmark (1995), found a predation cost of conspicuousness. They found that, during the breeding season, females disappeared in the same proportion as brightly coloured males, while no dull-coloured males disappeared (Slagsvold et al. 1995). Since females seem to have a lower probability to escape (Götmark 1992; Götmark 1995) but a lower detectability than bright males (Dale & Slagsvold 1996; but see Götmark & Hohlfält 1995) predation rate of females may be similar to that in males (Slagsvold et al. 1995). However, the lower detectability of dull males compared to bright ones, and their higher ability to escape than females would cause these males to show the lowest predation rate. Therefore, the results of Slagsvold et al. (1995) are consistent with the hypothesis of a higher predation risk due to increasing conspicuousness and a decrease in the ability to escape.

In another kind of experiments, Götmark (1994b) found that blackbirds (*Turdus merula*) with red-painted wings were avoided as prey. However, this result could in fact reflect the avoidance of a novel prey. Götmark and Olsson (1997) later found that red-painted great tits (*Parus major*) experienced increased predation compared with control birds. Post & Götmark (2006) studied predation of male and female pied flycatchers (*Ficedula hypoleuca*) and found that during the incubation and nestling stages males and females were equally predated by sparrowhawks, and a comparison with the chaffinch (*Fringilla coelebs*), where hawks took more females than males, led authors to conclude that differential predation risk of sexes was mainly related to timing of breeding, foraging behaviour and parental roles and not to plumage conspicuousness.

After the initial tests of Götmark and Slagsvold studying differential predation risk between sexes in one single species, some authors studied the more general relationship between conspicuousness and predation risk using comparative approaches. Rytkönen et al. (1998) studied prey remains from the surroundings of 12 sparrowhawk nests and found, using phylogenetic analyses, a positive correlation between prey vulnerability and plumage brightness after controlling for the effects of body mass and abundance of prey species. However, Huhta et al. (1998) studied predation rates of banded passerines and designed an experiment of prey choice using Eurasian kestrels (*Falco tinnunculus*) and found that dull coloured species and experimental great tits (*Parus major*) with bright parts painted black were equally selected than bright coloured species and normal birds, respectively. More recently Huhta et al. (2003) analyzed the relationship between predation risk and plumage brightness, body mass and density of prey species for a sample of 2,214 prey remains collected from sparrowhawk nests. They found that plumage brightness was the most important factor determining vulnerability to predation, and in adults, male brightness was more important than female brightness in explaining prey vulnerability. Møller and Nielsen (2006) studied the relationship between plumage dichromatism and prey vulnerability based on a comparative analysis with 31,745 prey individuals belonging to 66 species of birds. The found that prey vulnerability was predicted by sexual dichromatism, accounting for 23% of the variance in risk of predation among species, suggesting that sexual selection is an important evolutionary force affecting predator-prey interactions. Therefore, in general comparative analysis with many species show a positive relationship between conspicuousness and predation risk.

More recently, some studies in particular species have given new insights about the effect of conspicuous patches either in attracting or protecting prey from the attack of predators. Montgomerie et al. (2001) found that male rock ptarmigans (*Lagopus mutus*) retained their white plumage for three weeks after snow melted away from the tundra to attract females, thereby assuming a sexual selection related predation risk, and that when females began egg-laying, males soiled their white plumage to reduce conspicuousness sis-fold before they moulted to their cryptic summer plumage. Palleroni et al. (2005) showed that in feral pigeons (*Columba livia*) the white rump played an anti-predator role because it could disguise the initiation of the pigeon's evasive roll by contrasting conspicuous and cryptic targets, and they found that the relative abundance of this trait was related to the abundance of peregrine falcons (*Falco peregrinus*), which attack pigeons at high speeds and from above. Bokony et al. (2008) found in house sparrows that plumage ornaments of males (black throat patch and depigmented wing bar) did not reduce the short-term probability of survival. Therefore, conspicuous plumage patches, depending on prey species and predator behaviour, can either entail a predation cost, deter predator attacks or have no effect on predation risk.

As we have seen, the effect of conspicuous plumage coloration on predation risk is not straightforward. Even though there is enough evidence for a general rule of increased predation risk with conspicuousness, it can greatly vary between and even within species depending on the type of predator and the behaviour of prey.

On the other hand, bird conspicuousness is not such a simple concept as it may appear to be at first glance. It can be defined as bird detectability at long distances by predators in their natural habitat. Although colourful and bright birds have been usually considered to be conspicuous, conspicuousness in the above sense depends at least on the background in which birds are seen, on light conditions and on predators vision (Götmark & Unger 1994). Götmark and Hohlfält (1995) found that apparently conspicuous birds may be relatively cryptic in their environment. Hastad et al. (2005) found that passerines increase their conspicuousness to conspecifics but much less to avian predators (raptors and corvids) by exploiting the differences in colour vision between them (violet-sensitive cones vs. ultraviolet-

sensitive cones; Odeen & Hastad 2003). Moreover, since avian diurnal predators see in the ultraviolet light (Cuthill et al. 1999) to which humans are blind, conspicuousness to humans may be different than conspicuousness to avian predators (Eaton 2005; Hastad & Odeen 2008). Therefore, the existing difference between apparent conspicuousness (i.e. brightness and colourfulness) and real conspicuousness (i.e. long distance detectability by predators) may have misled the conclusions of some works studying the relationship between conspicuousness and predation risk, and may be the source of some apparently contradictory results.

Therefore, in studying the relationship between vigilance and conspicuousness, there are many different aspects to have in mind. We have to consider conspicuousness as detectability at long distance, according to predators' vision, in the usual habitat of prey and under the usual light conditions. We have to consider the behaviour of the different categories of prey (e.g. males and females), their escape potential as well as the behaviour of the main predators. Only after all these considerations we can draw a picture about which sex or species is in higher predation risk and therefore needs to compensate for this higher risk by increasing vigilance to predators.

Photo 3. Two male siskins, one perched on a thin branch and the other about to land. Notice the plumage coloration of males while flying and while perched, and the large black bib of the flying male.

■ Topic 3: Vigilance, predation risk and residence

Most wild animals, at least in some stage of their life cycle, move away from their natal area or usual or seasonal home range to go somewhere else. These movements can be classified, according to their dimension and regularity, as dispersal (Clobert et al. 2001) or migration (Milner-Gulland et al. 2011). There are many suggested benefits to these movements that may explain this widespread behaviour in most animal taxa. However, there are many reported (and sometimes obvious) costs too, so that animal movements are the outcome of a trade-off between these costs and benefits (Johnson & Gaines 1990; Bélichon et al. 1996; Coulton et al. 2011). Probably this is the reason why migratory behaviour can appear and disappear rapidly from bird species according to environmental conditions (Zink 2011).

Hinde (1956) suggested that one of the main benefits of territoriality was site familiarity, which could assist feeding, escape from predators and could increase fighting potentiality. In line with this pioneer hypothesis, higher predation risk (Alerstam 2011) and subordination to residents (Matthysen 1993) are considered the two main costs of transience. Probability of survival to dispersers is considered a critical factor in the evolution of dispersal (Johnson & Gaines 1990), while after settlement dispersers have both advantages and disadvantages when compared to philopatric individuals (Bélichon et al. 1996). Predation risk is one of the main reported costs of migratory behaviour, especially during the transient phase (Alerstam 2011). Transient individuals have been found to suffer higher mortality rates than residents in a wide range of taxa (e.g. Ambrose 1972; Isbell et al. 1993; López et al. 2000; Hoogland et al. 2006; Brown et al. 2008). Predation costs of transience have been related to higher movement rate and site unfamiliarity (Metzgar 1967; Yoder et al. 2004). This latter factor has been related to increased time to reach a refuge (Clarke et al. 1993; Hoogland et al. 2006), to worse knowledge of predators (Frair et al. 2007), to higher use of risky habitats (Koivunen et al. 1998) or to a combination of all (Yoder et al. 2004).

On the other hand, the subordination cost of transience is related to the prior residence effect (Maynard Smith & Parker 1976; Leimar & Enquist 1984), which states that the owner of a territory usually wins its contests with intruders. This effect has been proven in many species (e.g. Davies 1978; Cristol et al. 1990), and has been related either to an evolutionary stable strategy rule 'the resident always wins' (which lacks empirical support), to the fact that residents have superior resource-holding power (which applies to some species) or to the fact that the fitness payoff for defending a territory increases over time (e.g. dear enemy effect; demonstrated

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in some species) (Alcock 2009, p. 278-283). As we discuss below (see 'Vigilance and dominance status in social birds') dominance has an important effect both in improving the access to food resources and in reducing predation risk. Therefore, residents can obtain a great benefit in terms of dominance.

Transient animals facing a higher predation risk than residents (either because of site unfamiliarity or subordination to dominants) might have evolved anti-predator behaviours to compensate for this cost. Lind & Cresswell (2006) suggested that some of these behaviours could be joining larger flocks, changing patches, and/or allocating more time to anti-predatory behaviour (especially predator detection and vigilance; Lind 2004). According to that, we should expect transient birds to spend more time to vigilance to predators (Desportes et al. 1991).

Photo 4. Male siskin showing a large black bib below the beak and the yellow spot of the wing. The black bib is a melanin-based plumage coloration cue while the yellowish-greenish coloration is carotenoid-based. In this species, the black bib is a reliable signal of dominance, while the length of the yellow wing stripe formed by the inner visible 1/3 of the outer webs of the primaries is a signal of male parental quality.

■ TOPIC 4: VIGILANCE, PREDATION RISK AND PERSONALITY

Personality (or temperament) can be defined in a broad sense as "those characteristics of individuals that describe and account for consistent patterns of feeling, thinking and behaving" (Gosling 2001). This concept has traditionally been restricted to the study of human behaviour by psychologists. However, on the last decade it has been incorporated to the study of animal behaviour (Gosling 2001), and a large set of papers on this new field have been published to date (e.g. Réale et al. 2007). Animal personality is defined by a large set of animal traits traditionally studied alone that Réale et al. (2007) recently grouped in: (1) shyness-boldness, as an individual's reaction to any risky situation, but not new situations; (2) exploration-avoidance, as an individual's reaction to a new situation; (3) activity, as the general activity level of an individual; (4) aggressiveness, as an individual's agonistic reaction towards conspecifics; (5) sociability, as an individual's reaction to the presence or absence of conspecifics (excluding aggressive behaviour).

These different animal traits are not independent each other but they are correlated in the so called behavioural syndromes, which according to Sih et al. (2004) can be defined as "a suite of correlated behaviours reflecting between individual consistency in behaviour across multiple (two or more) situations". Then, we can say that a species or population exhibits a behavioural syndrome, and that a given individual has a behavioural type (Sih et al. 2004). Experimental studies have found a correlation between boldness and exploratory behaviour (Van Oers et al. 2004; Quinn & Cresswell 2005; Wolf et al. 2007; Dammhahn & Almeling 2012) and a correlation between exploratory behaviour, aggressiveness and dominance (Wolf et al. 2007; David et al. 2011; Mateos-González & Senar 2012; although dominance is not a personality trait, since it depends on the interaction between personality and the social context; Dingemanse & de Goede 2004). Hence, it is possible to talk about proactive individuals as those which exhibit simultaneously boldness, aggressiveness and exploratory behaviour, as opposed to reactive individuals, which exhibit the opposite behavioural traits (Sih et al. 2004). Proactive individuals would tend to outcompete reactive ones in a stable environment, while reactive individuals would respond better to changing ecological conditions (2004). The fact that personality traits are correlated implies a limitation in the behavioural plasticity of animals, that cannot exhibit perfect adaptation to the changing environmental conditions according to optimality models because of their behavioural carryovers or constraints (Sih et al. 2004).

By definition, a bold animal exposes himself to risky situations more easily than a shy animal. Hence, proactive individuals are risk-prone and assume a higher predation risk than reactive individuals (Van Oers et al. 2004; Quinn & Cresswell 2005; Jones & Godin 2010). Smith & Blumstein (2007) conducted a meta-analysis of published studies reporting fitness consequences of single personality traits and found that bolder individuals had increased reproductive success, particularly in males, but incurred a

survival cost. In a recent review of empirical studies, Biro & Stamps (2008) showed that proactivity traits minimized starvation risk at the cost of assuming a higher predation risk in a wide range of taxa, while reactivity resulted from a strategy that prioritized survival. Carter et al. (2010) found empirical support to this hypothesis working with Namibian rock agamas (*Agama planiceps*). Wolf et al. (2007) suggested that the variability in personality traits could evolutionary result from the simple principle that "the more an individual stands to lose, the more cautious that individual should be". According to that, proactivity traits would be associated to individuals with low future expectations. Therefore, we should expect proactive individuals in social foraging species that showed high food intake rates and allocated few time to vigilance to predators.

Contrary to the hypothesis of behavioural carryovers (Sih et al. 2004), bold individuals can evolve behavioural strategies (e.g. increase vigilance) to reduce their higher risk of predation. Couchoux & Cresswell (2012) studying redshanks (*Tringa totanus*) found no evidences for a behavioural syndrome related to risk management, and the only repeatable trait they found for this species was vigilance, which was adjusted in a flexible way to the riskiness of the situation. Godin & Dugatkin (1996) found that bold Trinidadian guppies (*Poecilia reticulata*), that were more conspicuous than drabber individuals, compensated for their higher detectability by having longer flight initiation distances. According to that, we should expect bold individuals to show higher proportion of time allocated to vigilance than shy individuals.

Maybe because of the need to compensate for boldness, in some species there are not behavioural syndromes in the sense of a correlation between boldness, exploratory behaviour and aggressiveness (Réale et al. 2007, p. 305). In wild chacma baboons (Carter et al. 2012) boldness and exploratory behaviour were found not to be correlated. Smith & Blumstein (2007) found in their meta-analysis review that survival was negatively correlated with boldness but positively correlated with exploratory behaviour and aggressiveness, from what we should conclude that these were independent traits.

Therefore, species may differ in the way how the different behavioural traits interact each other, so that exploratory behaviour and aggressiveness do not have to be necessarily correlated with boldness. On the other hand, boldness does not mean recklessness, so that bold individuals do not have to inevitably assume survival costs. In fact, they can compensate for their risk-prone behaviour by evolving behavioural strategies devoted to the reduction of this risk. Hence, the prediction of vigilance according to personality is not straightforward, and can depend on the particular interaction between personality traits in a given species and the presence or absence of compensation behaviours.

Photo 5. Male sparrowhawk (*Accipiter nisus*) plucking a male greenfinch (Carduelis chloris) before eating it. At the study area there was a male sparrowhawk hunting siskins and we found its plucking area with the remains of over 30 siskins.

◼ Topic 5: Body mass regulation, predation risk and residence

Body mass has a strong effect on birds' flying skills. An increase in body mass leads to an increase in wing loading reducing take-off speed and manoeuvrability (Witter & Cuthill 1993; Witter et al. 1994). Although there are some discrepancies about this general rule (Kullberg 1998; Veasey et al. 1998; MacLeod 2006), it is generally accepted that fat loads imply a cost in terms of flying performance, and this reduction is related to an increase in predation risk (Hedenström 1992; Witter et al. 1994; Kullberg et al. 1996; Burns & Ydenberg 2002). The body mass of birds results from a trade-off between the risks of starvation and predation (Lima 1986; McNamara & Houston 1990; Higginson et al. 2012). Therefore, birds increase their body reserves with increasing energetic demands (at mid winter: Bednekoff & Houston 1994; Cresswell 1998; Ratikainen & Wright 2013; at dusk: Metcalfe & Ure 1995; Kullberg 1998; and at coldest periods: Krams et al. 2010; Ratikainen & Wright 2013) and with increasing unpredictability (or scarcity) in food supply (Lima 1986). However, birds at any time tend to maintain the lowest possible fat loads necessary to avoid starvation in order to minimize predation risk (Schultner et al. 2013).

Several studies have found a reduction in body mass due to an increase in predation risk (Gosler et al. 1995; Carrascal & Polo 1999; Gentle & Gosler 2001; Zimmer et al.

2011). Carrascal & Polo (1999) compared the body mass variation of a group of captive coal tits (*Parus ater*) chased by the researchers and a control group non chased. Gentle & Gosler (2001) compared the body mass variation of great tits (*Parus major*) foraging in a feeder between weeks with high simulated predation risk (produced by flying a model sparrowhawk over the feeder while tits were feeding) and weeks without simulated predation risk. Zimmer et al. (2011) compared the body mass variation in captive groups of the common teal (*Anas creca*) and the tufted duck (*Aythya fuligula*) disturbed by a radio-controlled car running at high speed to the ducks as compared to groups of ducks non disturbed. In all these experiments the predation risk was not real and two of them were carried out in aviaries. Although, of course, it does not invalidate the results, it is difficult to know how these elements of artificiality could affect the behaviour of birds.

It is difficult to prove in the field the effect of real (not simulated) predation risk on the reduction of birds' body mass. Probably the best attempt to do so is the study of Gosler et al. (1995), who found a negative correlation between the variable abundance of sparrowhawks (*Accipiter nisus*) and the residual body mass of great tits (*Parus major*) at Wytham Woods from 1951 to 1993. This correlation was not found in wrens (*Troglodytes troglodytes*), which are very few caught by hawks, and the variation in residual mass of great tits was not observed in English and Welsh counties not affected by fluctuations in hawk abundance. Furthermore, at Wytham Woods great tits reduced their residual mass with beech mast availability, and to a national scale with artificial food supply, only when hawks were present. However, this study was based on the comparison of residual mass between different species, regions and periods of time. An ideal field test should compare individuals perceiving different predation risks but within the same area and period of time. This is, of course, difficult to attain.

Photo 6. Female siskin perched on a branch, showing its breast whitish coloration as compared with the yellowish coloration of male siskins. This probably makes females to be less conspicuous than males. Sexual dichromatism is common in many bird species.

◼ VIGILANCE AND DOMINANCE STATUS IN SOCIAL BIRDS

Birds foraging in groups, especially when resources are scarce and concentrated, compete to have access to the best foraging patches or resources and also to feed in the safest locations. Competing abilities of birds are variable, and depend either on genetically determined characters (e.g. sex), developmental characters (age), phenotypical characters (e.g. body size, personality), condition-dependent characters (e.g. body condition, plumage coloration) or ecological characters (e.g. prior residency) (e.g. Smith & Metcalfe 1994; Giraldeau 2008; see above for further discussion about the effect of each character on vigilance). In a given group of foraging birds it is possible to determine the dominance rank of each individual according to the outcome of its agonistic interactions with flockmates (Schneider 1984). Since dominance rank of an individual depends upon the competitive abilities of its companions, it is a relative trait, and it depends on the interaction between personality and environment (Dingemanse & de Goede 2004). However, in species where it is common to find many individuals foraging together that do not know each other, some signals of dominance status may have evolved (e.g. siskins; Senar 2006).

Dominant birds have priority of access to resources (both food and mates) but at the cost of keeping their status through competition with other high-ranking individuals (Senar 2006). However, while in some species dominants predominantly fight each other (i.e. feudal species), in other species dominants mostly fight with

subordinates (i.e. despotic species) (Senar & Domenech 2011). Whatever the case, being a dominant implies benefits but also costs that not all individuals are in condition to assume, and that is at least one of the reasons why not all individuals are 'hopeful dominants' (Rohwer 1982; Maynard Smith & Harper 1988).

Dominant birds have been shown to feed at the richest and safest food patches or locations, displacing subordinates to feed at poorer and more exposed places (e.g. Ekman 1987; Koivula et al. 1994). Moreover, since dominant birds have a predictable access to food resources, they can adjust their body reserves to the variable ecological conditions according to the predation and starvation risks trade-off (Lima 1986; McNamara & Houston 1990; Higginson et al. 2012). Body mass regulation depends on environmental conditions (Ekman 2004; Krams et al. 2010). Well fed dominant individuals feeding in rich food patches under mild conditions keep lower body reserves than subordinates, which have an unpredictable access to food and have to accumulate high fat loads at the cost of increasing predation risk (Clark & Ekman 1995; Gentle & Gosler 2001). Therefore, under these conditions we expect dominants to devote more time to vigilance and aggressions. However, dominant birds feeding under starvation risk (because of food scarcity or very low temperatures) highly increase fat loads, something than subordinates cannot do because of increased interference competition for food (Krams et al. 2010). Therefore, under these conditions we expect dominants to devote more time to feeding and less time to vigilance to predators than subordinates. Dominants may also have higher food intake rates and lower vigilance levels than subordinates soon in the morning to recover from the nightly energy expenditure, while may show the opposite trend at midday. Finally, dominants may show higher vigilance levels than subordinates when predation risk is very high.

Another important factor influencing vigilance levels of dominant and subordinate birds is competition. In feudal species (Senar & Domenech 2011), dominants may have higher aggression rates and therefore longer scan durations, lower scan rates and higher % of time spent scanning than subordinates. Conversely, in despotic species (Senar & Domenech 2011) the opposite trend may be found, with subordinates paying a high cost in terms of aggression avoidance.

Finally, it is important to point out that, in studying the effect of dominance over vigilance, feeding rate and body reserves regulation, it is much better to compare individuals of the same category (species, sex, age, residence status) differing only in dominance rank than to compare birds of different categories (as many studies to date have done; e.g. Ekman & Askenmo 1984; Hogstad 1988; Carrascal & Alonso 2006). Males and females, juveniles and adults, residents and transients and birds of different species do not only differ in dominance rank, but in many other aspects that could mask or distort the effect of dominance.

Eurasian siskins are small granivorous finches (Svensson 1992) easily attracted to feeders (Senar et al. 1992), easy to trap (Senar 1988) and easy to manipulate with low mortality risk (Senar 1989) that make important but irregular wintering irruptions to Catalonia (Senar & Guallar 2011). Siskins present a marked plumage sexual dichromatism: males have a melanin-based black bib and have a brighter and more extended carotenoid-based yellowish coloration than females (Svensson 1992; Martin & Badyaev 1996; Badyaev 1997). Wintering siskins are divided in two subpopulations: the residents (33% of the population), which are present in a given locality for extended periods, making only short-range movements (usually less than 3 km), and the transients (77% of the population), which stay in a given locality for only a few hours or days and that make movements of 10-40 km in a single day (Senar et al. 1992). Siskins have a hierarchical social organization (Senar 1989) which has been assimilated to a feudal system (Senar 1989; Senar & Domenech 2011) with agonistic interactions being more frequent between dominant individuals. Dominance status of males in this species is signaled by the area of the black bib (Senar et al. 1993; Senar & Camerino 1998). Large black bib individuals have a more exploratory personality (Mateos-González & Senar 2012). In siskins, males are dominant over females (Senar & Domenech 2011) and residents are dominant over transients (Senar et al. 1990). Contrary to melanin-based black bib coloration, carotenoid-based coloration (i.e. length of the yellow wing and tail stripe) in this species is related to mate choice but not to dominance status (Senar & Escobar 2002; Senar et al. 2005). Moreover, the more sexy males (i.e. with longer wing yellow stripe) are superior at solving a foraging problem (Mateos-González et al. 2011).

For all these characteristics, siskins are an ideal model species to test the effect of individual characters to vigilance: we can study the effect of dominance status and personality by comparing males with large black bib with males with small black bib; we can study the effect of plumage conspicuousness by comparing males and females; and we can study the effect of residency by comparing residents and transients. Siskins are also ideal to study the effect of environmental conditions to vigilance since they can be easily attracted to feeders differing in shape, area and distance to protective cover. And they can provide the chance to test in the field the body mass regulation according to predation risk by comparing the variation of resident and transient siskins between periods of time differing in real predation risk.

Objectives, hypotheses and predictions

(1) To design an experiment that allows us to clearly discriminate the differential effects of predation risk and competition over vigilance and foraging strategies according to all the relevant variables.

(2) To analyze how these strategies are affected by the individual characters of birds (sex, residence, dominance and personality).

(4) To relate the strategies of body reserves management according to predation risk with individual characters and vigilance.

