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Winter ecology of tits (*Paridae*) in boreal and subalpine forests: social organisation and the role of food hoarding

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A la meva mare i a la meva àvia...

...allò important no es veu amb els ulls...

“Fa milions d’anys que les flors fabriquen punxes. Fa milions d’anys que els xais es mengen les flors. I no n’és de seriós, tractar de comprendre per què les flors es preocupen tant de fabricar punxes que no els serveixen de res, oi ? I la guerra dels xais i les flors, tampoc no n’és d’important ?...”

El Petit Princep, Antoine de Saint-Exupéry.

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WINTER ECOLOGY OF TITS (*PARIDAE*) IN BOREAL AND SUBALPINE FORESTS: SOCIAL ORGANISATION AND THE ROLE OF FOOD HOARDING.

INTRODUCTION

For forest passerines inhabiting temperate habitats, winter is usually a limiting time. Resource availability is typically low (Janson et al. 1981, Spencer 1982) and weather conditions often adverse (Elkins 1993). However, during the non-breeding season birds are not directly involved in reproductive tasks, and therefore, individuals may increase their long term fitness (Darwin 1859, Maynard-Smith 1975) by maximising two separate fitness components: current survival and future reproduction (Williams 1966, Matthysen et al. 1992). The former may require most of an individual's effort, given that present survival must take priority over investments in a future that might never be known if subsistence is not assured. Whether birds migrate or not, whether they live in groups or not, whether individuals defend food resources or not, or whether individuals roost in tree cavities or among canopy needles are all options open to birds in order to maximise immediate survival. These processes commonly translate into enhanced predator avoidance or better foraging prospects leading to a lower risk of starvation (Pulliam & Millikan 1982, Lima & Dill 1990, Senar 1994). Such short-term factors might vary on a daily basis, as might the individual responses to such changes.

On the other hand, decisions taken during the non-breeding season may also significantly influence breeding prospects (Dhondt & Schillemans 1983, Lefebvre et al. 1992, Koivula et al. 1996). Individuals try to optimise the best positions within their social system in order to start reproduction with the best possible prospects (Black 1996). Indirect social constraints do not necessarily enhance survival expectations in the short term run, but rather increase future chances of successful breeding, or of offspring survival. Formation of a long-lasting pair (Orell et al. 1994, Black 1996, Delastrade 1999), sedentariness (Kaufman 1983, Lefebvre et al. 1992), or future dominance expectation through queuing strategies (Ekman 1989a, Koivula 1999) can increase a bird's future long-term fitness, especially in resident species or populations (Woolfenden & Fitzpatrick 1978, Greenwood and Harvey 1982, Smith 1978, 1984, Matthysen et al. 1992). Current behaviour related to future pay-offs rather than to present benefits may be hard to identify and place in the right context, and it may even seem non-adaptive at first sight (Pulliam & Millikan 1982, Koivula 1999).

Winter social organisation in a population, or a species, results from the behavioural set-up which maximises both, the probability of immediate survival and future reproductive output. But, individuals are exposed to different selection to pressures, and therefore, social outcomes will be individual dependent. Thus, the study of social organisation requires a detailed, multiscale approach in order to be properly understood. A suitable framework for studying problems of this kind is offered by passerine birds which live in groups during the non-breeding season (Pulliam & Caraco 1984, Senar 1994). The group of parids (*Paridae*) offers good opportunities for obtaining insight into social system variation in birds. Through a detailed study of this variation in species or populations in different environments, patterns can be established and the key factors ruling social systems at different levels identified.

All species of the *Paridae* studied to date live in social groups during the non-breeding season (Ekman 1989a, Matthysen 1990). The cost-benefit system associated with social life has been widely studied using a number of parids as models (Ekman 1989a, Matthysen 1990). The benefits of social life are related, in the first place, to an increased performance in antipredatory behaviour (Inman & Krebs 1987, Hogstad 1988a, 1988b), and second, to an increase in foraging efficiency derived from copying the behaviour of more experienced individuals (Mönkkönen & Koivula 1993), local enhancement (Hogstad 1988b), or the time saved using the reduced scanning rates associated with increased group size (Inman & Krebs 1987, Hogstad 1988b). However, competition costs impose a limit on group size (Ekman 1989b), and the dominance relationship between group members means individual benefits obtained are dependent on their dominance position in the system (Koivula 1999). Dominance is an almost inherent property of social systems. Individuals do not have equal abilities to compete which results in asymmetries in their resource holding potential (Piper 1998). Dominants monopolise resources but pay the costs of maintaining themselves at the top of their hierarchies (Roskaft et al. 1986, Hogstad 1987). Subordinate birds obtain benefits from flocking behaviour but may pay the costs of using poorer or more dangerous sites due to the dominants' behaviour (Scheneider 1984, Ekman 1987, Koivula et al. 1994).