■ HYPOTHESES AND PREDICTIONS

In order to achieve all these objectives we decided to test the following hypotheses:

Hypothesis 1. Environmental factors. *Social birds while foraging in groups adjust their vigilance system to the changing environmental conditions, employing different strategies depending on whether they are mainly concerned in the vigilance of predators or competitors.*

We studied the effect of an increase in predation risk by comparing two feeders at a different distance from protective cover (Caraco et al. 1980; Lazarus & Symonds 1992; Carrascal & Alonso 2006). We expected siskins:

1.a. To reduce mean inter-scan durations (i.e. mean duration of head down intervals) in order to detect approaching avian predators sooner (Hart & Lendrem 1984; Whittingham et al. 2004) and to increase mean scan durations (i.e. mean

duration of head up intervals) in order to scan a broader area (Carrascal & Moreno 1992). Both the percentage of time spent scanning (i.e. % of time with the head up) and the scan rate (i.e. number of scans per unit of time) were predicted to increase, which should decrease pecking rate (i.e. number of pecks per unit of time) (Carrascal et al. 1990; Fritz et al. 2002; Barta et al. 2004; Baker et al. 2011).

Alternatively, it could be that siskins responded to the increase in predation risk as chaffinches studied by Cresswell et al. (2003b). Then, we should expect siskins:

1.b. To increase pecking rate because of the increase in scan rate and the reduction of inter-scan durations (i.e. searching times).

It could also be possible that siskins did not change the head-up/head-down patterns with increasing predation risk and competition because vigilance and foraging were compatible behaviours (Fernández-Juricic et al. 2004) or because they used other kinds of head movement to scan for competitors and predators (Jones et al. 2007). Then we should expect siskins:

1.c. To not show differences between feeders in any of the analyzed variables.

Birds typically experience a higher rate of departures at locations with high predation risk (Lendrem 1983; Newman et al. 1988; Lima 1995; Barta et al. 2004). Then, when increasing predation risk we should expect siskins:

1.d. To reduce time on feeder.

We studied the effect of competition by comparing two feeders close to protective cover but which differed in surface area and shape, therefore increasing interference competition between flock members (Slotow 1996; Johnson et al. 2004). Since both the 'large' and the 'small' surface feeders were filled with thousands of seeds, we did not expect differences in scramble competition between them (Lima et al. 1999). We expected birds:

1.e. To react to increasing competition by increasing mean scan duration (and % of time scanning) in order to scan for both competitors and predators, while keeping mean inter-scan durations constant (Knight & Knight 1986; Knight & Skagen 1988).

1.f. To suffer a reduction in pecking rate (Cresswell 1997; Beauchamp 1998; Gauvin & Giraldeau 2004; Sansom et al. 2008) and time spent on the feeder (due to departures caused by aggression).

Hypothesis 2. Factor conspicuousness. *In species with a clear sexual dimorphism where one sex is much more conspicuous than the other and, as a consequence, is easier to detect by predators, individuals of this sex will be more affected by the risk of predation. Alternatively, and according to the 'unprofitable prey hypothesis', individuals of the most conspicuous sex show an aposematic coloration which is a signal of optimal flight performance and therefore difficulty to be caught, so that they will be avoided as prey by predators.*

We compared the colour, brightness and long distance detectability of male and female siskins, and we expected that:

2.a. Males will be more conspicuous than females (at least to humans, although we cannot say if also to avian predators; Eaton 2005; Hastad & Odeen 2008).

In small birds attacked by a bird of prey, escape probability depends on take-off speed and manoeuvrability (Witter et al. 1994; Metcalfe & Ure 1995), which are related to wing loading (Hedenström 1992; Witter & Cuthill 1993). This variable is the result of dividing body mass to wing area. The lower the wing loading, the higher the take-off speed and manoeuvrability (Witter & Cuthill 1993). Therefore, according to the unprofitable prey hypothesis, we expected that:

2.b. Males will have lower wing loadings than females.

If conspicuous males were unprofitable prey, then the UPH predicts predators to avoid them when attacking a foraging flock. Therefore, predation risk would be higher for females and we would expect them to evolve behavioural responses to compensate for such higher risk. Hence, we would expect that:

2.c. Females will avoid the feeder far from cover and will have shorter inter-scan times, higher proportions of time spent scanning and shorter foraging bout lengths than males, especially at the high predation risk feeder.

If males were not unprofitable, then the predation risk of conspicuous males would be higher, and therefore we would expect that:

2.d. Males will avoid the feeder far from cover and will have shorter inter-scan times, higher proportions of time spent scanning and shorter foraging bout lengths than females, especially at the high predation risk feeder.

In order to assess that the differences found in vigilance variables between male and female siskins were due to different predation risk and not to different interference

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competition, we studied vigilance behaviour, percentage of sexes, pecking rate, aggression rate and hopping rate of male and female siskins at three feeders which differed in predation risk and competition levels, and we tested the interaction between feeder and sex for each of these variables. If the differences between males and females were related to conspicuousness, we expected that:

2.e. The differences between sexes will be higher in the comparison between IL and OS feeders than in the comparison between IL and IS feeders, and higher for the predation related variables (especially inter-scan durations) than for the competition related variables (especially scan durations).

Alternatively, if the differences were related to dominance, we expected that:

2.f. The differences between sexes will be higher in the comparison between IL and IS feeders than in the comparison between IL and OS feeders, and higher for the competition related variables (especially scan durations) than for the predation related variables (especially inter-scan durations).

Moreover, we studied the relationship between carotenoid coloration and vigilance in males, which is related to conspicuousness but has nothing to do with dominance in wintering siskins (Senar & Escobar 2002), and compared it with the correlation found between melanin bib size and vigilance in males, which is highly related to dominance (Senar & Camerino 1998) and not to conspicuousness. If the differences found between sexes were related mainly to conspicuousness, we expected that:

2.g. We will find a higher correlation between plumage brightness and vigilance than between black bib size and vigilance in male siskins.

Alternatively, if the differences were related mainly to dominance we expected that:

2.h. We will find a higher correlation between black bib size and vigilance than between plumage brightness and vigilance in male siskins.

Finally, we provide predation data from a Eurasian sparrowhawk (*Accipiter nisus*) hunting in our study area in order to assess the sex bias in its prey selection. If conspicuousness increases predation risk we should expect that:

2.i. We will find a proportion of males in prey remains higher than expected.

Alternatively, if conspicuousness is an aposematic signal of unprofitability, we should expect that:

2.j. We will find a proportion of males in prey remains lower than expected.

Hypothesis 3. Factor residence. *In animals the residence, i.e. the fact of remaining in a familiar area without moving out, provides some advantages over transience because it provides a better knowledge of the foraging area and, therefore, a higher ability to detect and escape from predators.*

According to the unfamiliarity cost hypothesis, we should expect transient siskins:

3.a. To have a higher use of risky patches owing to their ignorance about safety sites (Koivunen et al. 1998; Yoder et al. 2004), to be more vigilant in order to compensate for their higher risk (Lind & Cresswell 2006) and as a consequence to reduce their food intake rate (Desportes et al. 1991). Moreover, we should expect transients to display longer scan durations to scan broader areas owing to their ignorance about the angle from which an attack may come (Desportes et al. 1991) and to display shorter inter-scan durations to reduce the time needed to detect an approaching predator (Hart & Lendrem 1984; Desportes et al. 1991; Whittingham et al. 2004).

According to the subordination cost hypothesis, we should find the same difference between residents and transients than between dominant and subordinate transients. Since in Topic 4 we compared dominant and subordinate transients, we should expect transients to show the same behaviours as subordinates, and therefore:

3.b. To have longer inter-scan durations and lower scan rates than resident siskins, to have equal % of time spent scanning, scan durations, pecking rate and foraging bout lengths, and to have equal relative proportions at feeders differing in exposition to predator attacks.

Hypothesis 4. Factor personality (related to dominance). *Large black bib males, with a proactive personality, adopt a vigilance strategy that allows them to compensate for the higher risk of predation associated to their personality trait. Alternatively, proactive siskins suffer a behavioural carryover that makes them to reduce the proportion of time allocated to the vigilance of predators.*

If large bib siskins, dominant, aggressive and fast explorers, showed a behavioural carryover leading to a reduction in the time allocated to predator vigilance, and therefore assumed a personality-related handicap (Sih et al. 2004; Jones & Godin 2010), then we should expect them:

    4.a. To have longer inter-scan durations, lower scan rates and/or lower % of time spent scanning, less disturbance-related departures and longer foraging bout lengths, especially at the high predation risk feeder.

Conversely, if large bib siskins showed a vigilance system that allowed them to compensate for the high risk of predation associated to their personality trait (Couchoux & Cresswell 2012, hypothesis (ii) of Jones & Godin 2010), we should expect them:

    4.b. To have shorter inter-scan durations, higher scan rates and/or higher % of time spent scanning, more disturbance-related departures and shorter foraging bout lengths, especially on the high predation risk feeder.

We also analyzed the food intake rates, aggression rates as well as the proportion of the different bib-size categories on the two feeders as relevant variables to the better understanding and interpretation of the results.

Hypothesis 5. Factor body mass. *Resident siskins adjust their body reserves in function of the predation risk at the area in order to manage their take-off speed and manoeuvrability in flight. However, transients cannot do it because of their ignorance about the predation risk at the area.*

We studied the consequences on resident and transient body mass of the appearance in midwinter of a sparrowhawk (*Accipiter nisus*) in our study area. The hawk remained hunting until the beginning of March (see below). This allowed us to compare, in the field, body mass in response to an increase in the real risk of predation, in two

subpopulations of the same species foraging at the same site and period of time, but with a different knowledge about the predation risk in the area.

If birds regulate their body reserves to the predation risk of the foraging area, then we should expect that:

    5.a. Resident siskins will reduce body mass from the period of the wintering season without avian predators to the period of the wintering season with the sparrowhawk regularly hunting.

If residence entails an advantage to transience in terms of familiarity with the area, we should expect that:

    5.b. Transients will not reduce their body mass from one period of the wintering season to the other because they are not aware of the predation risk at the area.

Alternatively, it could be that transient siskins could assess the predation risk at the area by looking at the vigilance behaviour of residents (as suggested by Desportes et al. 1991). Then, we should expect that:

    5.c. Transients will show the same body-mass regulation than residents.

Finally, it could be that the differences between residents and transients were related not to site familiarity but to dominance relationships. If dominance was the key factor, then we should expect that:

    5.d. When increasing the predation risk at the area, we will find the same pattern of variation in body mass between large and small black bib size siskins than between residents and transients.

Alternatively, if familiarity with the area was the key factor, then we should expect that:

    5.e. When increasing the predation risk at the area, we will find a different response of body mass regulation between residents and transients but not between large and small black bib size males.

Methods

The study was carried out in a permanent ringing station at Sarrià (41º24'21"N, 2º06'46"E), in the suburbs of Barcelona city (Catalonia, NE Spain), in an area surrounded by orchards, small pine woods (*Pinus halepensis*) and gardens (Fig. 2).
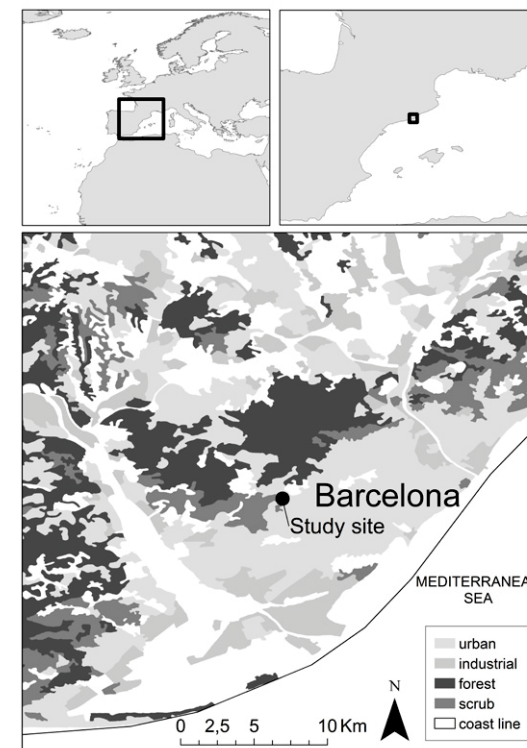

Figure 2. Location of the study site in the surroundings of Barcelona, western coast of the Mediterranean sea, southwestern Europe. The site is located at the suburban area of the city, near the scrub and forest lands of Collserola Natural Park.
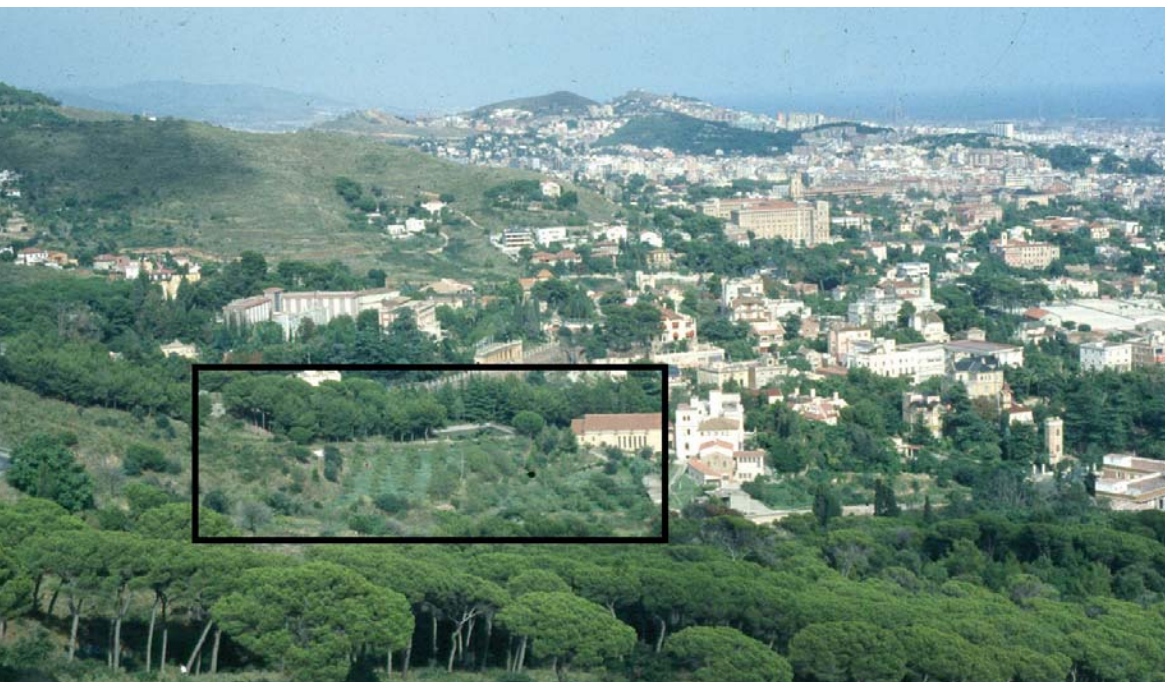
Photo 7. General view of the upper suburbs of Barcelona city with a black rectangle framing the study area where the feeders were located and the siskins were caught and ringed. Notice the mosaic landscape with orchards (centre of the rectangle), small pine woods (up), scrublands (left) and gardens (right). The plucking area of the sparrowhawk hunting at the ringing station was located inside the pine wood at the upper third of the rectangle. Feeders were located between the orchards and the pine wood, at the centre of the left half of the rectangle.

■ SISKINS RINGING AND MEASUREMENT

Data collected from siskins captured at the ringing station

Siskins were captured from 19th October 1996 to 22th March 1997, coinciding with their wintering permanence at the area. For each day of work at the ringing station we collected the average temperature (maximum temperature plus minimum temperature divided by 2) from the Observatori Fabra weather station, which is located at only 1.7 linear km from the ringing station. Siskins were trapped on a regular weekly basis at baited feeders using traps, mist and clap nets (Domènech & Senar 1997), and were marked with numbered aluminium rings.

Siskins were caught by expert bird ringers with the authorisation of the Ornithological Catalan Institute and the Catalan Government. Birds recaptured more than 15 days after the first capture (i.e. staying in the area as 'residents'; Senar et al. 1992) were additionally given unique colour ring combinations, allowing long

distance identification. Given the high trapping effort at the station, we classified as transients the siskins never recaptured more than 15 days after the first capture (Senar et al. 1992). In fact, most of the transients were captured only once.

From each siskin captured, we noted the day and time of capture, the sex and age (according to plumage coloration cues; Svensson 1992), number of the ring and code of colour rings (if resident). We measured its wing length (maximum cord, to the nearest 0.5 mm) and body mass (with an electronic balance, to the nearest 0.1 g). For some individuals, we also measured the black bib area (as the product of black bib height and width, in mm^2), the length of the yellow wing stripe and the length of the black tail stripe (instead of the yellow stripe, which is inversely correlated with it, because it was much easier to measure) (Fig. 3). All these plumage coloration cues differ between sexes (Senar et al. 2005) and can increase the detectability of males over females (see Topic 2).

Sample size for the study of body mass regulation

We captured a total of 1,117 siskins throughout the wintering season. We deleted from the database 35 siskins captured in October since on that month we only captured transients and we were interested in the comparison between residents and transients. We also deleted another 305 captures from which we did not have either the body mass or the wing length measured. Hence, in the end we had 812 captures with body mass and wing length measured. These captures corresponded to 510 different individuals, 101 residents and 409 transients. For each resident siskin we had several recaptures, while for most transient siskins we only had one capture. Therefore, and in order to avoid pseudoreplication, we grouped all the captures of each individual before and after the appearance of the sparrowhawk, and we randomly selected one of them for both periods (with a random generator: www.random.org). This way, the final sample size for the analysis was 542 captures corresponding to 510 different individuals. On the other hand, the black bib area was available for 299 captures from 295 different male siskins (56 residents and 239 transients).

Sample size for the correlation of conspicuousness and vigilance

We measured the plumage coloration on the yellow of the tail with a chromameter (see below) of 30 resident siskin males captured in the study area. Moreover, we measured the length of the yellow wing stripe and the length of the black tail stripe of 22 resident males, and the black bib area of 27 resident males. Unfortunately, on the video tapes we

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could only find 12 resident males with the coloration of the tail yellow patch measured, 10 resident males with the length of the yellow wing stripe and the black tail stripe measured and 11 resident males with the bib area measured. Still, we analysed the correlation between vigilance and coloration variables with the available males.

Test of differential long-distance detectability of male and female siskins

We studied the differential detectability of male and female siskins within four different habitats found in our study area (fruit orchards, dominated by green and grey colours; plowed lands, dominated by brown colours; woods and grasslands (both dominated by green colours). We used 10 male and 10 female siskin skins (five juveniles and five adults for each sex). We placed 10 pairs of siskin skins of the same age and different sex in each of the four habitats. The male and female of each pair were placed in a similarly hidden position in the trees or on the land, separated more than 1m and less than 4m. 28 people were individually placed in front of each of the areas where each stuffed model pair stood. Seven different people were used for each habitat test. At the two wooden habitats (i.e. orchards and wood), people were placed in front of the trees, initially at a distance of 8m from the stuffed pairs. At the two open habitats, people were individually and alternatively aligned with each of the stuffed pairs, initially at a distance of 40m. They scanned until they found one bird of the pair; if they did not find any, they moved closer to the pair until they discovered one. We recorded the sex of each of the 10 discovered birds for each person at each habitat.

Wing loading measurement of male and female siskins

For the study of plumage conspicuousness related to predation risk and vigilance (Topic 2), we measured the wing loading of 42 pairs of male and female resident siskins trapped together (each in a different capture event) at an experimental feeder as an estimate of manoeuvrability and take-off speed (Witter et al. 1994). We measured the length of the wing from the elbow to the tip of the longest primary (following Svensson 1992) and the distance of all the primary feathers to the tip of the wing. Then, we subtracted these distances from the length of the wing, and the resulting values were added, resulting in an index of the wing area (Evered 1990). We calculated wing loading by dividing body mass on estimated wing area (Norberg & Rayner 1987; Götmark & Unger 1994). We estimated the wing loading for pairs of males and females in order to remove the effect of the climate conditions over the body mass of birds.

Plumage brightness measurement of male and female siskins

We measured coloration on five points of the plumage for a sample of 52 siskins (23 females and 29 males). The points were chosen as those which a priori make the bird most visible from the back while it is flying (Fig. 3). Coloration was measured using a CR-200 Minolta chromameter with an eight mm diameter sensor. The chromameter provides for each bird independent values of hue, chroma and lightness, which are the parameters generally used to define a colour. Hue reflects its chromatic composition and corresponds to wavelength of light. Chroma, or saturation, refers to spectral variance, and determines the pureness of the colour. Lightness, or brightness, refers to percentage of white, and it is correlated with physical light intensity (Booth 1990). The higher the values for lightness and chroma of a particular part of the plumage, the higher its brightness.
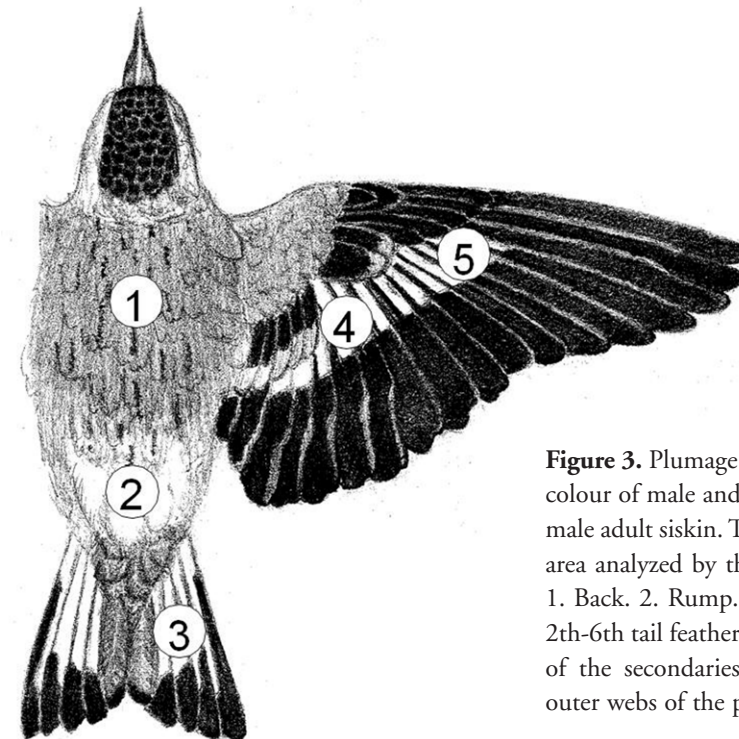
Figure 3. Plumage points where we measured the colour of male and female siskins, illustrated in a male adult siskin. The circles are equivalent to the area analyzed by the sensor of the chromameter. 1. Back. 2. Rump. 3. Basal-medium webs of the 2th-6th tail feathers. 4. Basal-medium outer webs of the secondaries. 5. Inner visible 1/3 of the outer webs of the primaries.

In addition to the brightness of a particular part of the plumage, the extent of this bright patch is also important. Two of the brightest plumage patches are the yellow wing stripe and the yellow of the base of the rectrices (Fig. 3). In males, the length

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of the yellow wing stripe formed by the inner visible 1/3 of the outer webs of the primaries and secondaries is larger than on females (pers. obs.), and the same is applicable to the length of the yellow in the base of the 2th-6th tail feathers (Senar et al. 2005).

Sparrowhawk presence/absence and prey selection at the study area

During all the wintering season, we captured siskins once a week from 7 AM to 13 PM, and we also visited the ringing station four additional days a week to provide food to feeders. From the 19th October 1996 to the 18th January 1997 we never saw an avian predator at the study area. The 20th January 1997 we could see for the first time an attack of a sparrowhawk (*Accipiter nisus*) to the siskins foraging at the feeders. Since we captured birds at the ringing station the 18th January and we visited the study site the 15th and 16th January without detecting the sparrowhawk, we can confidently say that it appeared at the area the 19th or 20th January. The 23rd January we could see a second attack of the hawk, and we could determine that it was a male. We witnessed additional attacks the 10th February and the 17th February. We found a plucking area of 20m x 10m in a wood next to the ringing station that was examined five days a week to look for siskin feathers. We found the remains of over 30 different siskins, and we could detect new remains until mid March. Therefore, we can confidently say that the sparrowhawk hunted siskins at the ringing station to at least the first week of March, and we classified the ringing dates from November to 18th January as 'absence' of the hawk, and the ringing dates from 25th January to mid-March as 'presence' of it.