Social patterns in parids

In addition to the trade-offs associated with social life, an interesting pattern of variation seems to appear in the spacing systems and flocking composition of the different species (Ekman 1989a). Two main types of organisation have been described (figure 1).

In the first type, groups of birds form territorial flocks of largely consistent membership and high site fidelity. In this framework, territoriality is related to the exclusive use of home ranges by resident individuals (Kaufman 1983, Matthysen 1990). Flocks seem to have an internal structure, that is by no means random in origin, and are commonly composed of a mated adult pair and a variable number of juveniles that are also paired (Ekman 1979, Koivula & Orell 1988). In the second type of social system, the "basic flock system" (Saitou 1988), groups are not territorial and group membership is much looser, resulting in groups of a highly variable composition and large temporary aggregations. However, in this type of organisation, temporary flocks seem to be formed around more sedentary mated adult pairs. In this case, the number of juveniles might vary considerably and neighbouring groups often inter-mix.

Figure 1. Schematic representation of different levels of social organization in two species of parids. The Willow tit, group territorial species ; and the Great tit, a basic flock species. These levels are (A) individual bonds, (B) group coherence, and (C) between group interactions. From Matthysen 1990.

Stable patterns of social organisation do not commonly arise from a direct response to increased immediate survival, but rather they owe their existence to concrete strategies of future territory acquisition or maintenance, and improved future breeding opportunities. In the case of parids, the long-lasting associations involving breeding individuals (Dhondt and Schillemans 1983, Black 1996) and the settlement strategies of juveniles to recruit into the existing population structure (Ekman 1989a, Matthysen 1990), seem to be associated with the patterns described. Ekman (1989a, 1989b) suggested that in closed populations, where vacancies within the social system are few and the habitat quality gradient is large, juveniles might be opting for the best of a bad option by remaining with adults in small territorial groups (Hogstad 1990). Queuing for a new opening in the social system might constitute the only mean by which such juveniles can obtain a breeding position in the following season (Koivula et al. 1996).

Hoarding and its possible role in non-breeding social systems

The habit of hoarding has also been widely studied in parids (Haftorn 1956 a, b, Källander and Smith 1990, Brodin 1994 a, b, Sherry 1996, Lahti et al. 1998), and its presence extensively recorded in almost all the species of the group studied so far, with the exceptions of the Great (*Parus major*) and the Blue tit (*P. caeruleus*). Individuals of hoarding species store food items in moments of high food supply and later withdraw it in order to reduce the possible consequences of food shortage (Van der Wall 1990). Because of the benefits obtained, it has been suggested that hoarding is a key factor in determining the social structure of parids (Ekman 1989a, Källander and Smith 1990). Given the benefits of cache recovery, the exclusive use of territories where caches are to be located clearly increases the benefits to be gained from. In fact, the two non-hoarding species mentioned above have been shown to present a loose, and non-territorial system during winter. Therefore, the dichotomy in the non-breeding social systems of parids is sometimes assumed to be strongly a consequence of the hoarding habit (Ekman 1989a, Slikas et al. 1996). However, although certainly present, the exact role of hoarding in shaping social patterns in parids is far from clear.

In a recent paper, Smulders (1998) presented a dynamic model which suggested that hoarding could have originated in a non-territorial population of tits without need for an elaborate memory system. The relationship between non-breeding social organisation and the hoarding habit clearly needs clarification. Given our current understanding, the study of hoarding populations of parids with different non-breeding social structures is essential in order to shed some light on the evolutionary origin and ensuing pathways of hoarding behaviour in this group of passerines.

Objectives of the thesis

The main objective of this thesis is to analyse the variation in non-breeding social systems within the group of parids and to identify the main factors involved. More specifically, I studied the role of food hoarding on the structure of winter social systems at different scales. The study was focused on the social patterns and hoarding of two species of tits inhabiting boreal (the Willow tit, *Parus montanus,* box 1) and montane subalpine forests (the Coal tit, *Parus ater,* box 2). The results included in this thesis are mainly concerned with the Coal tit, because the Willow tit has been studied in some detail by other researchers in the same study area described below (see chapter 5). Therefore, most of the points here investigated for the Coal tit were already studied for the Willow tit.