Every day of work at the ringing station from the end of January to the mid-March (5-7 days a week) we scrupulously examined the plucking area. All the prey remains that we could find were collected and lumped together. We then determined, for each day, the minimum number of individuals by matching wing and tail feathers (following Götmark & Post 1996). In order to identify the sex of the individuals, we used a combination of the colour intensity and length of the yellow band of the rectrices, primaries and secondaries, using the feathers collection from the Natural History Museum of Barcelona.

We designed an experiment to separate the differential effects of predation risk and competition over vigilance and foraging behaviour. We placed three feeders in one single site at a height of 1 m from the ground (see Fig. 4). They had a border of 1.5 cm and were filled with turnip (*Brassica rapa*) seeds to 0.5 cm every day, so we can assume the same density of food for all. Birds foraging at the feeders were videotaped from a hide with a S-VHS-C movie camera Panasonic NV-S7E equipped with digital zoom x16. In total 133 flocks were recorded at feeders on 28 different days from 10th January to 11th March 1997, between 11.00 AM and 17.00 PM.
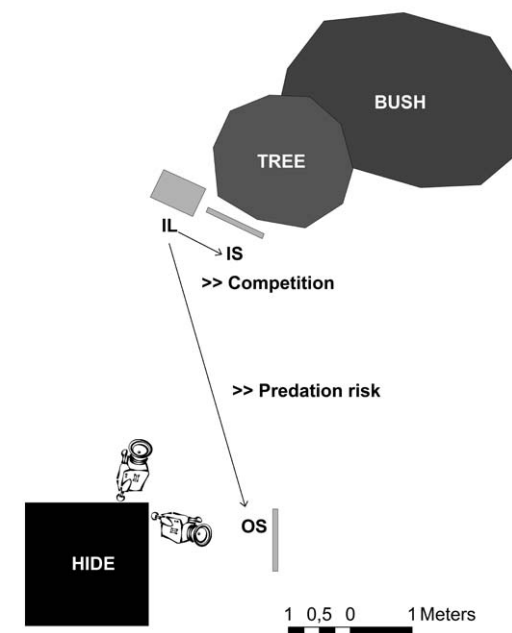
Figure 4. Experimental set up showing the location of the feeders, the vegetation (i.e. protective cover) and the hide from which the siskins were video recorded. The reduction of area between the inner large feeder (IL) and the inner small feeder (IS) allowed us to study the effect of an increase in interference competition over vigilance variables and foraging success, while the increase of distance to protective cover between the IL and the outer small feeder (OS) allowed us to study the effect of an increase in predation risk. When recording siskins at the IL feeder the other two feeders were emptied of food. IS and OS feeders were recorded simultaneously with the IL feeder emptied of food.

The three bird table feeders differed in their surface (i.e. expected interference competition; Elgar 1987; Johnson et al. 2004) and in the distance from protective cover (i.e. expected predation risk; Caraco et al. 1980; Lima et al. 1987; Lima & Dill 1990; Lazarus & Symonds 1992). We did not expect differences in scramble competition between feeders because each of them was filled with so many seeds that could not be depleted in a whole day (Lima et al. 1999). We did not expect

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scrounging behaviour since the food was visible and evenly distributed on the surface of feeders, so siskins did not have to search for it (Barta et al. 2004). Two feeders differing in surface (and hence expected interference rate) were placed below an almond tree, close to a big and dense bush (i.e. low expected predation risk; Fig. 4). The inner large (IL) feeder was 0.75 x 0.5m, while the inner small (IS) feeder was 0.08 x 1m. The third feeder (outer small: OS) was placed at 4.75m from the tree and the bush (so had a high expected predation risk; Fig. 4) and was the same size and shape as IS. The IL feeder was designed in such a way, in order to have a low density of birds (large surface) and a low aggression rate (square shape). The OS feeder was expected to attract few birds to feed, and was designed in that way in order to produce a similar bird density (small surface) and interaction rate (rectangular shape) as the IL feeder. Finally, the IS feeder was expected to attract many birds, and was designed specifically to have a higher density (small surface) and aggression rate (rectangular shape) than the IL feeder. Therefore, IL was intended to be a feeding patch with low predation risk and low competition, IS a patch with low predation risk and high competition, and OS a site with low competition and high predation risk.

The hide from where birds were videotaped was placed at 1.97m from OS and at 4.85m from IL and IS, at the opposite direction of the bush. Therefore, if the hide was perceived as a possible source of predators, it would further increase the perceived predation risk at OS compared with the risk at IL and IS. We recorded birds at IS and OS simultaneously with two video cameras placed inside the hide; while recording them, IL was emptied of food in order to force the birds to feed either at IS or OS. Conversely, IS and OS were emptied of food when recording IL. We filmed only half the length of the feeders when videotaping IS and OS, since they were too long to be recorded in the same image. Therefore, in order to prevent any biases and increase the number of individuals recorded, we shifted the video camera every 2 minutes from one half of the feeder to the other. In the study area (at 7 km from the Mediterranean Sea) the temperature was mild and very constant throughout the winter and most days were sunny; no video recordings were made on the few rainy days.

■ DATA OBTAINED FROM TAPES

Use of paired data for the different comparisons

In the Topic 1 we compared the behaviour of siskins between the three feeders. In Topics 2, 3 and 4 we compared the vigilance and foraging behaviour of male vs female siskins, residents vs transients and large black bib vs small black bib males, respectively. Therefore, we looked for pairs of birds foraging simultaneously (or at least in the same foraging group) and belonging to the two different categories to compare. This way, their behaviour was directly comparable and was not affected by environmental conditions (date, time of day, temperature, number and density of birds on the feeder, etc.). We considered the variables obtained from both individuals as paired data.

Feeders and subpopulations selected for the comparisons between groups

At the OS feeder there were few different residents filmed. Therefore, in the comparison of vigilance between the three feeders (Topic 1) we preferred to select only transients because this way we could have a large and homogeneous sample size for all the feeders with a very low probability of pseudoreplication given the high number of transient siskins foraging simultaneously and their short stay in the area. In the comparison between large and small black bib males (Topic 4), we only could visually assess this variable in the IS and OS feeders, since they presented few birds foraging together (as compared to IL feeder) and their body position facilitated the observation of the black bib. Therefore, we only selected birds from these two feeders and we only selected transients because for them the sample size was higher and the black bib is more informative than for residents (which know each other; Senar 2006). In the comparisons residents vs transients (Topic 3) and males vs females (Topic 2) we worked with the three feeders. In Topic 2 we selected only residents because they were aware of the presence of a sparrowhawk hunting at the area and we could obtain enough pairs of different individually identified siskins.

Data collected, subsamples selected and sample sizes obtained for the study of vigilance and foraging behaviour

We selected two different samples of siskins from the recordings for each of the comparisons. To the so called 'random subsample', the focal birds were randomly selected according to their individual characters (i.e. that they belonged to one of

the two categories to compare, that one bird of the other category was foraging simultaneously with them and that they were clearly visible). On the other hand, for the so called 'undisturbed subsample' we only selected birds (or pairs of birds) which stayed more than 30 seconds foraging on the feeder almost without fighting or moving around for at least this period of time. We applied this restriction because, in order to estimate the vigilance variables for each bird, we analysed a period of 30 seconds, and because, if we wanted the vigilance variables (mean scan duration, mean inter-scan duration and scan rate) to be comparable between birds, they had to be calculated when they only pecked and scanned.

The vigilance variables estimations were based on the undisturbed subsample. For each focal bird, we analysed a 30 second period of videotape during which virtually all of its time was spent foraging (head-down, i.e. looking for food and pecking) and scanning (head-up, i.e. looking for predators and conspecifics while handling food). This period of time was long enough to characterise the vigilance and feeding behaviour of siskins and was short enough to fit the short stays of birds at tables just feeding. Behaviours other than foraging and scanning (agonistic interactions and hops) comprised less than the 1% of the analysed recordings. We analysed the behaviour of each bird using the frame by frame function of the video (25 frames per second) and we recorded the following variables: % of time scanning (as the number of frames with the tip of the beak raised to eye level or higher; Lendrem 1983), mean scan duration (measured in frames), mean inter-scan duration (measured in frames), scan rate (as the total number of head up intervals per 30 seconds), pecking rate (as the total number of pecks per 30 seconds; as an estimate of food intake rate) and time spent by the bird on the feeder (in seconds; for correlational purposes only).

We analysed the random subsample to estimate the variables that were highly affected by the selection conditions of the undisturbed subsample: time spent by birds on the feeders (in seconds) and the proportion of time spent in aggressive interactions (as the number of frames each bird spent in aggressions divided by the total number of frames the bird was seen on the feeder). Then we subtracted this % of time spent in aggressions from the % of time spent scanning and pecking rate to obtain the adjusted values for these two variables.

In the table 1 there are summarized the sample sizes used for each of the comparisons of vigilance and feeding variables between groups of the thesis, both for the random and undisturbed subsamples.

Table 1. Number of focal siskins and number of pairs of focal birds used in the comparisons of the 5 topics of the thesis. All the topics except the number 5 were based on analysis of siskins foraging at feeders, and we selected two kinds of subsamples: random, selecting randomly a sample of individuals, and undisturbed, selecting only birds which stayed more than 30 seconds at the feeder almost only foraging and scanning. Topic 5 was based on siskins captured and measured at the ringing station. IL: inner large feeder, IS: inner small feeder, OS: outer small feeder.

	Focals	Sample	# Pairs				# Siskins				Captures	Individuals		Total number
			IL	IS	OS	N	IL	IS	OS	N		Res	Trans	
Topic 1: environmental factors	transients	Random					30	30	30	90				180
		Undisturbed					30	30	30	90				
Topic 2: factor sex	residents	Random					56	42	24	122				194
		Undisturbed	16	14	6	36								
Topic 3: factor residence	both	Random	56	42	24	122								368
		Undisturbed	28	20	14	62								
Topic 4: factor bib size	transients	Random						22	20	42				164
		Undisturbed						26	14	40				
Topic 5: factor body mass	both										812	101	409	510

Validation of the experimental design

The experimental set-up itself could not guarantee the achievement of the pretended goals of the experiment, i.e. that the comparison IL vs IS allowed us to test the effect of competition over vigilance, and that the comparison IL vs OS allowed us to test the effect of predation risk. In order to test for the validity of the experimental set-up and to rule out the possible effect of confounding factors, we decided to test the differences between feeders in aggression rates, departure reasons, number of hops, number of birds foraging and density of birds.

We recorded the proportion of time spent in aggressions and the total number of hops for a sample of 90 focal individuals (30 for each feeder) selected from the random subsample of birds during the entire time they spent on the feeder. We also recorded, for each focal bird, the number of birds foraging on the feeder and the density of birds (as number of birds per m^2). On IS and OS we only recorded half the feeder, so we doubled the number of visible birds on the recordings to estimate the number of birds foraging on them.

Additionally, we recorded the presumed reasons for the departure of the 90 individuals of the random subsample, which were classified as: 'aggression' if the bird departed upon being attacked, 'disturbance' if the focal bird and other flock

members departed suddenly and quickly (usually because of an alarm call emitted by a conspecific or heterospecific bird) or 'individual based' if they were not forced either by aggressions or by sudden disturbance departures.

Test of cohort distribution between feeders

We tested whether or not siskins foraging at the different feeders belonged to different cohorts of residence status (residents or transients), sexes (males or females), ages (adults or juveniles) or dominance status (large black bib dominants or small black bib subordinates; Senar & Camerino 1998).

During the videorecordings, we identified the age of some siskins at the IS and OS feeders according to plumage coloration cues. From the tapes, we looked for groups of birds from which we had transient siskins with the age identified at both feeders simultaneously. We obtained, for 10 different groups in 4 different days, 34 and 20 transient siskins with the age identified foraging simultaneously at the IS and OS feeders, respectively. For the IL feeder, we found 45 transient siskins with the age identified in the videorecordings (but for different days and groups than the birds at the other two feeders). We computed the proportion of adults at each feeder.

During the videorecordings, we visually classified the black bib size of male siskins at the IS and OS feeders in a 10 categories range, from 1 (no bib) to 10 (immense bib). As we commented before, at the IL feeder there were too many birds foraging and we could not identify the black bib size of males. Then, when analyzing the videorecordings of the IS and OS feeders, we looked for foraging groups with transient siskins with the black bib size identified feeding simultaneously at the two feeders. We found 30 different groups in 8 different days with siskins at both feeders with the black bib size identified. We then grouped the 10 categories of black bib of these individuals in only 3 ('small' as the individuals of the former categories 1 to 4, 'medium' as the individuals of the former categories 5 to 7 and 'large' as the individuals of the former categories 8 to 10) and we counted the number of transient male siskins of every category at each feeder. We obtained 220 transient male siskins at the IS feeder and 81 at the OS feeder.

When analyzing the videorecordings at the three feeders we also counted, for each foraging group at each feeder, the sex and residence status of all the individuals for which we had identified these traits on the field. For the IL feeder, we had 41 different groups in 13 different days, and for the IS and OS feeders, we had 16 groups in 6 different days

that were foraging simultaneously at both feeders. We could identify the sex of many more birds than the residence status. At the IS and OS feeders, we could obtain the residence status for a big proportion of the birds foraging at any time, since there were few birds and their position in the feeder allowed us to easily assess whether they were colour ringed or not. However, at the IL feeder there were many birds, for most of them it was impossible to see whether they were colour ringed or not and during the recordings we were mainly concerned in finding colour ringed individuals, so we could not estimate the proportion of residents for this feeder. We classified the residence status of siskins in three categories: 'residents' if they had colour rings, 'ringed' if they had numbered aluminium rings but not colour rings and 'transients' if they were not ringed. For the comparison of the proportion of males (in siskins) between feeders, we obtained 1,213 individuals at the IL feeder, 318 at the IS feeder and 346 individuals at the OS feeder. Otherwise, for the comparison of the proportion of residents between feeders, in males we obtained 147 individuals at the IS feeder and 96 individuals at the OS feeder, and in females we obtained 119 individuals at the IS feeder and 125 individuals at the OS feeder.

■ **Data analysis and transformation**

Statistical software

All the analyses were carried out with the program Statistica 8.0 (StatSoft, Inc.).

General data transformation

Many variables of the thesis did not fit normality in the distribution of frequencies. We tried to normalize them by applying mathematical transformations: logarithm, square root, power, etc. However, some variables could not be normalized with these operations. When we needed to use parametric statistics with them, we applied a Type 1 rank transformation (Conover 1981). We ranked data from the different feeders and groups together in order to obtain both within and between feeders information. The results of the statistical comparisons, given the partitioning of ranks into blocks, were conditionally distribution free (Conover 1981). When we did not need to use parametric statistic methods, then we used the corresponding nonparametric tests.

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Time on feeder estimation

This variable was incomplete for many focal birds foraging on IS and OS feeders, since in these feeders we shifted the video camera every two minutes from one side to the other (see above), often before focal birds departed. Time on feeder was also incomplete for some birds foraging on IL because the video tape (or the battery of the video camera) finished during the recording of these birds. As choosing only birds with complete times on feeder would have been biasing the data towards birds with short values for this variable, we applied the survival analysis treating incomplete times on feeder as censored data and taking feeder as grouping variable. In some comparisons we computed the survival scores for each bird (according to Mantel's procedure) as the estimation of their time on feeder, and we used this estimation in the corresponding analyses. In other occasions, we compared times on feeder between feeders using the Comparing two samples or Comparing multiple samples functions of the survival analysis in Statistica 8.0 (StatSoft, Inc.). These tests are an extension of Gehan's generalised Wilcoxon test. First, a score is assigned to each survival time using Mantel's procedure; next a chi-square value is computed based on the sums (for each group) of this score.

Inter-correlations between vigilance and feeding variables

Since one of our goals was to set the relationship between all the vigilance and feeding variables describing the foraging behaviour of siskins, and how they were adjusted to predation risk and competition, we performed a correlation matrix with all of them at the three feeders of the study, and we analysed which of the correlations were significant with the Product-Moment and Partial Correlations function of the software Statistica 8.0 (Statsoft, Inc.). Since we performed 45 P estimates from the same data, we set the probability to 0.00111 using Bonferroni adjustment. In order to estimate the relationship between all the vigilance and foraging variables, these had to be calculated for the same individuals and for the same periods of time. Therefore, in this analysis we used the non-adjusted pecking rates, the non-adjusted % of time scanning and the times on feeder of the undisturbed subsample. In order to cope with the problem of the incomplete times on feeder, we used the survival scores of a survival analysis, and in order to normalise the distribution of data we used the squared survival scores of times on feeder.

Correlation between plumage coloration and vigilance

In analysing the relationship between plumage coloration and vigilance behaviour in resident males, we computed the Product-Moment Correlations using the program Statistica 8.0 (StatSoft, Inc.) and we adjusted the level of significance to the number of correlations tested ($P = 0.05 / 12 = 0.0042$). We only used % time spent in vigilance and mean inter-scan duration as the variables most related to the predation risk of siskins (Pascual & Senar 2013).

Comparisons between feeders

For the comparison of % of time spent in aggressions, number of hops, number of birds and density of birds between the three feeders, since these variables did not fit the assumption of normality, we carried out Kruskal-Wallis ANOVAs.

For the comparison of the vigilance and foraging variables between feeders, we carried out a MANOVA with feeders as the predictor variable (factor) and the vigilance variables and adjusted pecking rate as the dependent variables. We performed post hoc comparisons (Tukey HSD test) in order to compare the means of the dependent variables between the three feeders.

For the comparison of the proportions of the different categories of species, residence status, sex, age and black bib size between the different feeders, we applied the Pearson chi-square test of the function Tables and Banners of the software Statistica 8.0 (StatSoft, Inc.).

For the comparison of departure reasons between feeders for the 90 individuals of the random subsample we applied a Pearson chi-square test.

Comparison between sexes of vigilance and foraging variables

For the comparison of times on feeder of males and females, we applied the two-sample test of a survival analysis treating incomplete times on feeder as censored data and taking sex as grouping variable. We compared the times on feeder of males and females for all the feeders together and for every one independently.

We compared the three variables of aggression (aggression given rate, aggression received rate and % of time spent in aggressions) between sexes for the three feeders together and for every one independently (only IS and OS) by applying the Mann-Whitney U-test, since the distribution of these variables was highly skewed to zero or to low values near zero.

We compared the hopping rate of siskins between sexes and analysed the possible interaction between feeder and sex by applying a Factorial ANOVA. We used a logarithmic transformation of the dependent variable.

Scan durations, inter-scan durations and pecking rates did not fit the assumption of normality in the distribution of frequencies, and we applied logarithmic transformations in order to normalize their distributions. As we wanted to compare the values of the vigilance and feeding variables between the two individuals of each pair at each feeder, we computed Repeated Measures ANOVAs for each vigilance and foraging variable.

Comparison between residents and transients of vigilance and foraging variables

We compared the % of time spent in aggressions between residents and transients for the three feeders together and for every one independently (only IS and OS) by applying the Wilcoxon Matched pairs Test.

We computed the survival scores of time on feeder for all the resident and transient focal siskins together and we ranked them. We used the minus inverse of mean inter-scan durations and the logarithm of adjusted pecking rates in order to normalize them. We computed Repeated Measures ANOVAs for each vigilance and foraging variable (i.e. adjusted proportion of time spent scanning, logarithm of the adjusted pecking rate, ranked scores of time on feeder, mean scan duration and minus inverse of mean inter-scan duration) taking feeder as categorical factor and residence as within-effects.

Comparison between large and small bib size males of vigilance and foraging variables

We computed survival scores of time on feeder with a survival analysis. We applied a Type 1 rank transformation to % of time spent in aggressions and to survival scores of time on feeder. We also used the following transformations: cube of % of time scanning, reciprocal of inter-scan duration and logarithm of pecking rate.

We compared the vigilance and feeding variables, aggression rates and times on feeder of large and small bib size siskins with Repeated Measures ANOVAs, taking feeder as categorical factor and bib size as within-effects.

For the comparison of departure reasons, we grouped the male transient siskins in three categories of bib size: 'small' as the individuals of the former categories 1

to 4, 'medium' as the individuals of the former categories 5 to 7 and 'large' as the individuals of the former categories 8 to 10. Then we compared departure reasons between feeders and between bib sizes with the Pearson chi-square test.

Comparison between sexes of wing loading, plumage brightness and detectability

When comparing wing loading, wing area and body mass of male and female residents, and in order to avoid the confounding effect of temporal variation in body mass, we calculated the mean values of all the resident males and all the resident females simultaneously trapped in the same foraging group at the IL feeder, and we compared these values as paired data using the Wilcoxon Matched Pairs Test. Males and females of each pair were of the same age.

Some of the variables of lightness, chroma and hue for the five measured plumage patches of siskins (Fig. 3) were transformed applying logarithmic and power operations. We then performed a principal components analysis (PCA) from the correlation matrix with all these variables, and we computed factor scores for each individual from factor loadings of unrotated principal axes. We used the negative scores on the first axis as the values of brightness for each individual (we changed the sign of the scores because all the variables had negative scores with that axis). We carried out a Mann-Whitney U-test to compare the brightness of males and females. We also calculated the mean correlation between all the variables to estimate their degree of inter-correlation.

In the long-distance detectability study, we applied a t-test for dependent samples with the number of males and females found for each person as variables to see whether males were more frequently detected than females. We analysed data both from the four habitats together and from each habitat independently.

In order to quantify prey selection by the *sparrowhawk* hunting at the study area, we compared the proportion of males trapped on the IL feeder in the period when the remains were collected, with the proportion of males found in the prey remains. We analyzed the significance of this difference with the Difference Between Two Proportions function of the program Statistica (StatSoft, Inc.).

Test of the effect of residence and bib size in predation-related body mass regulation

In order to explore the differential variation in body mass of resident and transient siskins with and without the presence of the sparrowhawk, we applied a General Linear Model (GLM) with body mass as the dependent variable; month, sparrowhawk presence, residence status, sex and age as categorical predictors; and environmental data and wing length as continuous predictors. Specifically, as environmental data we considered mean temperature and time of capture, which are known to have a strong influence in body mass (Lima 1986; Metcalfe & Ure 1995; Cresswell 1998). Month was added to the model in order to control for the phenological variation in siskin body mass during the winter (Senar et al. 1992). Wing length was added to the model in order to control for the effect of body size on body mass (Jakob et al. 1996). Sex and age were also added to the model because they can affect the body mass regulation of birds (e.g. Cresswell 1998). Finally, we introduced to the model the two key variables of our study, the residence status of the siskins and the presence of the sparrowhawk, whose specific interaction we wanted to test with the analysis. In the GLM we also included the two-way interactions between month and residence, sex and age, and between sparrowhawk presence, sex and age, as well as the three-way interactions between month, residence and sex and between sparrowhawk presence, residence and sex.

In order to determine whether the differences found between residents and transients in body mass regulation were related to the previous knowledge of the area (Hinde 1956) or to the dominance of residents over transients (Senar & Camerino 1998), we explored the relationship between body mass and dominance in the periods with absence and presence of the predator. We estimated the dominance rank of males according to the black bib area, and we categorized it as 'small' (when it was lower than 30 mm^2; 163 cases) and 'big' (when it was equal or higher than 30 mm^2; 136 cases). Then we applied a General Linear Model with the same variables as before but without sex (because we only had males) and with the addition of black bib size as a categorical predictor. We tested the interaction between sparrowhawk presence and bib size, and we also included to the model the two-way interactions between month, age and bib size, and between sparrowhawk presence, age and bib size. We did not include the three-way interactions because the sample sizes for some contrasts were too small.
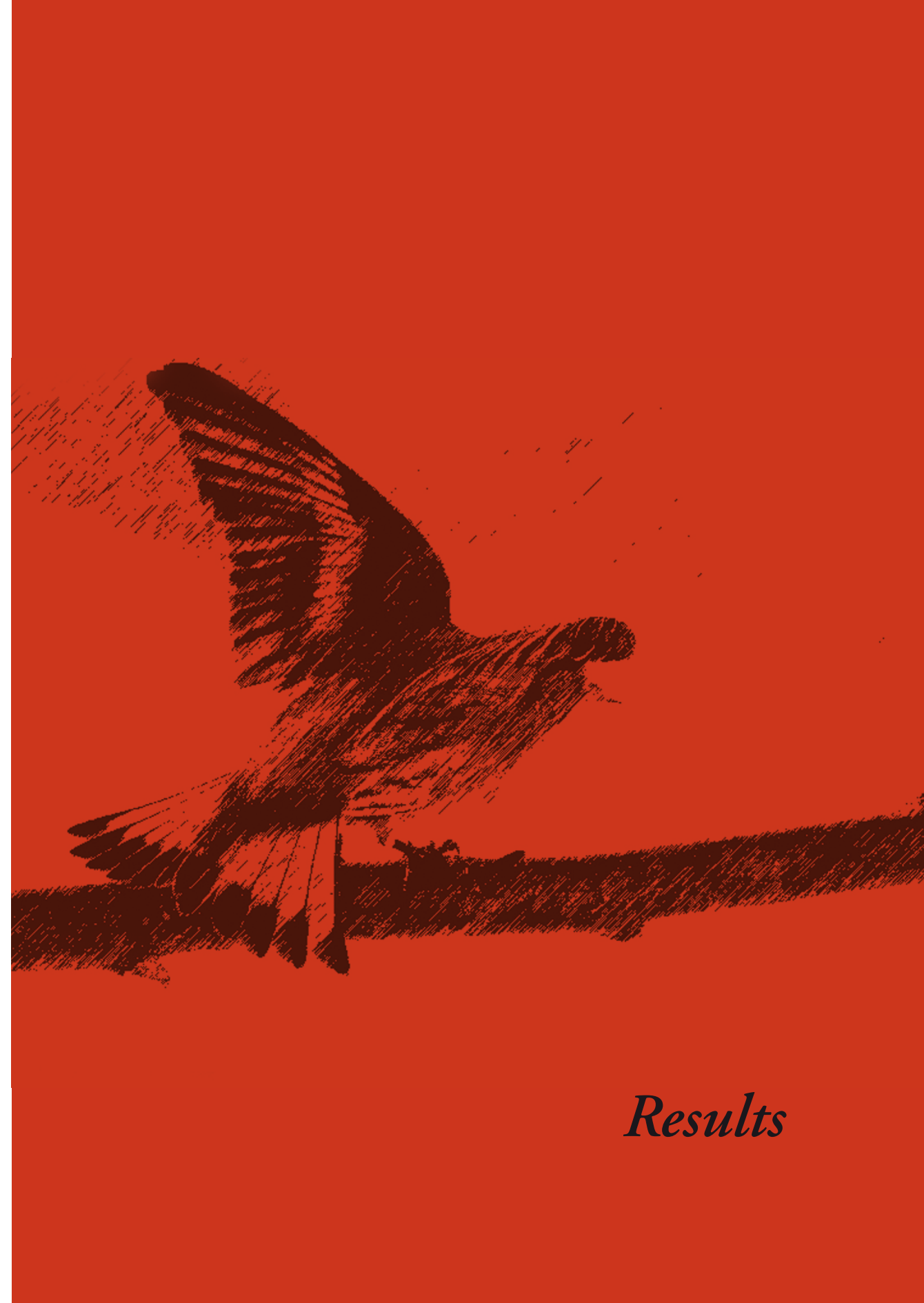

Results

Validation of the experimental set-up

Percentage of time spent in aggressions was significantly different between feeders (Kruskal-Wallis ANOVA: $H_{2,90}$=55.5, P<0.0001). Aggressive interaction times were higher on IS than on IL (Kruskal-Wallis ANOVA: P<0.0001) and were higher on IS than on OS (Kruskal-Wallis ANOVA: P=0.013)(Fig. 5). Moreover, they were also higher on OS than on IL (Kruskal-Wallis ANOVA: P<0.0001).

Figure 5. Mean ± Standard Error of the % of time spent in aggressions (total frames fighting divided by total frames the bird is visible in the recordings) of siskins at the three experimental feeders (IL: inner large feeder, IS: inner small feeder, OS: outer small feeder) differing both in predation risk and competition levels. N=90. *P<0.05; **P<0.01; ***P<0.001.
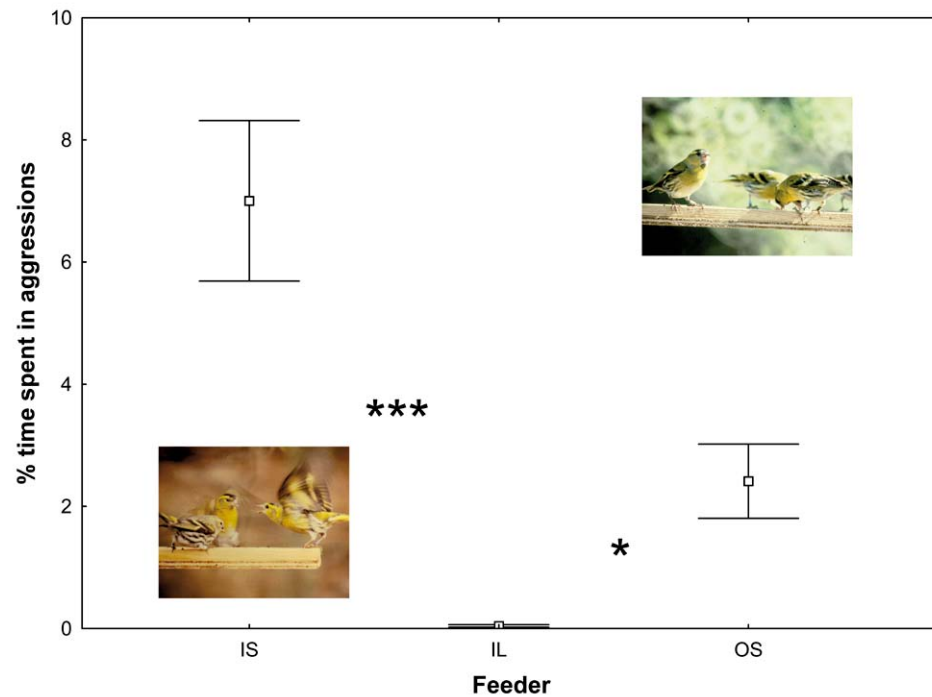
The group size also differed between feeders (Kruskal-Wallis ANOVA: $H_{2,90}$=20.0 P<0.0001). The number of birds foraging on the IL feeder (Mean=14.6 birds, SE=1.29) was higher than the mean number of birds feeding on IS (Mean=9.10 birds, SE=0.38) and OS (Mean=7.87 birds, SE=0.44), while the mean density was lower on IL (Mean=38.84 birds/m², SE=3.43) than on IS (Mean=113.75 birds/m², SE=4.81) and OS (Mean=98.33 birds/m², SE=5.45) (Kruskal-Wallis ANOVA: $H_{2,90}$=53.97, P<0.0001). The maximum number of birds recorded on the three feeders (35 on IL, 15 on IS and 12 on OS) was much higher than the mean, so the feeders normally were not used to their full capacity (although in all the recorded foraging events there were many birds perched around the feeders in addition to the birds foraging on them). The reasons for departure were very different on the three feeders (Table 2). The main reason for departure on IL was 'individual based', on IS was 'aggression received' and on OS was 'disturbance' (related to alarm calls).

Table 2. Observed and expected (in brackets) frequencies of the different reasons for departure of birds foraging at the three feeders. N=30 for each feeder.

Departure reason	Inner Small	Inner Large	Outer Small
Individual based	8 (11.00)	22 (11.00)	3 (11.00)
Disturbance	4 (9.33)	8 (9.33)	16 (9.33)
Aggression received	18 (9.67)	0 (9.67)	11 (9.67)

Pearson chi-square test: X^2_4 = 42.67, P<0.000001

We found no differences between the three feeders either in the frequency of age classes (Pearson chi-square test: x^2_2 = 3.14, p=0.21) or in the frequency of bib size categories (see Topic 4). Therefore, and given that the other individual traits were controlled for in the experiment (species, sex and residence status), we can conclude that we should not expect any difference in the phenotype of the focal birds between feeders. Hence, when we compare the behaviour of focal birds a the different feeders, we compare the same kind of birds but foraging in different environmental conditions, as we intended to do.

From these results we can conclude that: (1) the comparison IL vs IS feeders allowed us to estimate the effect of competition over vigilance; (2) the comparison of IL vs OS feeders allowed us to estimate the effect of predation risk over vigilance; (3) aggression rates were higher at OS than at IL, but the effect of competition over vigilance in this comparison could almost be discarded when the differences found between these two feeders were in the opposite direction to the differences found between IL vs IS.

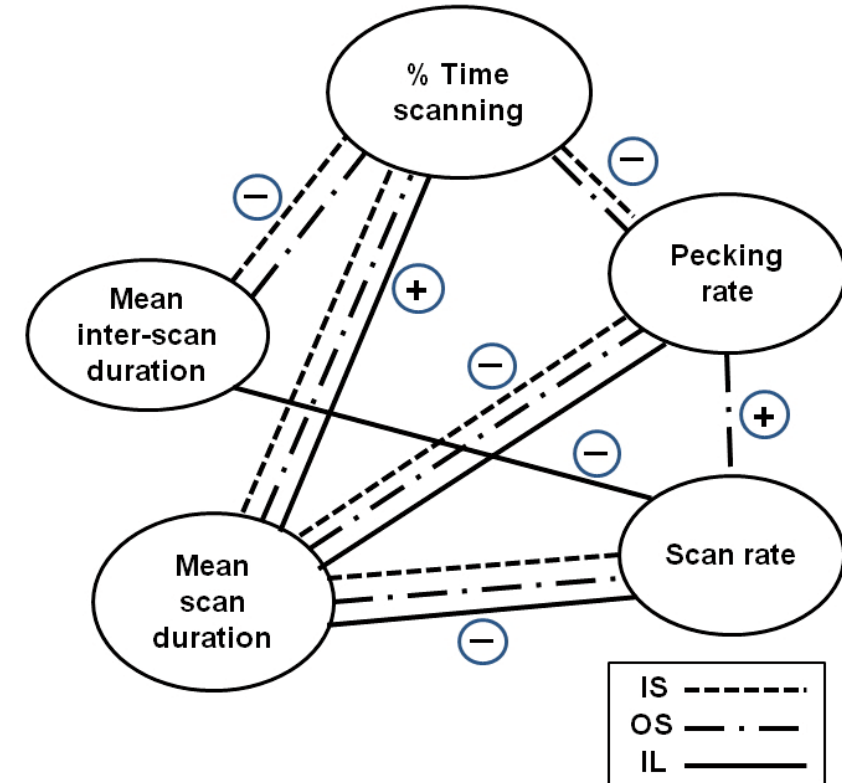## Inter-correlations between variables at the different feeders

The inter-correlations between the vigilance variables were high (Table 3, Fig. 6). Mean scan duration had high correlations with % of time scanning and scan rate, but not with mean inter-scan durations, which were highly correlated only with % of time scanning. Interestingly, scan rate and mean inter-scan durations were only correlated at the IL feeder. Pecking rate and scan rate were positively correlated at the OS feeder but not at the others. On the other hand, pecking rate and mean inter-scan duration were marginally and positively correlated at the IS feeder but not at the others. In any case, pecking rate was negatively correlated both with % of time scanning and mean scan duration at all the feeders (only marginally at the IL feeder). The time on feeder was only marginally (and negatively) correlated with % of time scanning and mean scan duration at the OS feeder, but not at the IL feeder. Time on feeder was also marginally and positively correlated with pecking rate at the two small feeders, while it was marginally and negatively correlated with pecking rate at the large feeder.

Table 3. Correlations between all the vigilance variables, pecking rate and time on feeder at the three feeders (IL: inner large, IS: inner small, OS: outer small). The values of all the variables were transformed to fit the assumptions of the parametric statistics, except for the scan rate. The values of time on feeder were the scores of a survival analysis treating incomplete times on feeder as censored data. Significant differences (*P*<0.0011) are shown with asterisks (the number indicate the level of significance) and tendencies (*P*<0.05) are shown in italics.

	Feeder	%Time scanning	Mean scan duration	Mean inter-scan duration	Scan rate	Pecking rate
Mean scan duration	IL	0.70**				
	IS	0.84**				
	OS	0.81**				
Mean inter-scan duration	IL	*-0.56*	0.11			
	IS	-0.76**	-0.35			
	OS	-0.60*	-0.08			
Scan rate	IL	0.05	-0.63*	-0.79**		
	IS	-0.29	-0.66**	-0.35		
	OS	*-0.42*	-0.84**	*-0.44*		
Pecking rate	IL	*-0.46*	-0.60*	0.14	0.26	
	IS	-0.77**	-0.70**	*0.55*	0.19	
	OS	-0.76**	-0.82**	0.23	0.64*	
Time on feeder	IL	-0.09	0.13	0.06	-0.19	*-0.44*
	IS	-0.19	*-0.39*	-0.05	*0.37*	*0.37*
	OS	*-0.47*	*-0.53*	0.15	*0.33*	*0.33*

P<0.0011 *, *P*<0.0001 **

Comparison between feeders in vigilance and foraging variables

MANOVA results showed significant differences between feeders in the five variables that describe the behaviour of birds while foraging (Wilks' lambda=0.58, $F_{10,166}$ = 3.40, *P*<0.0001). When increasing competition levels (IS compared to IL), the siskins increased mean scan duration (Table 4, Fig. 7a) and (marginally) reduced scan rate (Table 4, Fig. 7d), while keeping mean inter-scan duration constant (Table 4, Fig. 7b). On the other hand, when increasing predation risk (OS compared to IL; there was some increase in competition too), siskins decreased mean inter-scan duration (Table 4, Fig. 7b) while keeping mean scan duration constant (Table 4, Fig. 7a). Adjusted pecking rate was not affected by predation risk but was reduced by competition (Table 4, Fig. 8a).

Figure 7. Mean ± Standard Error of (a) mean scan duration, (b) mean inter-scan duration, (c) adjusted % of time scanning and (d) scan rate at the three experimental feeders (IL: inner large, IS: inner small, OS: outer small) differing both in predation risk and competition levels. The values of (a) and (b) are given in seconds. Scan rate is given in number of scans per second. *N*=90. ns *P*≥0.05; * *P*<0.05.
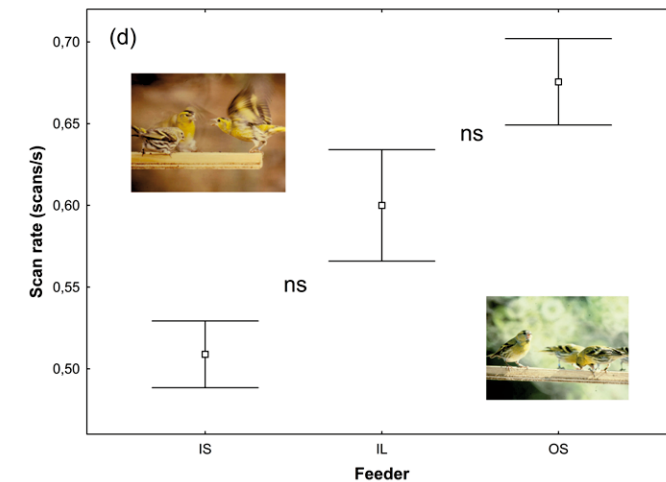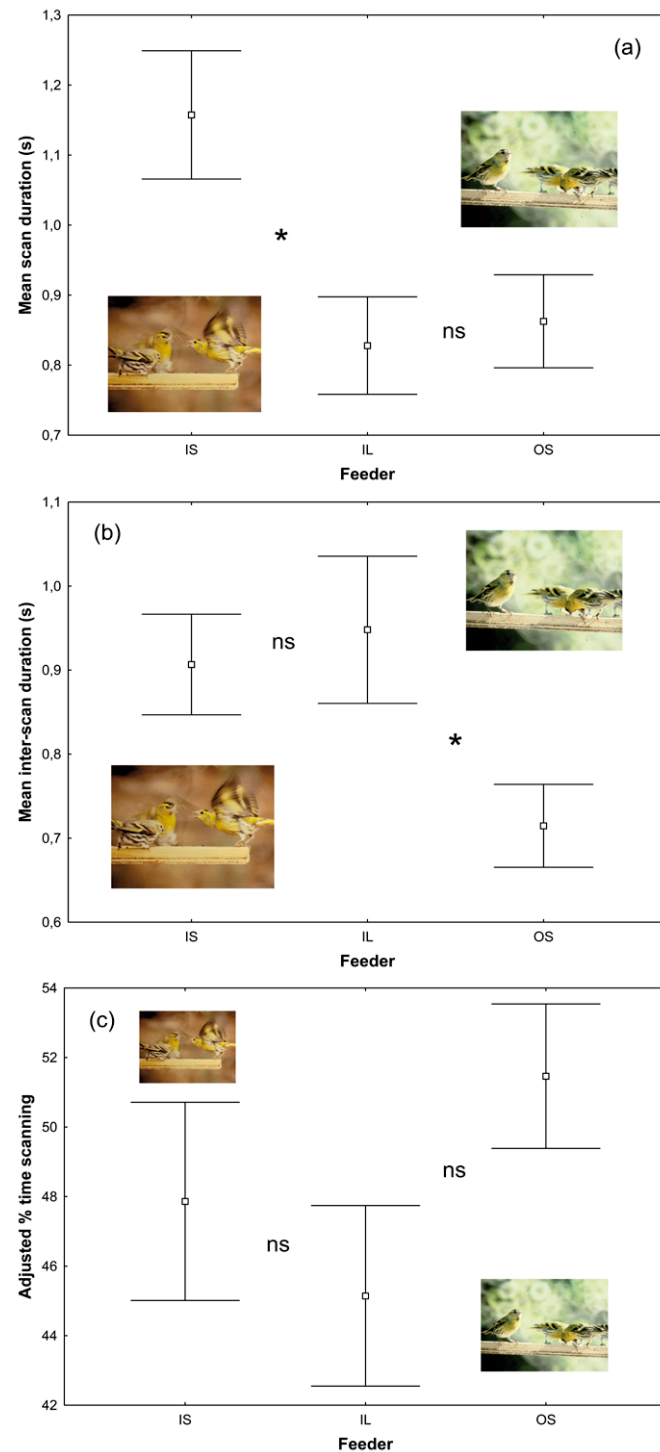
Table 4. MANOVA Post Hoc Comparisons between feeders (IL: inner large, IS: inner small and OS: outer small) of the 5 variables describing the behaviour of birds while foraging (mean scan duration, mean inter-scan duration, % of time scanning, scan rate and pecking rate). The values of all the variables except for scan rate were transformed to fit the assumptions of the parametric statistics, and % of time scanning and pecking rate were adjusted (ad) to the % of time spent in aggressions. Significant differences (*P*<0.05) are shown in bold and tendencies (*P*<0.1) are shown in italics.

| Variables | | IS vs IL | | OS vs IL | | IS vs OS | |
| | | Tukey HSD test | | Tukey HSD test | | Tukey HSD test | |
	Between MS	DF	P	DF	P	DF	P
Mean scan duration	0.19350	87	**0.010**	87	0.811	87	*0.052*
Mean inter-scan duration	0.14517	87	0.990	87	**0.015**	87	**0.022**
% of time scanning (ad)	1564000	87	0.637	87	0.221	87	0.725
Scan rate	0.02276	87	*0.056*	87	0.134	87	**0.000**
Pecking rate (ad)	0.14426	87	**0.015**	87	0.770	87	*0.085*

The only vigilance variable that showed no significant differences between feeders was adjusted % of time scanning ($F_{2,87}$ = 1.40, *P*=0.25; Table 4, Fig. 7c). In fact, for the period of 30 seconds analysed in the undisturbed subsample, the increase in mean scan durations did actually imply a concomitant increase in % of time scanning (before adjustment) when comparing IS and IL feeders (Tukey HSD test: *P*=0.013), and the decrease in mean inter-scan durations did actually imply a marginal increase in % of time scanning when comparing OS and IL feeders (Tukey HSD test: *P*=0.066). However, when subtracting the mean % of time spent in aggressions at each feeder to the % of time scanning, these increases were neutralised because of the higher aggression rates on the small feeders.

Times on feeder were reduced both by predation risk and competition (chi-square=19.52, *df*=2, *P*<0.0001; Fig. 8b).

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Figure 8. (a) Mean ± Standard Error of the adjusted pecking rate (pecks/s) at the three experimental feeders (IL: inner large, IS: inner small, OS: outer small) differing both in predation risk and competition levels. *N*=90. ns *P*≥0.05; *P*<0.05. (b) Cumulative proportion of birds surviving up to the respective interval of time on feeder (in seconds) at the three experimental feeders. *N*=90. Chi-square=19.52, *df*=2, *P*<0.0001.
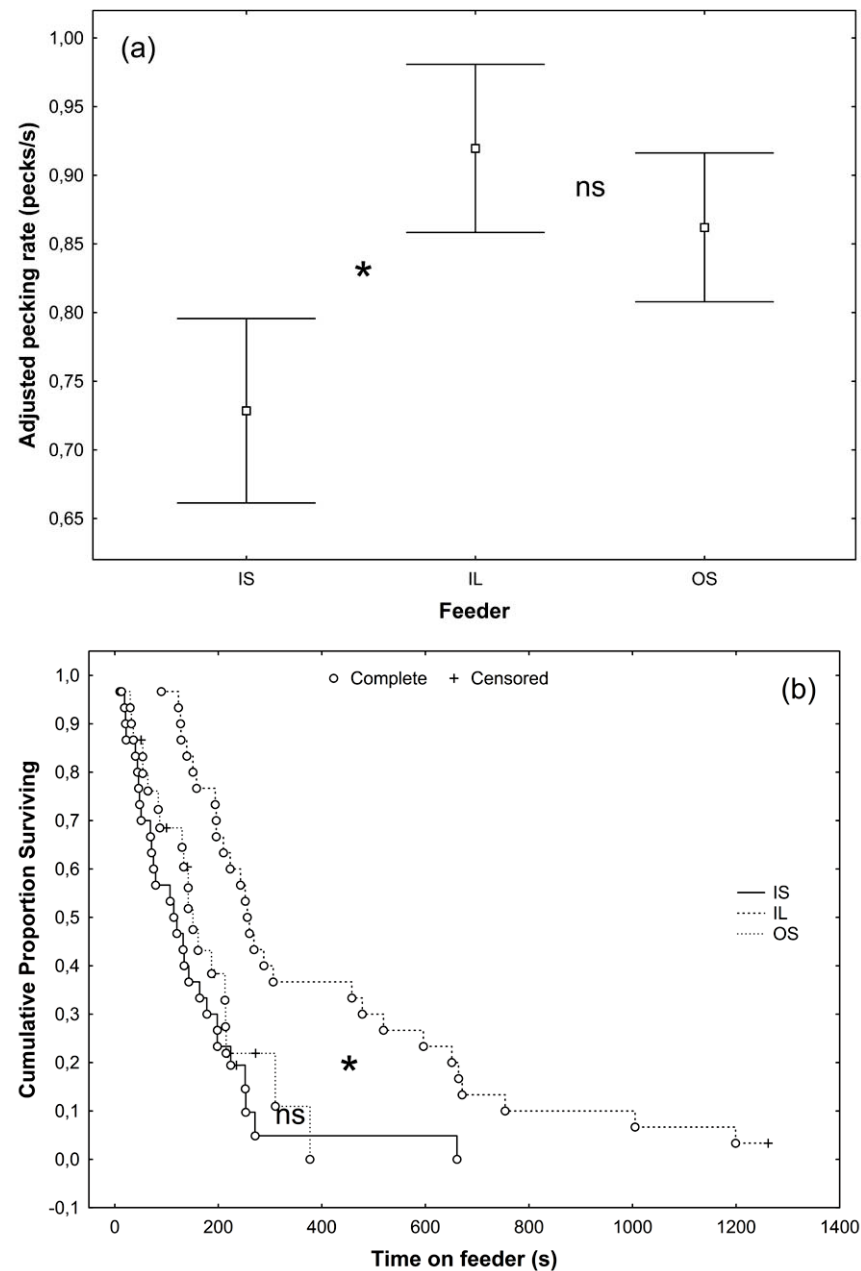
Between-sexes differences in plumage brightness

The first principal component of the PCA on lightness, chroma and hue for the five measured plumage points of siskins accounted for 51% of the total variance (eigenvalue = 7.69). All the variables showed high positive correlations with that axis (except rump hue and lightness of secondaries; Table 5), and could therefore confidently be interpreted as a factor of general brightness of plumage coloration. The comparison between the sexes for this factor showed that males had higher scores than females, i.e. males were brighter than females (mean score of males: 0.70, mean score of females: -0.89; *U* = 28, *Z* = -5.63, *P* < 0.0001). All females had negative scores for the factor, while all the males but three had positive scores. Only these three individuals from the total of 52 could not be correctly sexed according to their factor score. The average ratio male/female for all the different measures on all the plumage points was 1.36, and it was 1.47 when considering only lightness and chroma, which are more related to brightness (Table 5). Siskin males displayed a more saturated plumage colour than females (83% more saturated, on average; 141% more for tail and 147% more on primaries) and a slightly higher percentage of white than females (14% more, on average; 34% more for tail and 17% for primaries)(Table 5).

Table 5. Mean male and female value ± Standard Error of lightness, chroma and hue of the coloration of the plumage points of siskins illustrated in Fig.3, and ratio 'mean value of males/mean value of females'. *N*=29 for males and *N*=23 for females. Also included are the factor score loadings for the first principal component (PC1) from the PCA on lightness, chroma and hue. Eigenvalue = 7.69, %Explained variance = 51%. Mean correlations between variables = 0.41, SE=0.03, *N*=105.

Plumage point PC1	Variable	Males mean±SE	Females mean±SE	Ratio M/F	Factor loading
	Lightness	58.10±1.17	43.27±0.95	1.34	0.88
Tail	Chroma	29.71±1.73	12.31±1.11	2.41	0.89
	Hue	96.88±0.86	91.51±2.01	1.06	0.57
	Lightness	39.88±0.24	39.31±0.30	1.01	0.44
Back	Chroma	11.13±0.42	7.80±0.31	1.43	0.76
	Hue	92.56±0.56	81.75±1.19	1.13	0.84
	Lightness	54.11±0.92	49.92±0.63	1.08	0.65
Rump	Chroma	32.64±1.34	20.45±0.86	1.6	0.84
	Hue	95.88±0.20	95.82±0.32	1	0.03

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Primaries	Lightness	41.47±0.79	35.37±0.58	1.17	0.83
	Chroma	11.83±1.07	5.00±0.52	2.37	0.89
	Hue	85.38±2.68	58.07±5.09	1.47	0.88
Secondaries	Lightness	56.46±0.78	56.82±0.51	0.99	0.07
	Chroma	19.74±1.27	14.99±0.94	1.32	0.62
	Hue	95.14±0.52	90.05±1.06	1.6	0.73

Between-sexes differences in detectability

Males were found to be earlier detected than females (Table 6). However, if we analyze the difference in detectability in each of the four habitats independently, this difference was only significant at the fruit orchards habitat. Males tended to be more detectable than females at the plowed lands and forest habitats (where the differences would probably be significant with a higher sample size) while at the grasslands habitat there were not any detectability differences.

Table 6. Summary of the results from the experimental test comparing the siskin sexes long-distance detectability by human observers. Male and female siskin mounts were presented in 10 pairs to 28 different observers at the different habitats found in the study area, and we recorded the sex of the individual of each pair detected first. In 5 tests both sexes were detected simultaneously and were excluded.

	All habitats		Fruit orchards		Plowed lands		Forest		Grasslands	
Number of times detected first	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
280 pairs (5 ties excluded)	159	116	46	24	40	28	39	30	34	34
Sex most detected first	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
28 observers (6 ties excluded)	17	5	7	0	4	1	3	2	3	2
t-test										
T	2.67		5.68		1.22		0.97		-0.00	
Significance (P)	0.013		0.001		0.270		0.368		1	
N	28		7		7		7		7	

Between-sexes differences in profitability (wing loading)

Body mass of males was higher than body mass of females, but wing area was also higher for males, so that they did not differ in wing loading (Table 7).

Table 7. Wilcoxon Matched Pairs Test results of the comparison between sexes of body mass, index of wing area and wing loading of 42 pairs of resident siskins trapped together (each in a different capture event) on the IL feeder. Significant differences are highlighted in bold.

	Valid N	Mean (SE)		T	Z	P
		Males	Females			
Body mass (g)	42	12.81 (0.08)	12.58 (0.14)	271	2.26	**0.024**
Index of wing area (mm)	42	452 (3.6)	441 (3.8)	233	2.56	**0.010**
Wing loading (g/mm)	42	0.0285 (0.0003)	0.0287 (0.0004)	423	0.36	0.722

Between-sexes differences in predation-related vigilance variables

We did not find significant differences between sexes in % time scanning ($F_{1.33}$=1.83, P=0.19; Table 8a and Fig. 9a). On the other hand, we found that males had shorter inter-scan durations than females ($F_{1.33}$=12.4, P=0.001; Table 8a) and that the difference between sexes was significant at the high predation risk and intermediate competition feeder (Tukey HSD test (OS): P=0.032) and marginally at the low competition and low predation risk feeder (Tukey HSD test (IL): P=0.056) but that sexes did not differ in this variable at the high competition and low predation risk feeder (Tukey HSD test (IS): P=0.997)(interaction feeder x sex: $F_{1.33}$=5.17, P=0.011; Table 8b, Fig. 9d). Times on feeder of males and females did not differ in general (Test statistic=0.01, P=0.99) and on none of the feeders (IL: Test statistic=-0.86, P=0.39; IS: Test statistic=0.78, P=0.44; OS: Test statistic=-0.27, P=0.78). We found significant differences between the three feeders in the proportion of sexes (Pearson chi-square test: X^2_2 = 16.01, P=0.0003). The proportion of males was higher at the feeders IS (56%) and IL (53%) than at the feeder OS (42%).

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Table 8. Tukey HSD results for Post-hoc comparisons of Repeated Measures ANOVAs for the vigilance variables and pecking rate of paired male and female siskins foraging at three feeders differing in predation risk and competition. We show the results of the comparisons (a) between sexes (all feeders) and (b) the results of the interaction between sex and feeder for inter-scan durations on the OS feeder (the only interaction which was found to be significant). N = 16 pairs at IL feeder, N = 14 pairs at IS feeder and N = 6 pairs at OS feeder. Significant differences ($P < 0.05$) are highlighted in bold, tendencies ($P < 0.1$) are shown in italics.

a) BETWEEN SEXES

Variable	Sex	Mean	Std.Err.	Significance (P) Males
Pecking rate	Males	0.90	0.07	
	Females	0.86	0.05	0.484
% Time scanning	Males	0.51	0.02	
	Females	0.47	0.02	0.491
Mean scan duration	Males	0.79	0.06	
	Females	0.84	0.07	0.443
Mean inter-scan duration	Males	0.64	0.04	
	Females	0.74	0.03	**0.005**

b) FEEDER X SEX

Variable Mean inter-scan duration	Feeder	Mean	Std.Err.	IS Males	IS Females	IL Males	IL Females	OS Males	OS Females
IS	Males	0.67	0.05						
IS	Females	0.63	0.04	0.997					
IL	Males	0.70	0.05	0.986	0.916				
IL	Females	0.83	0.04	*0.089*	**0.039**	*0.056*			
OS	Males	0.54	0.08	0.722	0.857	0.391	**0.011**		
OS	Females	0.77	0.06	0.778	0.624	0.960	0.976	**0.032**	

Figure 9. Mean ± Standard Error of the adjusted % of time scanning (a), adjusted pecking rate (b), mean scan duration (c) and mean inter-scan duration (d) of paired male and female siskins at three feeders differing in predation risk and competition. IL: N = 16, IS: N = 14; OS: N = 6.
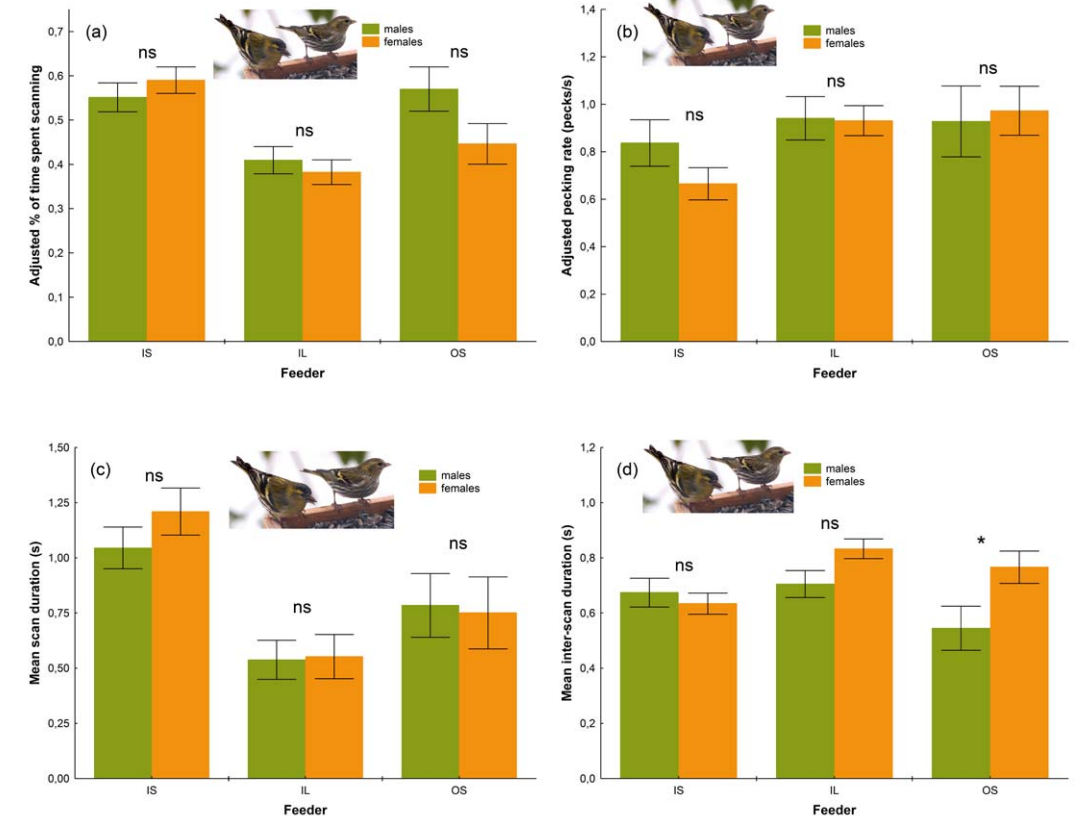
Between-sexes differences in competition-related vigilance and foraging variables

Male and female siskins did not differ in either pecking rate ($F_{1.33}$=0.31, P=0.58; Table 8a and Fig. 9b) or mean scan duration ($F_{1.33}$=0.21, P=0.65; Table 8a and Fig. 9c). There were not differences between sexes in the rate of aggressions given and in the % time spent in aggressions (U=1672, Z adjusted=-0.97, P=0.33 and U=1569, Z adjusted=-1.47, P=0.14, respectively). However, females had higher rates of aggressions received than males (U=1477, Z adjusted=-2.07, P=0.04). Male and

female siskins did not differ in the hopping rate on the feeders ($F_{1.110}$=1.93, P=0.17) and there was not a significant interaction between feeders and sexes for this variable ($F_{2.110}$=1.08, P=0.34).

Within-males correlations between plumage coloration and vigilance variables

The males had higher proportions of time spent scanning when the black tail stripe was shorter (and therefore the yellow tail stripe was longer; R = -0.90, P < 0.001; Table 9 and Fig. 10a) and the lightness of the tail yellow was higher (R = 0.78, P = 0.003; Table 9 and Fig. 10b). Mean inter-scan durations marginally decreased with the length of the tail black stripe (i.e. they tended to be shorter when the length of the yellow tail stripe was longer; R = 0.70, P = 0.024 NS). Bib area, length of the wing yellow stripe and chroma and hue of the tail yellow stripe had lower and non-significant correlations with both vigilance variables.

Table 9. Correlations of vigilance and coloration variables measured for siskin resident males. We considered the hue, chroma and lightness of the colour of the yellow tail stripe (measured with a chromameter) and the length of the yellow wing stripe and the black tail stripe (inversely correlated to the yellow tail stripe) as the variables more related to the detectability of siskins by an avian predator. We also considered bib area as a colour trait related to dominance. N = 12 males for chromameter coloration measures, N = 10 for wing and tail stripe measures and N = 11 for bib area. Significant correlations (P < 0.0042) are highlighted in bold and tendencies (P < 0.05) are marked in italics.

	Length wing yellow stripe	Length tail black stripe	Lightness tail	Chroma tail	Hue tail	Bib area (mm²)
% Time spent scanning	0.38	**-0.90**	**0.78**	0.53	0.06	-0.50
Mean inter-scan duration	-0.43	*0.70*	-0.28	-0.14	-0.40	0.34

Figure 10. A: Correlation between the length of the black tail stripe (inversely correlated to the yellow tail stripe) and the proportion of time spent scanning in male resident siskins. Spearman R = -0.90, P < 0.05, N = 10. B: Correlation between the lightness of the yellow tail stripe (measured with a chromameter) and the proportion of time spent scanning in male resident siskins. Spearman R = 0.81, P < 0.05, N = 12.
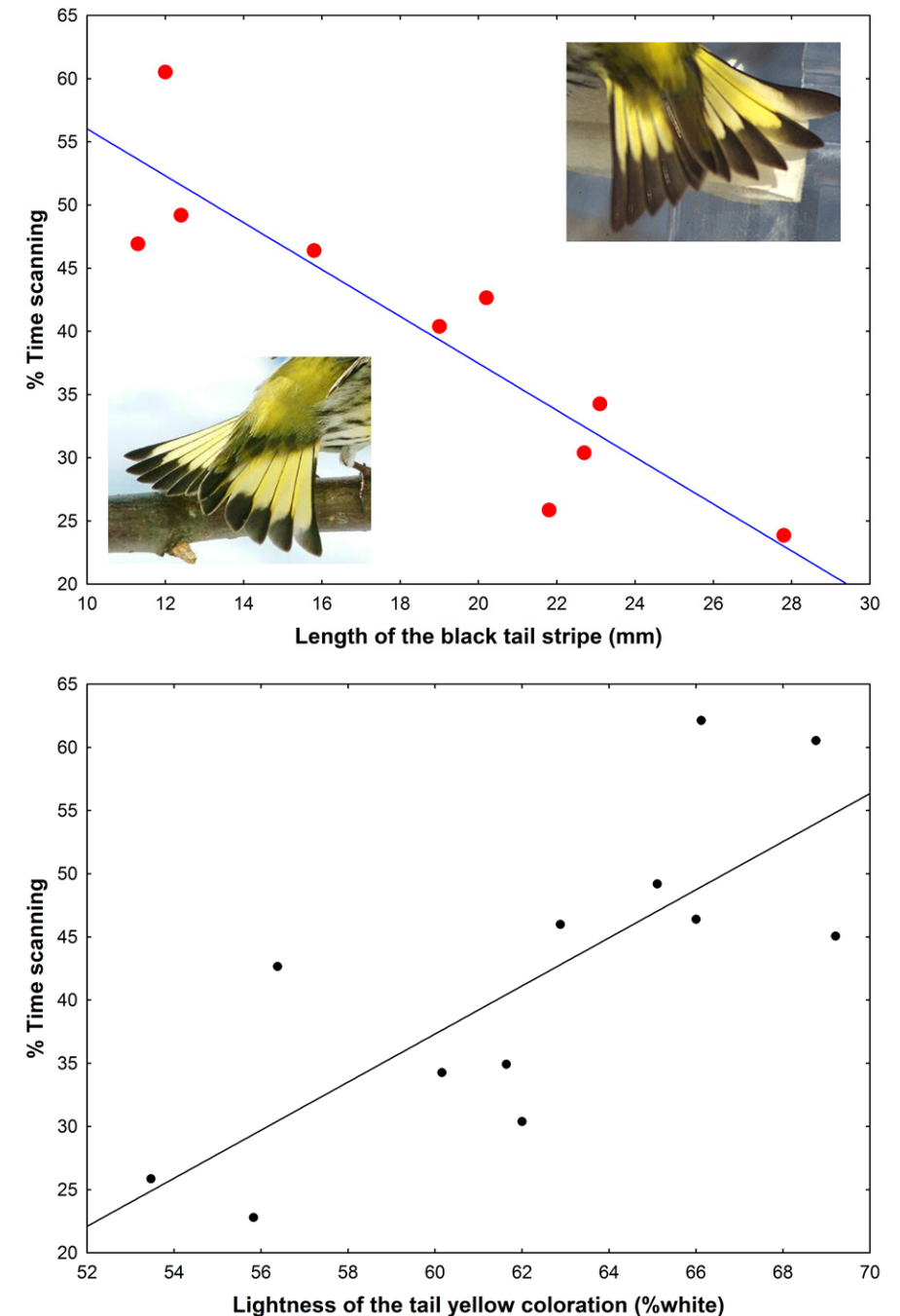
Between-sexes difference in prey selection

The proportion of males (both residents and transients) from the sample of birds trapped at the IL feeder was 55% (349 out of 635 individuals captured), while the proportion of males found in the prey remains was 80% (20 out of 25 birds identified). These two percentages differed significantly ($P = 0.014$), and therefore males were more abundant in prey remains than expected by the null hypothesis of equal predation risk.

■ TOPIC 3: VIGILANCE, PREDATION RISK AND RESIDENCE

Comparison of resident and transient frequencies at feeders

The proportion of resident siskins did not differ between the IS (22%) and OS (17%) feeders when considering both sexes together (Pearson chi-square test: $X^2_2 = 2.00$, $P = 0.37$, $N = 487$). However, when considering the sexes separately, we found that in males, residents had higher frequencies at the low than at the high predation risk feeder (Pearson chi-square test: $X^2_2 = 14.60$, $P = 0.0007$, $N = 243$; Table 10). We also found that ringed transients (that probably had spent more days at the foraging area) presented higher frequencies at the low predation risk feeder than not ringed transients. In females there were no differences in the proportion of residents between both feeders (Pearson chi-square test: $X^2_2 = 5.19$, $P = 0.07$, $N = 244$; Table 10). However, between female transients we observed the opposite tendency that in males: ringed birds tended to be more abundant at the high predation risk feeder than not ringed birds.

Table 10. Frequency (and proportion) of resident and transient (ringed and non-ringed) siskins at two feeders of the same size and shape and video recorded simultaneously but located near (IS) and far (OS) from protective cover.

Sex	Feeder	Residents	Transients	
			Ringed	Not ringed
Males	IS	31 (21%)	50 (34%)	66 (45%)
	OS	12 (13%)	17 (18%)	67 (70%)
Females	IS	27 (23%)	29 (24%)	63 (53%)
	OS	26 (21%)	47 (38%)	52 (42%)

Comparison of aggressive interaction rates

Resident and transient siskins did not differ in % of time spent in aggressions either at all the feeders (Wilcoxon Matched Pairs Test: $T = 1300$, $Z = 0.84$, $P = 0.40$, $N = 122$) or at the feeders IS (Wilcoxon Matches Pairs Test: $T = 388$, $Z = 0.03$, $P = 0.98$, $N = 42$) and OS (Wilcoxon Matched Pairs Test: $T = 73$, $Z = 1.48$, $P = 0.14$, $N = 24$).

Comparison of times on feeder and pecking rate

Transient siskins had longer foraging bouts than residents, especially at the IL feeder (Table 11, Fig. 11a). Pecking rates did not differ between transients and residents, but there was an almost significant interaction between residence and feeder (Table 11) so that transients increased pecking rate when increasing predation risk while residents did the opposite (Fig. 11b).

Table 11. Results of Repeated Measures ANOVAs with different vigilance and foraging variables as dependent variables, feeder as categorical predictor and residence (difference between paired residents and transients) as within-effects. Time on feeder: $N = 56$ pairs for IL feeder, $N = 42$ for IS and $N = 24$ for OS. All other dependent variables: $N = 28$ for IL, $N = 20$ for IS and $N = 14$ for OS.

	df (df Error)	F	P
Ranked survival scores of time on feeder			
Feeder	2 (119)	17.56	<0.0001
Residence	1 (119)	4.38	0.0385
Feeder x Residence	2 (119)	0.20	0.8163
Logarithm adjusted pecking rate			
Feeder	2 (59)	12.3	<0.0001
Residence	1 (59)	0.06	0.8143
Feeder x Residence	2 (59)	2.89	0.0634
Adjusted % time scanning			
Feeder	2 (59)	7.13	0.0017
Residence	1 (59)	0.4	0.5283
Feeder x Residence	2 (59)	1.45	0.2428
Scan rate			
Feeder	2 (59)	6.63	0.0025
Residence	1 (59)	19.84	<0.0001
Feeder x Residence	2 (59)	0.52	0.5992

Mean scan duration			
Feeder	2 (59)	9.55	0.0003
Residence	1 (59)	14.85	0.0003
Feeder x Residence	2 (59)	0.36	0.6994
Minus inverse of mean inter-scan duration			
Feeder	2 (59)	6.06	0.004
Residence	1 (59)	5.56	0.0218
Feeder x Residence	2 (59)	2.56	0.0858

Figure 11. Mean ± Standard Error of (a) time on feeder, (b) adjusted pecking rate, (c) mean scan duration and (d) mean inter-scan duration for resident and transient siskins foraging at three different feeders differing in predation risk and competition. IL: N = 28 pairs; N = 20 pairs; OS: N = 14 pairs.
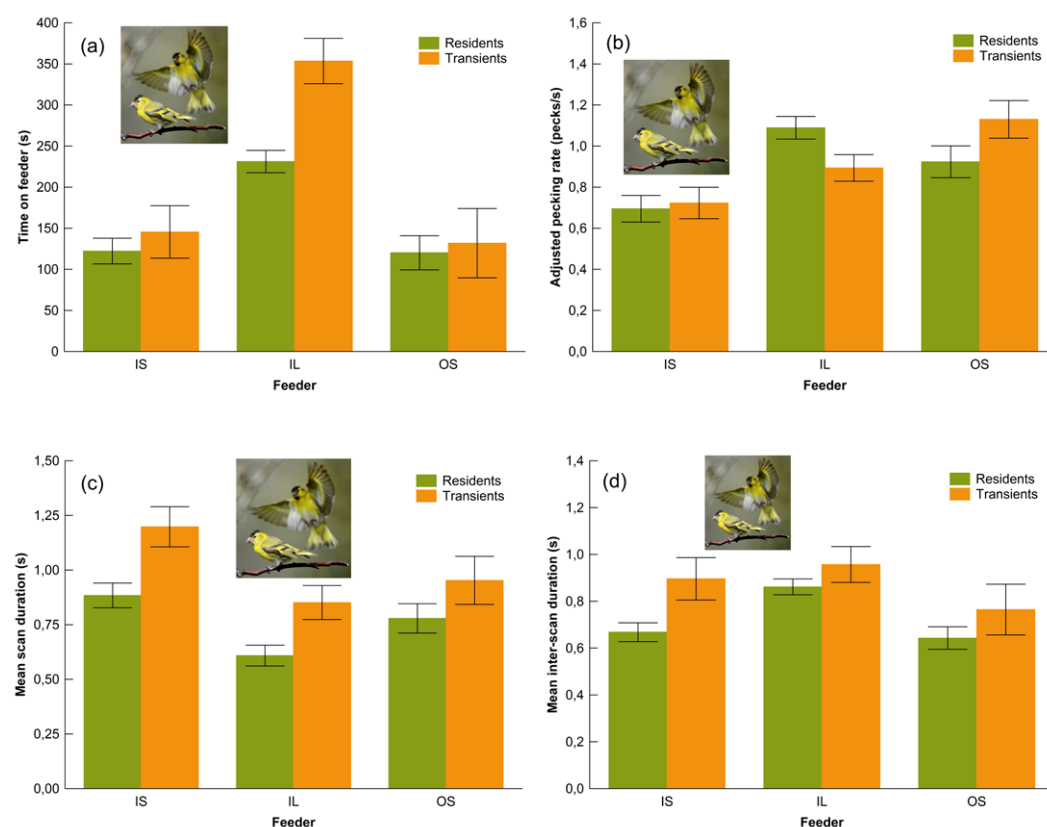
Comparison of vigilance variables

Adjusted % of time spent scanning did not differ between residents and transients at none of the feeders (Table 11). However, transients showed a lower scan rate and longer mean scan and inter-scan durations than residents (Table 11, Fig. 11c,d). There were no significant interactions between vigilance variables and feeder (Table 11).

■ TOPIC 4: VIGILANCE, PREDATION RISK AND PERSONALITY

Siskins with large black bibs showed a vigilance system with shorter inter-scan durations and higher scan rates than siskins with small black bibs (Table 12, Fig. 12). Proportion of time scanning, pecking rate, time on feeder and proportion of time spent in aggressions did not differ between the two bib size categories (Table 12). Mean inter-scan durations (in seconds) were shorter at the OS feeder (mean = 0.65 ± 0.07, N = 14) than at the IS feeder (mean = 0.88 ± 0.05, N = 26), scan rates (in number of scans per minute) were higher at the OS feeder (mean = 24.94 ± 1.16, N = 14) than at the IS feeder (mean = 19.96 ± 0.85, N = 26) and survival scores of time on feeder were smaller at the OS feeder (mean = -11.7 ± 7.79, N = 20) than at the IS feeder (mean = 12.82 ± 7.42, N = 22), but we did not find any interaction between bib size and feeder for any of the analyzed variables (Table 12). Departure reasons did not significantly differ between bib size categories either at the IS or at the OS feeders (Table 13). However, the large black bib size males had the lowest aggression departure frequencies and the highest disturbance departure frequencies (Table 13). Finally, we did not find significant differences in the proportion of bib size categories between feeders (IS: small = 34%, medium = 34% and large = 32%, N = 220; OS: small = 38%, medium = 28% and large = 33%, N = 81; Pearson chi-square test: X^2_2 = 0.82, P = 0.66).

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Table 12. Results of Repeated Measures ANOVAs for the comparison of different vigilance, foraging and aggressive behaviours between pairs of siskins differing in bib size and foraging in two feeders with different predation risk. Most variables were transformed so that we could apply parametric statistics. The first four variables were estimated from the undisturbed subsample (N=26 pairs for IS feeder and N=14 pairs for OS feeder) and the last two variables were estimated from the random subsample (N=22 pairs for IS feeder and N=20 pairs for OS feeder).

		F	df	P
reciprocal of inter-scan duration	(Intercept)	660.4	1, 38	0.0000***
	Feeder	12.1	1, 38	0.0013**
	Bib	7.4	1, 38	0.0099**
	Bib x Feeder	0.6	1, 38	0.4620
scan rate	(Intercept)	981.9	1, 38	0.0000***
	Feeder	12.1	1, 38	0.0013**
	Bib	4.2	1, 38	0.0472*
	Bib x Feeder	0.0	1, 38	0.8470
cube of % of time scanning	(Intercept)	198.8	1, 38	0.0000***
	Feeder	0.3	1, 38	0.5705
	Bib	1.6	1, 38	0.2165
	Bib x Feeder	0.1	1, 38	0.7691
logarithm of pecking rate	(Intercept)	10.6	1, 38	0.0024**
	Feeder	0.2	1, 38	0.6588
	Bib	1.0	1, 38	0.3246
	Bib x Feeder	0.0	1, 38	0.9843
ranked survival scores of time on feeder	(Intercept)	266.8	1, 40	0.0000***
	Feeder	7.3	1, 40	0.0099**
	Bib	2.1	1, 40	0.1542
	Bib x Feeder	0.1	1, 40	0.7062
ranked % of time spent in aggressions	(Intercept)	169.8	1, 40	0.0000***
	Feeder	0.9	1, 40	0.3397
	Bib	0.9	1, 40	0.3425
	Bib x Feeder	2.6	1, 40	0.1116

*P<0.05; **P<0.01; ***P<0.001

Figure 12. Mean ± Standard Error of (a) mean inter-scan duration and (b) scan rate of paired male transient siskins differing in black bib size. N = 40 pairs. P level was calculated from a Repeated Measures ANOVA with the transformed variables.
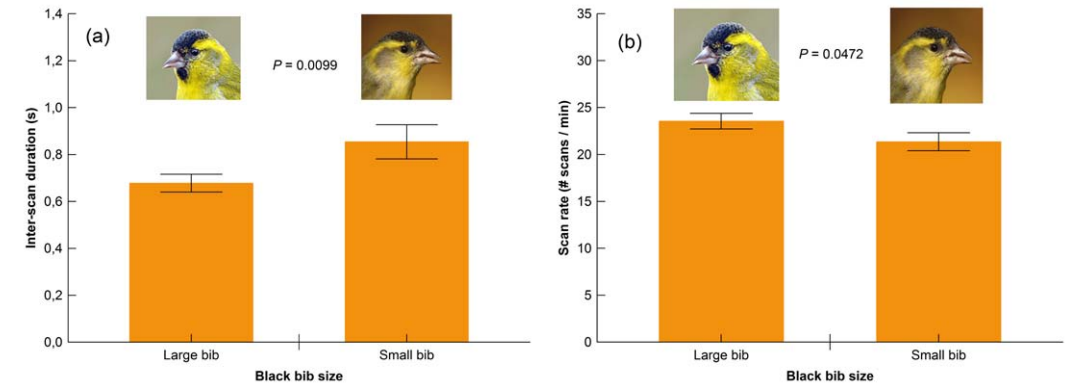
Table 13. Observed and expected (in brackets) departure reasons of male transient siskins belonging to different black bib size categories and foraging on two feeders of different predation risk, and proportion of departure reasons for each category. N = 47 for the low predation risk feeder (IS) and N = 39 for the high predation risk feeder (OS).

Feeder	Bib size category	Departure reason		
		Aggression	Individual based	Disturbance
Low predation risk (IS)	Small	10 (7.5)	4 (4.4)	2 (4.1)
	Medium	6 (5.6)	3 (3.3)	3 (3.1)
	Large	6 (8.9)	6 (5.3)	7 (4.9)
High predation risk (OS)	Small	6 (7.3)	4 (2.9)	9 (8.8)
	Medium	5 (3.1)	0 (1.2)	3 (3.7)
	Large	4 (4.6)	2 (1.8)	6 (4.9)
Proportion of departures (both feeders)	Small	46%	23%	31%
	Medium	55%	15%	30%
	Large	32%	26%	42%

IS: Pearson chi-square test: X^2_4 = 4.00, P = 0.41

OS: Pearson chi-square test: X^2_4 = 3.33, P = 0.50

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A General Linear Model (between effects whole model R^2 = 17.8%, $F_{31,510}$ = 3.57, P < 0.000001; Table 14) showed a significant interaction between sparrowhawk presence and residence status over the body mass of siskins (Fig. 13). However, a similar General Linear Model but only with males with black bib size measured (between effects whole model R^2 = 15.4%, $F_{18,280}$ = 2.82, P = 0.0002) showed no significant interaction between dominance status (estimated from the black bib size) and the presence of the sparrowhawk over the body mass of male siskins (sum of squares = 0.36, $F_{1,280}$ = 0.54, P = 0.46).

Table 14. Results of a General Linear Model with body mass as dependent variable. We specifically tested the effect of *Accipiter nisus* presence on the body mass regulation of resident and transient siskins. N = 542 captures from 510 different individuals.

	Sum of Squares	df	F	P
Intercept	1.08	1	1.50	0.2207
Month	2.01	4	0.70	0.5953
Daily mean Temperature	0.33	1	0.46	0.4965
Time of capture	23.89	1	33.14	<0.0001
A. nisus pres.	3.70	1	5.14	0.0238
Wing length	14.96	1	20.75	<0.0001
Residence	0.00	1	0.00	0.9877
Sex	0.91	1	1.26	0.2625
Age	0.13	1	0.18	0.6713
Month*Residence	2.87	4	0.99	0.4098
Month*Sex	2.76	4	0.96	0.4307
Month*Age	2.88	4	1.00	0.4076
A.nisus*Residence	3.65	1	5.06	0.0249
A.nisus*Sex	2.02	1	2.80	0.0947
A.nisus*Age	0.00	1	0.00	0.9491
Month*Residence*Sex	1.41	4	0.49	0.7445
A.nisus*Residence*Sex	0.15	1	0.21	0.6498
Error	367.65	510		

Figure 13. Mean ± Standard Error of body mass of resident and transient siskins for two periods of the wintering season, one with absence of avian predators and another one with the presence of a sparrowhawk (*Accipiter nisus*) hunting at the study area. *N* = 542 captures from 510 different individuals.

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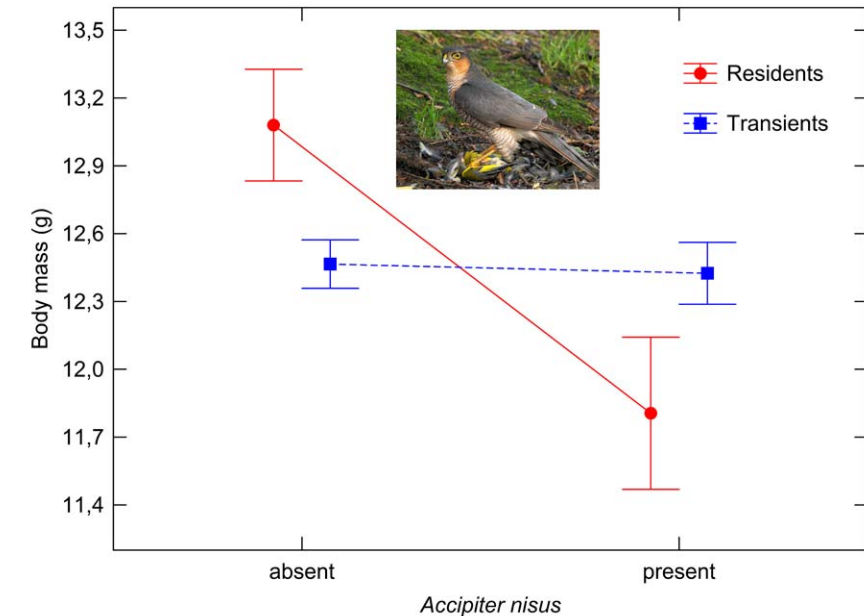
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Photo 8. Couple of males involved in a high-intensity struggle. Male siskins start the fight by opening the wings and beak towards the receiver, and if it does not surrender the two individuals stand one in front of the other the more stretched as possible, trying to have the head and beak above the adversary (and maybe showing their black bib size). If there is not a winner, then they lift the flight trying to be above the fighting mate and crush it with its beak until it flees.

■ TOPIC 1: VIGILANCE AND ENVIRONMENTAL FACTORS: PREDATION RISK AND COMPETITION

Vigilance strategies

At all the feeders, we found that % of time scanning was highly correlated with mean scan and inter-scan durations (which were poorly correlated to each other). However, % of time scanning was not correlated to scan rate. This means that siskins adjusted their level of vigilance by modifying mean scan and inter-scan durations, rather than the frequency of scans. These two variables have rarely been measured simultaneously in previous studies (e.g. Ekman 1987; Carrascal et al. 1990; Pöysä 1994), so many of them have probably lost an important piece of information about the effects of the different studied factors on vigilance. In fact, some studies reporting no effects of some factors on vigilance (e.g. flock size, food density, distance from cover; Barnard 1980b; Elgar et al. 1986; Saino 1994; Slotow & Coumi 2000), may be wrong in their conclusions, as birds may change vigilance strategies without altering the total amount of time spent scanning or the scan rate. Moreover, as a change in mean scan

duration and/or mean inter-scan duration may imply a correlated change in scan rate, the apparent effects of competition or predation risk over scan rate, quoted in many studies (e.g. Powell 1974; Petit & Bildstein 1987; Cassini 1991), may in fact reflect adjustments of the two key variables (mean scan and inter-scan duration).

Foraging strategies

We found that birds foraging at the low predation risk and low competition feeder (IL) tended to adjust their times on feeder to the pecking rate, so that birds with higher rates tended to remain less time. At the other feeders (IS and OS), birds departed sooner compared to IL because of disturbances and/or aggressions. At these two feeders, the birds with higher pecking rates (and lower % of time scanning) tended to remain there for a longer period of time. It is possible that these were dominant birds, who could keep a higher food intake rate without being displaced by subordinate birds. However, at the high predation risk feeder it could be that they were hungry individuals who were more willing to assume a risk to be caught by predators (Kotler et al. 2004).

Pecking rate was negatively correlated to % of time scanning and to mean scan duration, so that the most vigilant birds had a lower food intake rate. This applied to all three feeders. However, we found that an increase in scan rate did not entail a reduction in pecking rate, which supports a previous study showing a higher reduction of food intake rate due to an increase in mean scan duration rather than due to an increase in scan rate (for an equal % of time scanning; Fritz et al. 2002). Pecking rate and scan rate, in fact, were positively correlated at the high predation risk feeder (OS) (in line with the results of Cresswell et al. 2003b).

The effect of competition on vigilance strategy and feeding success

As stated by prediction 1.e, siskins responded to increased competition by increasing their mean scan duration while keeping constant their mean inter-scan duration. Mean scan duration depends both on time spent on vigilance and time spent husking the seeds (Desportes et al. 1990). These behaviours are nonexclusive (Fernández-Juricic et al. 2004), but the time spent husking a seed sets the minimum value for mean scan duration. Since we can assume that handling time is the same at the three feeders, we can interpret the increase in mean scan duration as birds having to be vigilant for both other flock members and predators (Fernández-Juricic et al. 2005).

Given that the absolute number of birds foraging at IS feeder was lower than at IL feeder, the longer mean scan durations at the former could be expected due to a reduction of the flock size (Beauchamp 2008). However, since the number of disturbance departures was the same or even higher at IL than at IS (see Table 2), it seems that the perceived flock size at IS was the same as at IL due to the proximity of the birds waiting around IS (many of them at less than 2.5m, on the almond tree, inside the visual range of birds; Fernández-Juricic et al. 2007). Therefore, the increase in mean scan durations probably reflects an increase in interference competition rather than a reduction in the number of birds scanning for predators.

The 'long scans' vigilance system at IS, combined with the higher rates of aggression found at this feeder, implied a reduction in pecking rate, as the birds had to spend a lot of time being vigilant and fighting. As we pointed out before, this system is more costly than increasing scan rate (Fritz et al. 2002). Moreover, competition involved a high reduction in time on feeder, because birds were ejected from the feeder by aggressions of conspecifics. Therefore, we may conclude that competition decreases the food intake per visit to the feeder, supporting the prediction 1.f.

The fact that the costs of group foraging were found at the small but not at the large feeder, despite the much higher number of birds foraging on the latter, demonstrates that these costs are related to interference competition rather than to the group size itself. Therefore, our results do not contradict the general rule of an increase in food intake rate with group size (Beauchamp 1998). In fact, our results correspond to the conclusions of other studies reporting a reduction in food intake rate with increasing flock size when there is a concomitant increase in interference competition between flock members (due to a small feeder size (Elgar 1987), an increase in seed density (Johnson et al. 2001) or because of foraging in small defendable food patches (Beauchamp 1998)). Nevertheless, our results do contradict the predictions of the 'competition hypothesis', since increasing competition did not increase pecking rate nor reduce handling time and vigilance (Beauchamp & Livoreil 1997; Lima et al. 1999). However, this apparent contradiction may in fact reflect the absence of scramble competition in our unlimited food supply experiment.

The effect of predation risk on vigilance strategy and feeding success

Birds responded to increased predation risk levels by decreasing mean inter-scan duration while keeping mean scan duration constant, supporting the prediction 1.a and not the prediction 1.c. These results are opposed to those obtained when testing

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the effects of competition, and are in line with the studies reporting a reduction of mean inter-scan durations when increasing predation risk but not with the studies reporting an increase in mean scan durations. Nonetheless, since the different variables are intercorrelated, it is possible that the birds react to a reduction in flock size either by increasing mean scan durations or by reducing mean inter-scan durations. In fact, the studies which reported a change in one variable due to a reduction or an increase of the flock size did not report any change in the other (Elgar et al. 1984; Knight & Knight 1986; Elgar 1989; Carrascal et al. 1990; Carrascal & Moreno 1992; Saino 1994; Roberts 1995). The use of one strategy or the other might depend on the birds' main kind of predator (increase of mean scan duration with stalking predators and decrease of mean inter-scan durations with fast moving predators; Scannell et al. 2001; Bednekoff & Lima 2002; Cresswell et al. 2003a; Whittingham et al. 2004).

Pecking rate did not decrease significantly when increasing predation risk. This could be due to the high correlation found between this variable and scan rate at the OS feeder (Fritz et al. 2002). Here, siskins would be good both at foraging and at detecting predators, as found by Cresswell et al. (2003b) and in accordance with the prediction 1.b. Mean inter-scan duration has a minimum value due to the handling constraint (i.e. the minimum time needed to obtain a seed from the feeder; Lendrem 1983). It is likely that both mean scan and inter-scan durations were set to the minimum at the high predation risk feeder (OS) in order to minimise the effects of vigilance on feeding success while optimising the vigilance to predators.

Time on feeder decreased, both because of the higher rates of disturbances and the higher aggression rates, supporting the prediction 1.d. Therefore, the reduction in times on feeder was not voluntary. If we had only taken into account pecking rates and not time on feeder, we would have concluded that predation risk does not affect foraging success, while in fact it does have an impact by reducing time on feeder. This illustrates the importance of taking both variables into account when studying foraging success.

Photo 9. Male siskin in an agonistic display showing its long tail yellow stripe..

■ TOPIC 2: VIGILANCE, PREDATION RISK AND CONSPICUOUSNESS

Plumage brightness

According to the results of the plumage coloration analysis, and supporting the prediction 2.a, we can say that, on average, siskin males were 50% brighter than females, and this value was even higher according to the plumage patch under consideration. The quantitative and objective value of dichromatism obtained in this study by the use of a chromameter is higher than the semiquantitative values obtained by using several observers rating the brightness of birds from bird book illustrations (12% for the siskin; Martin & Badyaev 1996; Badyaev 1997). This difference is probably due to the fact that we specifically sampled the yellowish body parts from the back (which we think that are

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the most related to detectability by an avian predator attacking from above) and not all the patches of the siskins' body (neither the blackish patches from the back).

Long-distance detectability

Siskin males were more detectable than females analyzing the four habitats found in our study area together. However, analyzing the four habitats individually, the difference in detectability between sexes was only significant at the fruit orchards habitat, and at the grasslands habitat there was not any difference in detectability between them. At the forest and the plowed lands males tended to be more detectable, and we would probably find significant differences with a higher sample size. The orchards area is dominated by green and gray colours. Since the grayish-white colour of females is similar to the one of the trunks of many fruit trees, females are probably less detectable at the fruit orchards. This suggests that with greenish backgrounds grayish-white (females) and yellow (males) colours are similarly detectable, while with brown backgrounds yellow tends to be more detectable than grayish-white. Hence, our results support the conclusions of Götmark & Hohlfält (1995) in that conspicuousness of a particular colour in natural conditions highly depends on the background.

It is important to point out that in social foraging species the important factor is short-distance detectability. If wing and tail yellow patches of males are brighter, more saturated and have a larger extent (Senar et al. 2005) than the ones of females, we expect birds of prey to turn their attention to males when close to a flying flock of siskins. According to the confusion effect (Pulliam & Caraco 1984), and in this case, they should most probably be easier to isolate than the duller mass of females and, therefore, they should be more suitable to be pursued by the bird of prey. However, we cannot exclude the possibility that the contrast between bright yellow and black patches may serve an antipredator function (as found in pigeons by Palleroni et al. 2005).

Vigilance, time on feeder and proportion of males at the feeders

Males spent roughly the same proportion of time scanning as females, but males used a vigilance strategy with shorter mean inter-scan durations than females, especially at the feeder with high predation risk (OS), supporting the predictions 2.d and 2.e and contrary to the predictions 2.c and 2.f. This should allow males to detect the predator sooner than females (Hart & Lendrem 1984). Although at the time of an attack the whole foraging flock departs, the birds which are vigilant (both the birds that detect the predator and the non-detector ones) flush to cover sooner

than non-vigilant birds, and therefore they have higher chances of escaping from the predator (Lima 1994). On the other hand, male and female siskins did not differ in times on feeder, but the proportion of males on the high predation risk feeder (OS) was lower than on the other feeders, supporting the prediction 2.d and contrary to the prediction 2.c. Therefore, wintering siskins seem to behave as expected if males 'perceive' or have some 'evolutionary knowledge' that they are in higher predation risk than the less bright females. This supports the Darwin view of a predation cost to plumage brightness (Darwin 1871; Slagsvold et al. 1995). The trend may be reversed during the breeding season for those species in which females incur a high parental investment (e.g. chaffinches *Fringilla coelebs*; Götmark et al. 1997), although given that in cardueline finches males provide most of food to the breeding female and a great deal of parental investment (Newton 1972; Badyaev 1997) the trend for siskins may be similar in both seasons. In spite of their low predation risk, females would still be cryptic in order not to be seen in the nest during the incubation period, or maybe because they are not subject to sexual selection favouring brightness.

Discrimination of conspicuousness and dominance effects

Male and female wintering siskins do not only differ in plumage brightness but also in social positions (Senar 1985). In fact, in our study we found that females received more aggressions than males, although sexes did not differ either in percentage of time spent in aggressions, pecking rate or hopping rate. A difference in dominance can have an important influence in vigilance rates (e.g. Waite 1987a; Waite 1987b). However, we have many reasons to believe that dominance does not account for our results. On the one hand, differences between sexes were found in inter-scan duration, the variable most related to predation risk, and not in scan duration, a variable more related to competition (Hart & Lendrem 1984; Knight & Knight 1986; Knight & Skagen 1988; Pascual & Senar 2013), supporting the prediction 2.e and contrary to the prediction 2.f. On the other hand, differences between inter-scan durations of male and female siskins were found in the pooled data and in the high predation risk feeder, but not at the high competition feeder. The differences found in the proportion of males between feeders could be related to dominance and not to predation risk. However, we found no differences in this proportion between the high and the low competition feeders near protective cover, while the percentages of males for both were higher than at the high predation risk feeder. Finally, we found that the more brightly coloured was a resident male (longer tail yellow stripe, with a lighter

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yellow colour) the more time it spent in vigilance, and marginally the shorter were its inter-scan durations, in line with the prediction 2.g and contrary to the prediction 2.h. Carotenoid coloration in siskins is related to mate choice but not to dominance status (Senar & Escobar 2002; Senar et al. 2005), which in this species is signalled by the black bib size in males (Senar & Camerino 1998), and therefore we cannot expect the relationship we found between carotenoid coloration and vigilance to be related to competition. Moreover, we found a high correlation of vigilance with tail yellow coloration but not with bib area, and we can expect the former to be much more related to detectability by an avian predator attacking a flying flock of birds. If the difference between sexes in vigilance was related to competition, we would have expected to find the opposite trend (a higher correlation with bib area).

Unprofitability

The escaping stage of a bird is mainly related to take-off speed and manoeuvrability (Witter et al. 1994; Metcalfe & Ure 1995). Since male and female siskins did not differ in wing loading (contrary to prediction 2.b), then males and females are not expected to differ in their profitability. Moreover, it is not likely that males were more distasteful than females (Götmark 1992; Götmark & Unger 1994), because males were the most common prey of the sparrowhawk hunting in our study area (see below).

Prey selection by the sparrowhawk present in the study area

Males were taken more often than females when compared to expectation based on the sex ratio of the foraging flocks, supporting prediction 2.i and contrary to prediction 2.j. This is not in itself a demonstration that siskin males are more hunted than females by sparrowhawks in general, since the sample unit in such a predation study should be sparrowhawks and not prey (Götmark & Post 1996). However, the obtained result is in accordance with that from the analysis of vigilance rates and the view that plumage brightness involves a predation cost.

Photo 10. Flying juvenile sparrowhawk. This species is the main predator of siskins in the wild.

■ **Topic 3: Vigilance, predation risk and residence**

Subpopulation distribution between feeders

The proportion of transient siskins increased with distance to protective cover in males but not in females, giving a partial support to prediction 3.a. However, this result could easily be interpreted in terms of subordination. Males were probably more affected by competition in a feudal species like siskins (Senar & Domenech 2011). The displacement of subordinates to food patches more exposed to predation is common in many species of small forest birds (Koivula et al. 1994; Carrascal & Alonso 2006). In any case, the fact that this tendency was found in the comparison between resident and transient males and not in the comparison between dominant and subordinate transient males (see Topic 4), suggests that there was some effect of unfamiliarity, too. In Topic 2 we found that males had higher frequencies at the low predation risk feeder. Considering all these results together, the most straightforward interpretation is that male resident siskins, dominant and familiar with the area, tried to feed at the safest feeder, which was also characterized by high competition levels. They probably displaced females (both transient and resident) and transient males

(both dominant and subordinate) to the riskiest feeder. Therefore, our results seem to be better explained by combining both the dominance and familiarity advantages of residence.

Differences between subpopulations in vigilance and foraging strategies

Resident and transient siskins did not differ in % of time allocated to vigilance. This was contrary to the prediction 3.a of a higher vigilance in transients as a way to compensate for their higher predation risk due to unfamiliarity with the area (Lind & Cresswell 2006). When increasing predation risk, transient siskins highly reduced time on feeder but only slightly increased % of time spent scanning and even increased pecking rate. On the other hand, residents showed a lower reduction in time on feeder but a higher increase in % of time spent scanning and a reduction in pecking rate. These results probably reflect a different strategic response to the increase in predation risk between resident and transient siskins. Residents know the predation risk of the area and the direction from which an attack may come (Hinde 1956). Therefore, for them the vigilance is a very effective way to reduce predation risk, and so they highly increase vigilance to predators at the cost of reducing pecking rate. On the other hand, transients are unfamiliar with the foraging area, so the vigilance for them is less effective and hence they prefer to reduce foraging bouts and this way to reduce the probability of encounter with predators (Newman et al. 1988; Endler 1991). This is in line with what Lima (1987a) found in house sparrows (*Passer domesticus*), which increased pecking rate and reduced vigilance with distance to cover when the distances were too long to make escape likely in case of an attack and when there were visual obstructions that prevented predator detection (i.e. when vigilance was not useful).

Resident and transient siskins used different vigilance strategies. Residents showed a vigilance system with higher scan rates, as expected by prediction 3.b. This allowed them to reduce predation risk while maintaining the pecking rate (and therefore being good foragers and also good in detecting predators; Cresswell et al. 2003b). This is the same vigilance system that showed dominant males in comparison to subordinates (see Topic 4). However, in that study the higher scan rate of male dominants was mainly associated to their shorter inter-scan durations (probably to detect sooner an approaching predator; Hart & Lendrem 1984; Whittingham et al. 2004), while dominants and subordinates did not differ in mean scan duration. On the other hand, in the present study the higher scan rate of residents was associated to both their shorter scan and inter-scan durations. Considering that the longer scans

of transients were found at all the feeders (and not especially at the high competition feeder) and that the residents were only a small percentage of the foraging birds (11% and 21% at the OS and IS feeders, where we could estimate it; 23% in Senar et al. 1992), we think that the longer scans of transients found in this study were related to their need to scan a broader area because of their ignorance about the direction of a possible attack (Desportes et al. 1991) and not to the need to keep residents under surveillance (Knight & Knight 1986; Knight & Skagen 1988). This finding gives support to prediction 3.a.

Predation-risk related costs of transience

Our results provide much evidence for a cost of transience in terms of predation risk. Transients vigilance and feeding behaviour made them more vulnerable to the attacks of predators because of their longer foraging bouts (Barta et al. 2004), longer inter-scan durations (Hart & Lendrem 1984; Whittingham et al. 2004) and lower scan rates (Cresswell et al. 2003b). In addition to these costs, unfamiliarity with the foraging area probably makes them even more vulnerable in terms of ignorance about the type of predators (Frair et al. 2007), escape routes (Clarke et al. 1993; Hoogland et al. 2006) and safety zones (Koivunen et al. 1998; Yoder et al. 2004). Another reported cost of transience is related to body mass regulation (see Topic 5). Transient siskins keep lower body reserves than residents throughout the wintering season (Senar et al. 1992) and they do so irrespective of the access to food sources (Senar et al. 2001). However, residents are able to adjust their body reserves to the actual predation risk at the area, reducing it when increasing predation risk, while transients are not, probably because of their unfamiliarity with the area. Considering all these handicaps of transience together, and also given the fact that these birds form three quarters of the population (Senar et al. 1992), we expect the dilution effect (Bertram 1978) to highly benefit residents. That is probably why these siskins give contact calls to attract transients (Senar & Metcalfe 1988). These birds, in turn, would still benefit from the association with residents because of their knowledge about the food sources (Clark & Mangel 1984) and predators (Desportes et al. 1991) at the area.

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Photo 11. Male siskin showing the melanin-based black bib below the beak, which is a reliable signal of dominance in this species.

■ TOPIC 4: VIGILANCE, PREDATION RISK AND PERSONALITY

In this study of wintering siskins we found that a plumage coloration signal (the black bib), which is positively correlated to exploratory behaviour (Mateos-González & Senar 2012), aggressiveness (Senar & Domenech 2011) and dominance (Senar et al. 1993) (i.e. proactive personality trait; Sih et al. 2004), was also related to anti-predatory vigilance behaviour. However, vigilance was not found to be a carryover of a behavioural syndrome, in terms of a non-adaptive product of the personality trait (Sih et al. 2004), but rather it was found to be flexibly adjusted to the predation risk faced by birds (Couchoux & Cresswell 2012). We found that male siskins reduced the inter-scan duration, increased the scan rate and reduced the foraging bout lengths in response to an increase in predation risk (i.e. from the low to the high predation risk feeders: see Topic 1).

In line with the prediction 4.b, and contrary to the prediction 4.a, we found that large bib males (i.e. proactive individuals), as compared to small bib males (i.e. reactive individuals), adopted a vigilance strategy (i.e. shorter inter-scan durations

and higher scan rates) that reduced the predation risk by reducing the time to detect a predator attack (Cresswell et al. 2003b).

The departure reasons of male transient siskins did not significantly differ between bib size categories, but the birds with large bibs showed the highest proportions of disturbance departures. Therefore, these results also provide some support to the prediction 4.b, and would probably be significant with a higher sample size.

The large black bib siskins enhanced their vigilance to predators in a way that was not costly in terms of foraging efficiency, as found by Cresswell et al. (2003b) for chaffinches (*Fringilla coelebs*). They did not increase the proportion of time spent scanning and they did not reduce either the pecking rate or the foraging bout lengths as compared to small black bib males. Additionally, in spite of the feudal social system of siskins (Senar & Domenech 2011), males with large black bib size (i.e. dominants) did not show a higher proportion of time spent in aggressions than subordinates at none of the two feeders, and showed (non-significant) lower frequencies of aggression-driven departures. All these findings together suggest that in siskins, proactive males were both good at foraging and at detecting predators (Cresswell et al. 2003b).

The proportion of bib size categories was not found to be different between feeders, and therefore the large black bib size siskins did not avoid the high predation risk feeder. In terms of boldness (Réale et al. 2007), we should expect them to be more prone to feed on the high predation risk feeder (Carter et al. 2010). It could be said that in terms of dominance we should expect the opposite (i.e. that small bib size subordinates were displaced to the riskiest foraging patch; e.g. Ekman 1987; Koivula et al. 1994). However, small bib size siskins, while subordinates to large bib size males, were dominant over female siskins and over male and female serins (*Serinus serinus*) (Senar & Domenech 2011) foraging with them. Therefore, in fact they were not expected to be relegated to the high predation risk patch. The lack of difference between bib size categories in the proportion at both feeders probably reflects the combined effects of boldness and compensation of predation risk in male transient siskins, giving some additional support to the prediction 4.b. On the other hand, it could reflect the effect of group cohesion in this gregarious species (i.e. that the siskins tend to feed with flock companions irrespective of the predation risk of the patch) or the fact that transient males, both with large and small bib size, were subordinate to resident males, which were found to avoid the high predation risk feeder (see Topic 3).

Our results are opposite to the findings of Jones & Godin (2010) for juvenile convict cichlids (*Amatitlania nigrofasciata*), where fast explorer individuals were shown to be slow reactors to a predator attack. However, they are in accordance with the

findings of Godin & Dugatkin (1996) for the Trinidadian guppies (*Poecilia reticulata*). In this species, conspicuous individuals are preferentially attacked by cichlid fish predators, and they compensate for this handicap by having a higher inspection rate of predators (i.e. by being bolder, but in fact deterring a predator attack) and having a longer flight initiation distance. Therefore, to be bold in the sense of having a lower anxiety in the presence of predators (or risk-aversion), does not imply to be reckless. In siskins, small bib size individuals were found to have a higher metabolic rate in daylight but not in darkness than large bib size males (Senar et al. 2000), which may in fact indicate that they have a higher anxiety, like drab guppy males. Carter et al. (2012) studying wild chacma baboons (*Papio ursinus*) found that the response of individuals to a threat (a model snake) was driven by anxiety and not by exploratory behaviour (i.e. the response to a novel object), which were different (uncorrelated) traits. However, in their discussion they commented that in rats and mice anxiety correlated negatively with aggressiveness and exploratory behaviour. Therefore, we think that being fast explorer and bold should not be confounded by being reckless or incautious, but with having a lower anxiety in front of novel or risky situations, respectively, which in fact may be useful for reducing predation risk.

Photo 12. Male sparrowhawk scanning for prey. Vigilance strategies of birds are different depending on predator strategy. Sparrowhawks are usually fast moving predators, although sometimes they also may stalk, like in this picture.

■ TOPIC 5: BODY MASS REGULATION, PREDATION RISK AND RESIDENCE

We found that resident siskins foraging at the study area reduced their body mass between a wintering period without avian predators (November-mid January) and a wintering period with the presence of a sparrowhawk regularly hunting (end of January-March), supporting the prediction 5.a. This pattern, however, was not found in transient siskins foraging at the study area together with residents, since their body mass did not vary between the two periods of the wintering season, supporting the prediction 5.b and contrary to the prediction 5.c. In our model we considered wing length and month in order to correct body mass for the confounding effects of body size and phenology (Senar et al. 1992). In the winters of 1985-86 and 1988-89 the body condition (i.e. body mass divided by the third potency of wing length) of resident and transient siskins was studied in the same ringing station with the same feeders and the same methodology of capture (Senar et al. 1992). In that winters, no avian predators were observed in the study area in 78 capture days, and resident and transient siskins showed exactly the same phenological pattern in body condition throughout all the wintering season, with no reduction at all of the body condition of

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residents as compared to transients from November-mid January to the end of January-March (Senar et al. 1992). Therefore, both the reduction in body mass between these two periods found in this study in residents but not in transients, and the absence of this pattern in two wintering seasons without the presence of avian predators, strongly suggest (although accepting the limitations of our correlational study) that there was a direct link between this reduction of body mass and the predation risk related to the absence/presence of the sparrowhawk. According to that, resident siskins in our study reduced their body mass probably in order to improve their flight performance and as a result to reduce their probability of capture (Hedenström 1992; Witter et al. 1994; Kullberg et al. 1996; Burns & Ydenberg 2002).

Additionally, our findings give support to the hypothesis that residence, in providing familiarity with the area, may improve predator avoidance (Hinde 1956). Resident wintering siskins, which remain in the same area for several weeks or months (Senar et al. 1992), have a good knowledge of the actual predation risk, and therefore can adjust their body reserves accordingly. On the other hand, transients, which spend all the wintering season continuously moving from one foraging site to the other, remaining at each site for only a few hours or days (Senar et al. 1992), are not aware of the predation risk at each location where they feed, and therefore cannot adjust their body reserves specifically. Our results are in line with Yoder et al. (2004), who found in the ruffed grouse (*Bonasa umbellus*) a predation cost of site unfamiliarity and suggested that it was related to a reduced ability to locate cover or a willingness to inhabit dangerous areas.

The better body condition of residents in the 1985-86 and 1988-89 winters was interpreted in terms of a dominance advantage of residents over transients (Senar et al. 1990), or alternatively to a need of transients to be 'lean and fit' (Schultner et al. 2013) in order to reduce energetic costs of flight associated to their nomad life style (Senar et al. 1992). In view of the results of the present study, we suggest another possible explanation related to body mass regulation according to the predation and starvation risks hypothesis (Lima 1986; McNamara & Houston 1990). When facing a low predation risk at the foraging area, residents could keep high body reserves and this way increase their probability of overnight survival, something that transients foraging in the same area could not do because they ignore the risk of predation of the area.

Alternatively, it could be said that transients could determine the predation risk of the area by observing the vigilance behaviour of residents (as suggested by Desportes et al. 1991), and that the advantages of residents over transients in terms of body mass regulation found in this study were related to the fact that residents

are dominant over transients (Senar et al. 1990). Dominant birds, because having a more predictable access to food sources, can keep lower body reserves in front of a high predation risk than subordinates, especially when weather conditions are mild (Clark & Ekman 1995; Gentle & Gosler 2001; Ekman 2004; Krams et al. 2010). Therefore, the lack of reduction of body mass observed in transients with the presence of the hawk, could be the result not of their ignorance about the predation risk of the area but of their higher concern in reducing starvation risk. However, we found no differences in the relationship between body mass and dominance (estimated from the black bib size in males; Senar et al. 1993; Senar & Camerino 1998) with the absence and presence of predators, supporting the prediction 5.e and contrary to the prediction 5.d. Moreover, in another study (see Topic 3) we found that transient birds showed a different vigilance and foraging strategy than residents. Therefore, we strongly believe that the difference between residents and transients is related to the knowledge of the actual predation risk of the area and not to the different level of dominance.

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General Discussion

Siskins foraging at feeders in our study area adjusted their vigilance behaviour specifically to the environmental conditions. Hence, vigilance was not the outcome of a behavioural carryover (Sih et al. 2004) but a variable optimally adapted to current environmental conditions (e.g. Couchoux & Cresswell 2012). Siskins' vigilance strategy while foraging was very different when they were mainly concerned in scanning for predators than when they primarily monitored competing flock companions. Vigilance to predators was related to short inter-scan durations (e.g. Hart & Lendrem 1984; Whittingham et al. 2004) and high scan rates (e.g. Cresswell et al. 2003b), while vigilance to flockmates was related to long scan durations (e.g. Knight & Knight 1986; Knight & Skagen 1988). The increase in vigilance through shortening of inter-scans was done at no cost in terms of pecking rate (Cresswell et al. 2003b). However, the increase in vigilance through lengthening of scan durations implied a correlated reduction in food intake rate. Time on feeder was reduced both by competition (i.e. aggression related departures) and predation risk (i.e. disturbance related departures).

Siskin males were on average 50% more brightly coloured and were more detectable (to humans) than females, while sexes did not differ in wing loading. Proportion of males was lower at the high predation risk feeder. Males had shorter mean inter-scan times than females, especially at the higher predation risk feeding site (that was avoided by them). Yellow tail stripe length and brightness of males were positively correlated with proportion of time spent scanning. The sparrowhawk hunting at the study area took 25% more males than expected from the sex ratio found at the feeders. All these data reject the hypothesis that plumage brightness was an aposematic signal of unprofitability (Baker & Parker 1979; Endler 1991), and supports the view that conspicuousness implies a cost in terms of increased detectability to predators (e.g. Montgomerie et al. 2001; Huhta et al. 2003).

The proportion of transient siskins increased with distance to cover in males but not in females, probably because resident males displaced subordinate females and male transients from the safest feeder. Transient siskins did not allocate more time to vigilance than residents, and even increased pecking rate with distance to cover, while residents did the opposite. However, transients reduced foraging bouts more than residents with distance to cover. These different strategies probably reflect the different usefulness of vigilance to both categories of birds (Lima 1987a). Transient siskins showed a vigilance system with longer inter-scan durations, lower scan rates and longer foraging bouts, which probably increased their vulnerability to a predator attack. They also showed longer scan

durations, probably in order to scan a broader area owing to their unfamiliarity with the area (Desportes et al. 1991). Our results support the existence of predation-related costs of transience associated both to unfamiliarity with the area (e.g. Yoder et al. 2004; Hoogland et al. 2006) and subordination to residents (e.g. Matthysen 1993).

Proactive large black bib male siskins showed a vigilance system with shorter inter-scan durations and higher scan rates than reactive siskins. Therefore, they compensated for the higher predation risk associated to their behavioural trait with a vigilance strategy which improves the detection of a predator attack (Godin & Dugatkin 1996), although they did not avoid the high predation risk feeder as predicted (maybe because of the compensation of the boldness and dominance effects; Koivula et al. 1994; Carter et al. 2010). This anti-predatory vigilance system did not imply a reduction in food intake rate, so that proactive birds were both good at detecting predators and at foraging (Cresswell et al. 2003b). These results show that proactive individuals do not have to necessarily pay a predation cost, and therefore that being fast explorer and bold does not imply to be reckless.

We found that resident siskins reduced their body mass with the presence of a sparrowhawk hunting at the area, while transients did not. Since in a previous study with no avian predators at the study area it was found that the difference in body condition between residents and transients did not vary throughout the wintering season, we can confidently say that the reduction in body mass observed in this study was directly linked to the presence of the hawk. This reduction was not associated to the dominance of residents over transients but to their familiarity with the area, showing an advantage of residence to transience related to the possibility to regulate body mass in function of the actual predation risk at the area. Our results strongly support the mass-dependent predation hypothesis (McNamara & Houston 1990; Gosler et al. 1995).

■ LOOKING FOR TRANSVERSE PATTERNS: A DISCUSSION ON THE EFFECT OF DOMINANCE

It is possible to interpret the results of every topic of this thesis independently, as we did before, or to try to find transverse patterns. The main general trend arising from the comparisons for sex, residence and personality is that dominant siskins (i.e. males, Senar & Domenech 2011; residents, Senar et al. 1990; and proactive large black bib males, Senar et al. 1993; Mateos-González & Senar 2012) used a vigilance strategy

with shorter inter-scan durations and higher scan rates (see Table 15). Short inter-scans allow birds to detect sooner the attack of an avian predator (Hart & Lendrem 1984; Whittingham et al. 2004), and in fact we found in Topic 1 that siskins reduced inter-scans when increasing predation risk (Fig. 7b). Moreover, the reduction in inter-scans by dominant siskins was achieved by increasing scan rate and without increasing % of time spent scanning, so that they could maintain pecking rate (Table 15). This strategy allowed dominant siskins to be good both at foraging and at detecting predators, as reported for the chaffinch (*Fringilla coelebs*) by Cresswell et al. (2003b).

Table 15. Summary of the results of the topics 2, 3 and 4 for the vigilance and foraging variables. Significant differences are highlighted. Notes show result statistics of Repeated Measures ANOVAs for the comparisons not included in the topics.

Variable	Males (in residents)				Residents				Proactive (in transients)			
	All	IS	IL	OS	All	IS	IL	OS	All	IS	IL	OS
Proportion at feeders		higher	higher	lower		higher (males)	no data	lower (males)		equal	no data	equal
% of time scanning	equal				equal				equal			
scan rate	higher[1]				higher				higher			
mean scan duration	equal				shorter				equal[2]			
mean inter-scan duration	shorter	equal	shorter (ns)	shorter	shorter				shorter			
pecking rate	equal				equal		R: IL>OS, T: IL<OS		equal			
time on feeder	equal	equal	equal	equal	shorter		much shorter		equal			

[1] $F_{1,33} = 5.77$, $P = 0.022$

[2] $F_{1,38} = 0.44$, $P = 0.510$

If subordinate siskins (i.e. females, transients and small black bib reactive males) did not show this optimal vigilance system was probably because they could not. Cresswell et al. (2003b) suggested that the key parameter in foraging behaviour was feeding rate and not vigilance, so that individuals with high scan rates and short inter-scan durations were in fact individuals with short searching for food and handling food times. Good foragers would be individuals with higher competitive ability because of differences in morphology and experience. In our study, however, males were not expected to have more experience than females, and large bib size males were not expected to have a different morphology than small bib size males. Moreover, the feeders were filled

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with thousands of seeds, so we did not expect differences in searching time between individuals. Maybe handling time could differ between residents (used to husk turnip seeds provided at feeders) and transients, but not between males and females. Therefore, we strongly believe that the differences found in this study between groups were related to vigilance and not to feeding skills. Subordinate individuals could be forced to maintain long mean scan durations to keep flockmates under surveillance, which did not allow them to increase scan rates. Or they could not reduce inter-scans because while with the head-down (i.e. while searching for food) they could still have to pay attention to flockmates with the lateral vision (Fernández-Juricic et al. 2005), but at the cost of being slower in searching for food (Fernández-Juricic et al. 2004).

Although in Topic 1 we found that the effect of interference competition was an increase in mean scan durations (Fig. 6b; Knight & Knight 1986; Knight & Skagen 1988), and therefore the vigilance to flockmates in addition to the vigilance to predators (Fernández-Juricic et al. 2005), the dominant siskins did not seem to take an advantage in terms of an increase in pecking rate by a reduction in the duration of scans, but in terms of a reduction in predation risk by reducing the duration of inter-scans. These results seem to be contrary to the view that proactive individuals prioritize feeding (i.e. reducing starvation risk) to predation risk (Smith & Blumstein 2007; Biro & Stamps 2008; Carter et al. 2010). However, opposite to the view of behavioural carryovers associated to behavioural traits (Sih et al. 2004), and as found by Couchoux & Cresswell (2012) for the redshanks (*Tringa totanus*), birds can adjust vigilance in a flexible way to the riskiness of the situation. Dominant and subordinate birds will show a completely different body-mass regulation in function of the environmental conditions (Ekman 2004), as in fact we found in Topic 5 (see Fig. 13). Therefore, if dominant siskins in our study faced a low starvation risk and a high predation risk, then it is not surprising that they prioritized vigilance rather than feeding. And this is probably what happened in our study area, since temperatures were mild (monthly mean temperature: January: 8.0ºC, February: 11.6ºC, March: 13.7ºC; data from Observatori Fabra meteorological station) and food availability and predictability were high (since we provided it in abundance throughout the winter).

In any case, we do not think that dominance alone can account for our results. In Topic 2, we found that the more brightly coloured was a male, the more time it spent in vigilance and marginally the shorter were its inter-scan durations. Since brightness in this species is related to carotenoid coloration, which is not related to dominance but to mate choice (Senar & Escobar 2002; Senar et al. 2005), these results must be explained in terms of the relationship between conspicuousness and predation risk. In Topic 3 we found that transients showed longer mean scan

durations than residents, something that was not found in the comparisons between sexes and personalities, supporting the view that they had to scan for a broader area since they did not know the direction from which an attack could come (Hinde 1956). Moreover, we also found an interaction between pecking rate and feeder when comparing residents and transients, which was not found in the comparisons between sexes and personalities. Transients prioritized a reduction in foraging bouts when increasing predation risk even increasing pecking rate, while residents prioritized an increase in vigilance at the cost of reducing food intake rate. These different strategies were probably related to the different usefulness of vigilance to both groups (Lima 1987a), in accordance with the site familiarity effect, and could not be explained in terms of dominance relationships. Finally, in Topic 5 we saw that residents adjusted body mass to the presence of a sparrowhawk hunting at the area while transients did not, and this could not be attributed to dominance relationships since we did not find such a pattern when comparing large black bib to small black bib males.

Therefore, only the comparison between personalities (i.e. between males differing in the size of the black bib) can be exclusively attributed to the effect of dominance (Senar & Camerino 1998). In the comparisons between males and females and between residents and transients there are also important effects of conspicuousness and site familiarity, respectively. And even in the comparison between black bib size categories, we think that it is better to focus on personality since dominance is not an individual character but the result of the interaction between personality and the social environment (Dingemanse & de Goede 2004). This is the reason why the Topics focused in the effects of conspicuousness, site familiarity and personality instead of focusing on the effect of dominance, although this was taken into account in all of them when it was considered relevant.

Conclusions

- Siskins foraging at feeders in our study area adjusted their vigilance behaviour specifically to the environmental conditions.

- Siskins' vigilance strategy while foraging was very different when they were mainly concerned in scanning for predators than when they primarily monitored competing flock companions.

- Vigilance to predators, related to an increase in scan rate and a reduction in inter-scan durations, was less costly in terms of food intake rate than vigilance to flockmates, related to an increase in scan durations.

- Siskin males were more brightly coloured and more detectable than females, and showed a vigilance system more oriented to the reduction in predation risk, supporting (together with the correlation found between coloration and vigilance in males) the view of a predation cost of conspicuousness.

- Resident and transient siskins showed a different vigilance and foraging strategy. Residents were more confident in vigilance to reduce predation risk while transients preferred to reduce foraging bout lengths. Transient siskins were in higher predation risk than residents according to their vigilance and foraging behaviour, and this was related both to their unfamiliarity with the area and their subordination to residents.

- Proactive male siskins showed a vigilance system that improved their ability to detect predators as compared with reactive males, supporting the view of a behavioural compensation for the higher predation risk associated to their behavioural trait. Therefore, to be bold does not imply to be reckless.

- Resident siskin males adjusted their body mass to the presence of predators at the foraging area, something that transients could not do because of their unfamiliarity with the area.

- In general, dominant individuals (whether males, residents and proactive birds) showed a vigilance and foraging behaviour that prioritized predation risk reduction to the increase in food intake rate, which could be expected according to the low starvation risk at the area. Dominants increased vigilance to predators at no cost in terms of food intake rate as compared to subordinates. These birds probably could not adopt this optimal behaviour because they had to be vigilant to flockmates in addition to predators they had to be vigilant to flockmates in addition to scan for predators.

- Dominance alone cannot account for our results, so in spite of the fact that it could have some effect in all the comparisons, it could not remove the effect of conspicuousness and site familiarity.

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■ INTRODUCCIÓ

Quan un ocell s'alimenta al seu hàbitat natural està sotmès a un cert risc de depredació, que depèn de moltes variables (visibilitat, distància a cobert, etc.; veure per ex. Lima 1987a). Per tal de reduir aquest risc, l'ocell en qüestió pot minimitzar el temps d'exposició al lloc d'alimentació (tot maximitzant la taxa d'ingestió d'aliment; Moreno & Carrascal 1991) o bé pot maximitzar el seu nivell de vigilància (a expenses d'una reducció en la taxa d'ingestió d'aliment i, en conseqüència, d'un augment del temps d'exposició al lloc d'alimentació; Fritz et al. 2002).

En aus socials, una altra manera de reduir el risc de depredació és alimentar-se en grups (Elgar 1989). Com més ocells s'alimenten junts, més ulls vigilen ('many eyes effect', Pulliam 1973), en cas d'atac el depredador es confon ('confusion effect', Miller 1922), els individus s'amaguen dins del grup ('selfish herd', Hamilton 1971) i es redueix la probabilitat de captura d'un individu concret ('dilution effect', Bertram 1978). A més, el fet d'alimentar-se en grup pot millorar la capacitat de trobar aliment (a través de l'intercanvi d'informació, Giraldeau 2008). No obstant, en augmentar la mida del grup també augmenta la competència per l'aliment (Beauchamp 1998), de manera que la quantitat total d'aliment ingerit per un cert individu dependrà d'un compromís entre el risc de depredació i la competència.

La majoria dels estudis d'alimentació fets fins ara s'han basat en determinar com varia la vigilància, la taxa d'alimentació i/o el temps al lloc d'alimentació en funció de la mida del grup (Beauchamp 2008), però com que aquesta variable està correlacionada tant amb el risc de depredació com amb la competència, s'han confós els efectes dels dos factors. Un repte important pels investigadors és el de poder discriminar els efectes del risc de depredació i de la competència sobre la vigilància i les estratègies d'alimentació dels ocells. D'altra banda, aquests dos factors no afecten per igual a tots els individus. Per tant, també resulta de molta importància el fet de poder

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determinar com les diferents espècies, sexes, classes d'edat, etc. ajusten el seu sistema de vigilància i d'alimentació a les variables condicions ambientals.

El risc de depredació varia en funció de la coloració del plomatge. Els ocells de colors més brillants i, per tant, més conspicus, sovint experimenten un risc de depredació major que no pas els ocells de colors més apagats (Huhta et al. 1998; Zuk & Kolluru 1998; Hill & McGraw 2006). La majoria d'espècies d'ocells són dimòrfiques, i el dimorfisme sexual en la coloració del plomatge està molt estès (Price & Birch 1996; Hill & McGraw 2006). El dimorfisme sexual està relacionat amb la selecció de parella (Andersson 1994; vegeu però Badyaev & Hill 2003), i per tant és el resultat d'un compromís entre la selecció sexual i el risc de depredació (Darwin 1871; Endler 1983; Butcher & Rohwer 1989; Montgomerie et al. 2001). Alguns autors han postulat una hipòtesi alternativa segons la qual la coloració del plomatge pot actuar com un senyal aposemàtic que indiqui que el ocells de colors vius són més difícils de caçar o menys comestibles (Baker & Parker 1979; Endler 1991). No obstant, aquesta hipòtesi gaudeix de molt poc suport experimental (Huhta et al. 2003).

La personalitat dels ocells també pot afectar el seu risc de depredació. En els últims anys s'han fet molts estudis que han demostrat la importància de la personalitat en el comportament animal (Réale et al. 2007). Es parla sovint de síndromes comportamentals, enteses com "un conjunt de trets de personalitat correlacionats que reflecteixen una consistència comportamental entre individus a l'hora d'afrontar múltiples situacions" (Sih et al. 2004). Així, també es parla d'arrossegaments comportamentals, entesos com a comportaments no òptims davant de situacions concretes provocats per l'existència d'una síndrome comportamental que condiciona la conducta dels animals (Sih et al. 2004). Entre els principals trets de personalitat, destaquen l'atreviment, el caràcter exploratori, l'agressivitat, l'activitat i la sociabilitat (Réale et al. 2007). En molt diversos tipus d'animals s'ha vist que hi ha una correlació entre atreviment, caràcter exploratori i agressivitat (Van Oers et al. 2004; Quinn & Cresswell 2005; Wolf et al. 2007), en el que s'ha anomenat com a personalitat proactiva (Sih et al. 2004). Els animals proactius tendeixen a assumir més riscos i per tant poden estar exposats a un major risc de depredació (Van Oers et al. 2004; Quinn & Cresswell 2005; Jones & Godin 2010). Ara bé, també és possible que adoptin certs comportaments de compensació per tal de reduir aquest major risc (Godin & Dugatkin 1996; Carter et al. 2012; Couchoux & Cresswell 2012).

El risc de depredació que experimenta un individu també pot estar relacionat amb el coneixement que té del territori on s'alimenta (Metzgar 1967; Ambrose 1972; Isbell et al. 1993; Yoder et al. 2004; Frair et al. 2007). Els animals residents en una zona coneixen bé quins depredadors hi ha, d'on vénen i com es comporten (Hinde

1956). Així, poden ajustar la seva vigilància i el seu comportament d'alimentació de tal manera que minimitzin el risc de ser capturats (Metzgar 1967). En canvi, els animals transeünts o nòmades no saben ni quins depredadors hi ha ni com es comporten a les diferents zones per on transiten i s'alimenten, i per tant no poden ajustar el seu comportament d'una manera específica. Si bé poden intentar copiar el comportament dels residents o bé barrejar-se amb ells (Desportes et al. 1991), difícilment podran escapar amb la mateixa eficàcia quan es produeixi un atac.

D'altra banda, el risc de depredació també es veu molt influït per la dominància. Els ocells dominants s'ha vist que desplacen als subordinats a llocs d'alimentació més exposats als atacs dels depredadors (Ekman 1987; Koivula et al. 1994). A més, la subordinació també condiciona la possibilitat d'ajustar el nivell de reserves corporals al nivell de risc. El pes dels ocells resulta d'un compromís entre el risc de depredació i el risc de morir de fam (Lima 1986; McNamara & Houston 1990; Higginson et al. 2012). Com més reserves corporals, més càrrega alar (Witter & Cuthill 1993) i per tant menys capacitat d'enlairada i de maniobrabilitat en vol, i menys capacitat de fugir dels depredadors (Hedenström 1992; Witter et al. 1994; Burns & Ydenberg 2002). Els ocells ajusten el pes corporal al risc de depredació (Gosler et al. 1995; Carrascal & Polo 1999; Gentle & Gosler 2001; Zimmer et al. 2011). Els subordinats, però, no disposen d'un accés predictible i garantit als recursos tròfics, i en conseqüència es veuen obligats a acumular més reserves que els dominants, assumint així un major risc de depredació (Clark & Ekman 1995; Gentle & Gosler 2001; Ekman 2004; Krams et al. 2010).

L'efecte de la competència per l'aliment tampoc no és igual per a tots els individus. Hi ha dos grans tipus de competència, la competència per interferència i la competència per esgotament de recursos (Beauchamp 2009). La competència per interferència està relacionada amb la capacitat de lluitar per la possessió d'un recurs (en el nostre cas, l'aliment), la qual està molt relacionada amb la dominància. La dominància no és un tret de personalitat com a tal, sinó que resulta de la interacció entre la personalitat i l'ambient social (Dingemanse & de Goede 2004). La dominància interespecífica depèn sobretot de la mida corporal (Morse 1978). Per la seva banda, la dominància intraespecífica varia normalment en funció del sexe i de l'edat, de manera que els mascles són dominants respecte de les femelles i els adults respecte dels joves (per ex. Catry et al. 2004; Arizaga & Bairlein 2011; Senar & Domenech 2011). L'efecte de la dominància de sexe sobre l'accés als recursos depèn de l'estructura social de l'espècie, que pot ser de tipus feudal (amb els mascles competint sobretot entre ells) o de tipus despòtic (amb els mascles enfrontant-se sobretot a les femelles; Senar & Domenech 2011). Finalment, la dominància també es veu molt afectada per

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la residència, de manera que els animals que es troben al seu territori són dominants respecte dels intrusos (Cristol et al. 1990; Senar et al. 1990; Dearborn & Wiley 1993).

En la present tesi es pretén testar si els ocells de les diferents categories individuals (sexe, estatus de residència, dominància i personalitat) ajusten les seves estratègies de vigilància, alimentació i regulació de pes a condicions variables de risc de depredació i de competència d'acord amb les prediccions plantejades a partir de la literatura. L'estudi se centra en el lluer (*Carduelis spinus*), un fringíl·lid social sexualment dimòrfic (Svensson 1992; Martin & Badyaev 1996; Badyaev 1997) molt estudiat durant el període d'hivernada a Catalunya. En lluers hi ha dues subpoblacions hivernals, els residents i els transeünts (Senar et al. 1992). En mascles, especialment transeünts, l'estatus de dominància es pot determinar visualment mitjançant la mida del pitet negre que tenen sota el bec (Senar et al. 1993; Senar & Camerino 1998). El pitet negre també està correlacionat positivament amb la personalitat de tipus exploratori/agressiu/proactiu (Mateos-González & Senar 2012). Per tant, aquesta espècie és ideal per tal de determinar l'efecte del sexe, la personalitat (o dominància) i la residència en el comportament de vigilància dels ocells.

■ Resultats, discussió i conclusions

Els lluers del nostre estudi van ajustar el seu comportament de vigilància específicament a les condicions ambientals. Per tant, la vigilància no va ser el subproducte d'un 'arrossegament comportamental' (Sih et al. 2004) sinó una variable òptimament ajustada a les condicions ambientals (veure per exemple Couchoux & Cresswell 2012). L'estratègia de vigilància dels lluers mentre s'alimentaven va ser molt diferent quan estaven dedicats sobretot a la vigilància dels depredadors que quan es dedicaven sobretot a controlar els companys d'alimentació. La vigilància dirigida als depredadors es va veure que estava relacionada amb intervals entre vigilàncies curts (per ex. Hart & Lendrem 1984; Whittingham et al. 2004) i taxes de vigilància altes (Cresswell et al. 2003b), mentre que la vigilància dirigida a companys d'estol estava relacionada amb durades de vigilància llargues (per ex. Knight & Knight 1986; Knight & Skagen 1988). L'increment en la vigilància a través de l'escurçament dels intervals entre vigilàncies no va suposar cap cost en termes de taxa de picoteig (Cresswell et al. 2003b). En canvi, l'increment de la vigilància a través de l'allargament de les vigilàncies va portar associada una reducció en la taxa d'alimentació. El temps d'estada a la menjadora es va veure reduït tant per la competència (sortides per agressions) com pel risc de depredació (fugides per espantades).

El plomatge dels mascles de lluer va presentar una coloració el doble de brillant i més fàcil de detectar (pels humans) que el de les femelles, mentre que els sexes no van diferir en càrrega alar. La proporció de mascles va ser més baixa a la menjadora amb més risc de depredació. Els mascles van presentar intervals entre vigilàncies més curts que les femelles, sobretot a la menjadora sotmesa a major risc de depredació (que com hem vist era evitada pels individus d'aquest sexe). La longitud i brillantor de la banda groga de la cua dels mascles va mostrar una correlació positiva amb el tant per cent de temps dedicat a vigilar. L'esparver que caçava a la zona d'estudi va capturar un 25% més de mascles del que s'esperava d'acord amb les proporcions de sexes observades a les menjadores. Tots aquests resultats refuten la hipòtesi que la brillantor del plomatge sigui un senyal aposemàtic que indica que els individus brillants són poc profitosos pel depredador, i en canvi donen suport a la hipòtesi que la conspicuïtat implica un cost en el sentit de facilitar la detecció dels ocells per part dels depredadors.

La proporció de lluers transeünts es va incrementar amb l'augment de la distància a cobert, segurament perquè els mascles residents van desplaçar les femelles subordinades i els transeünts de la menjadora més segura. Els lluers transeünts no van pas dedicar més temps a la vigilància que els residents, i fins i tot van incrementar la taxa de picoteig amb la distància a cobert, mentre que els residents van fer tot el contrari. No obstant, els transeünts van reduir el temps d'estada a la menjadora més que no pas els residents en augmentar la distància a cobert. Aquestes estratègies diferents probablement reflecteixen la diferent utilitat de la vigilància per a ambdues classes d'ocells (Lima 1987a). Els lluers transeünts van mostrar un sistema de vigilància amb intervals entre vigilàncies més llargs, taxes de vigilància menors i temps d'estada a la menjadora majors, la qual cosa molt probablement va incrementar la seva vulnerabilitat respecte dels depredadors. A més, els transeünts van emprar vigilàncies més llargues, segurament per tal de vigilar una àrea més gran degut al seu desconeixement de la zona (Desportes et al. 1991). Els nostres resultats donen suport a l'existència de costos de nomadisme relacionats amb el risc de depredació, que estarien associats tant amb el desconeixement de la zona (per ex.. Yoder et al. 2004; Hoogland et al. 2006) com amb la subordinació als individus residents (Matthysen 1993).

Els lluers proactius, amb pitets grans, van mostrar un sistema de vigilància amb intervals entre vigilàncies més curts i taxes de vigilància majors que els lluers reactius. Per tant, van compensar el major risc de depredació associat al seu tret comportamental amb un sistema de vigilància que millora la detecció dels atacs dels depredadors (Godin & Dugatkin 1996), malgrat que no van evitar d'alimentar-se a la menjadora amb alt risc de depredació, tal i com havíem previst (potser degut a que el seu major atreviment va compensar l'efecte de la dominància; Koivula et al. 1994;

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Carter et al. 2010). Aquest sistema de vigilància dirigit a detectar aviat l'atac dels depredadors no va implicar una reducció en la taxa d'alimentació, de manera que els ocells proactius van resultar ser bons tant detectant depredadors com alimentant-se (Cresswell et al. 2003b). Aquests resultats mostren que els individus proactius no han de pagar necessàriament un preu en termes de major risc de depredació, i per tant que ser explorador i atrevit no implica pas ser temerari.

Els lluers residents van reduir la seva massa corporal amb la presència d'un esparver caçant a la zona, cosa que no van fer els transeünts. Com que en un estudi previ fet a la mateixa zona i sense depredadors aeris es va trobar que la diferència de condició física entre residents i transeünts no variava al llarg de l'estació d'hivernada, podem afirmar que la reducció en la massa corporal observada en el nostre estudi estava directament vinculada a la presència de l'esparver. Aquesta reducció no estava associada a la dominància dels residents sobre els transeünts sinó al seu coneixement de la zona, mostrant un avantatge de la residència en relació al nomadisme relacionat amb la possibilitat de regular la massa corporal en funció del risc de depredació real a la zona. Els nostres resultats donen un ferm suport a la hipòtesi de la depredació depenent de la massa corporal (McNamara & Houston 1990; Gosler et al. 1995).

Els resultats dels diferents temes que conformen la present tesi es poden interpretar un per un, com hem fet fins ara, o bé es poden buscar patrons transversals a tots ells. La tendència més general que es deriva de les comparacions per sexe, residència i personalitat és que els lluers dominants (ja siguin mascles, Senar & Domenech 2011; residents, Senar et al. 1990; o mascles proactius amb pitets grans, Senar et al. 1993; Mateos-González & Senar 2012) van emprar un sistema de vigilància amb durades dels intervals entre vigilàncies més curtes i amb majors taxes de vigilància (veure Taula 15). Els intervals entre vigilàncies curts permeten detectar aviat els atacs dels depredadors aeris (Hart & Lendrem 1984; Whittingham et al. 2004), i de fet vam veure al Tema 1 que els lluers reduïen aquests intervals quan el risc de depredació augmentava (Fig. 7b). A més, la reducció dels intervals entre vigilàncies per part dels lluers dominants es va assolir mitjançant l'augment de la taxa de vigilància i sense incrementar el tant per cent de temps dedicat a vigilar, de manera que van poder mantenir la taxa de picoteig (Taula 15). Aquesta estratègia va permetre als lluers dominants de ser bons tant alimentant-se com detectant depredadors, tal i com van trobar pels pinsans (*Fringilla coelebs*) en Cresswell i col·laboradors (2003b).

Si els lluers subordinats (és a dir, les femelles, els transeünts i els mascles reactius de pitet petit) no van mostrar aquest sistema de vigilància òptim va ser perquè segurament no van poder adoptar-lo. En Cresswell i col·laboradors (2003b) van suggerir que el que determinava el comportament d'alimentació era la taxa

d'alimentació i no pas la vigilància, de manera que els individus amb altes taxes de vigilància i curts intervals entre vigilàncies eren de fet individus amb curts temps de cerca i de manipulació de l'aliment. D'acord amb aquesta hipòtesi, els individus amb altes taxes d'alimentació serien individus amb una altra capacitat competitiva originada per diferències en morfologia i experiència. En el nostre estudi, però, no era d'esperar que els mascles fossin més experimentats que les femelles, ni que els mascles de pitets grans tinguessin una morfologia diferent que els mascles de pitet petit. A més, les menjadores estaven plenes de llavors, de manera que no era tampoc d'esperar que hi haguessin diferències en els temps de cerca de l'aliment entre uns i altres individus. Podria ser que el temps de manipulació de les llavors fos diferent per a residents (acostumats a pelar les llavors de nap de les menjadores) que per a transeünts, però no era d'esperar que diferís entre mascles i femelles. Per tant, pensem que les diferències observades entre grups estaven vinculades a la vigilància i no pas a les habilitats d'alimentació. Els individus subordinats probablement es van veure obligats a mantenir vigilàncies llargues per tal de mantenir sota control els companys d'estol, cosa que no els va permetre d'incrementar les taxes de vigilància. O és possible que no podessin reduir els intervals entre vigilàncies perquè mentre estaven amb el cap avall (buscant aliment) encara els calia estar atents als companys d'estol amb la visió lateral (Fernández-Juricic et al. 2005), al preu d'anar més lents en la cerca de l'aliment (Fernández-Juricic et al. 2004).

Si bé al Tema 1 vam veure que l'efecte de la competència per interferència era un increment de la durada de les vigilàncies (Fig. 7a; Knight & Knight 1986; Knight & Skagen 1988), degut a la vigilància dels companys d'estol sumada a la vigilància dels depredadors (Fernández-Juricic et al. 2005), les diferències observades entre lluers dominants i subordinats no se centren en una menor durada de les vigilàncies dels dominants (que els permetria tenir una major taxa d'alimentació) sinó en una menor durada dels intervals entre vigilàncies (que els permet reduir el risc de depredació). Aquests resultats semblen contradictoris amb la idea que els individus proactius prioritzen la reducció del risc d'inanició abans que la reducció del risc de depredació (Smith & Blumstein 2007; Biro & Stamps 2008; Carter et al. 2010). No obstant, tal i com van trobar en Couchoux & Cresswell (2012) per la gamba roja (*Tringa totanus*), i en contra de la idea d'un 'arrossegament comportamental' associat a la personalitat (Sih et al. 2004), els ocells poden ajustar la vigilància de manera flexible al grau de perill de la situació. Els ocells dominants i subordinats regulen la massa corporal de manera completament diferent en funció de les condicions ambientals (Ekman 2004), com de fet vam veure al Tema 5 (Fig. 13). Per tant, si els lluers dominants del nostre estudi experimentaven un risc d'inanició molt baix i en canvi patien un alt risc de

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depredació, aleshores és normal que prioritzessin la vigilància enlloc de l'alimentació. I és això probablement el que va passar en el nostre estudi, donat que les temperatures eren suaus (temperatura mitjana mensual: Gener: 8.0°C, Febrer: 11.6°C, Març: 13.7°C; dades de l'Observatori Fabra) i la disponibilitat i predictibilitat en l'accés a l'aliment eren altes (donat que els vam proporcionar menjar en abundància durant tot l'hivern).

En qualsevol cas, no creiem que la dominància per sí sola pugui explicar els resultats obtinguts en els diferents estudis d'aquesta tesi. Al Tema 2, vam veure que com més brillant era el plomatge d'un mascle, més temps dedicava a la vigilància i més curts eren els seus intervals entre vigilàncies. Com que la brillantor del plomatge en aquesta espècie està relacionada amb la coloració carotènica, que no està relacionada amb la dominància sinó amb l'elecció de parella (Senar & Escobar 2002; Senar et al. 2005), aquests resultats s'haurien d'explicar en termes de la relació entre conspicuïtat i risc de depredació. Al Tema 3 vam veure que els transeünts mostraven vigilàncies més llargues que els residents, cosa que no es va trobar en les comparacions entre sexes i entre personalitats, i això estaria relacionat amb el fet que haurien de vigilar una àrea més gran per desconeixement de la zona (Hinde 1956). A més, també vam trobar una interacció entre taxa de picoteig i menjadora en la comparació entre residents i transeünts, cosa que no vam trobar en les comparacions entre sexes i entre personalitats. Els transeünts van prioritzar una reducció en els temps d'estada a la menjadora quan s'incrementava el risc de depredació, mentre els residents prioritzaven un increment de la vigilància al preu de reduir la taxa d'alimentació. Aquestes diferents estratègies probablement tenien a veure amb la diferent utilitat de la vigilància per a uns i altres ocells (Lima 1987a), en concordança amb l'efecte de la familiaritat, i difícilment es poden entendre en termes de relacions de dominància. Finalment, al Tema 5 vam veure que els residents ajustaven la seva massa corporal a la presència d'un esparver caçant a la zona, mentre que els transeünts no ho feien, i això no podia ser atribuït a les relacions de dominància perquè no vam trobar aquest mateix patró en comparar mascles de pitet gran amb mascles de pitet petit.

Per tant, només la comparació entre personalitats (és a dir, entre mascles que difereixen en la mida del pitet) pot explicar-se exclusivament per l'efecte de la dominància (Senar & Camerino 1998). En les comparacions entre mascles i femelles i entre residents i transeünts hi ha també importants efectes de la conspicuïtat del plomatge i del coneixement de la zona, respectivament. I fins i tot en la comparació entre categories de mida de pitet, pensem que és millor d'interpretar els resultats en relació amb la personalitat degut a que la dominància no és un caràcter individual sinó el resultat de la interacció entre la personalitat i l'ambient social (Dingemanse

& de Goede 2004). Per aquesta raó els temes d'aquesta tesi se centren en els efectes de la conspicuïtat, el coneixement de la zona i la personalitat enlloc de centrar-se en l'efecte de la dominància, tot i que aquesta es pren en consideració en tots ells quan es considera rellevant.

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