Box 1. The Willow tit

The Willow tit is a small (weight 10-12 g), year-round resident passerine in the Paleartic region (Cramp and Perrins 1993). The species is one of the most abundant winter birds in boreal forests in northern Europe. The Willow tit spends the winter in stable, coherent flocks consisting typically of four to six individuals (e.g. Ekman 1979a, Koivula and Orell 1988). After settlement in the late summer-early autumn, the birds are highly site-tenacious throughout their lives (Ekman 1979a). Typically, the individuals in a flock exhibit a clear dominance hierarchy (Hostag 1987a, Koivula and Orell 1988; but see Lahti et al. 1993). The sedentariness and permanent group structure with non-transitive dominance relations enable the examination of the effect of sociality on many interesting ecological variables, such as reproductive success and survival (Koivula et al. 1996). It is a food hoarding species.

Box 2. The Coal tit

The Coal tit is also a small forest passerine (mean body mass is 9-10 g). A typical species of coniferous forests, it is widely distributed throughout Europe and large areas of central and north Asia. It is one of the most common breeding passerine species in montane subalpine forests and the most common resident species in these areas during winter. It is also a hoarding species. The winter social organisation of this species is largely unknown, in spite of being one of the most common tit species in Europe and having been studied in great detail during the breeding season. Some preliminary studies suggest that the Coal tit in Scandinavia might have a territorial system similar to that of the Willow tit (Ekman 1989a). However, other studies do not agree with this view and have found populations exhibiting much looser and non-territorial social patterns (Nakamura 1975). Therefore, being a hoarding species, the social organisation of the Coal tit is largely unknown although an interesting variation seems to appear.

I first described the non-breeding social organisation of the Coal tit in an optimal habitat (i.e. coniferous subalpine forest) in order to confirm non-territoriality in the population and shed light on the spacing mechanisms of individuals in that environment (Chapter 2). I further analysed in detail and experimentally the role of status signalling mechanisms in dominance determination under different social conditions in mountain populations of the Coal tit (Chapter 3). Given the loose organisation and the large associations of individuals detected, status signalling is predicted of special importance in determining dominance outcomes among birds that lack previous knowledge of opponents.

I also studied the foraging behaviour of tit populations under conditions of stress caused by weather or decreased food availability (Chapter 4 and 5). In these chapters, I analysed the role of stressful episodes on the winter ecology, hoarding patterns and, indirectly, on the social organisation of tits.

Hoarding alters the distribution of food in the bird's environment. Therefore, if food distribution is a significant factor in shaping the foraging behaviour of individuals, hoarding is predicted to play a decisive role. I analysed the impact of hoarding patterns in the possible foraging behaviour of individuals (Chapter 6) and furthermore, I analysed the most likely uses of hoarding on tit populations differing in sociality and environmental conditions (Chapter 7, 8).

Hoarding is predicted to be beneficial to the hoarder when it has a higher probability of recovering stores than its neighbours. In a non-territorial population, the presence of large associations of birds imposes a high potential hazard on stores hoarded by individuals. I analysed the behavioural strategies that individuals in non-territorial high density populations utilise in order to increase selfish benefits of hoarding behaviour and make hoarding compatible with a non-exclusive use of home ranges (Chapter 7).

The constraints imposed by a non-breeding social organisation might be of special importance in shaping life history traits of bird populations. In species where autumn juvenile settlement is time constrained due to the existence of a territorially closed system, fecundity may be limited because late produced offspring are of much lower competitive value than earlier individuals. Therefore, I finally addressed the question of the possible indirect effects of winter social organisation on the life history strategies of parids. More specifically, I tested the possible evolutionary influence of winter territoriality on the fecundity of different species of the *Paridae* (Chapter 8) and on the eruptive habit that some of them present (Chapter 9).

ECOLOGIA HIVERNAL DE LES MALLERENGUES (*PARIDAE*) EN BOSCOS BOREALS I SUBALPINS: L'ORGANITZACIÓ SOCIAL I EL PAPER DE L'EMMAGATZEMAMENT DE MENJAR

INTRODUCCIÓ

Pels passeriformes habitants d'hàbitats temperats, l'hivern és sovint una època de limitacions. En general, la disponibilitat de recursos és baixa (Janson et al. 1981, Spencer 1982) i les condicions atmosfèriques adverses (Elkins 1993). Durant l'estació no reproductora, els ocells no estan directament involucrats en tasques reproductores i així, incrementen la seva eficàcia biològica (Darwin 1859, Maynard-Smith 1975) maximitzant dos dels seus components: la supervivència immediata i la reproducció futura (Williams 1966, Matthysen et al. 1992). La supervivència immediata sembla centrar l'interès dels individus, ja que aquesta te preferència sobre inversions futures que depenen de la supervivència actual. Si els ocells migren o no, si els ocells formen grups o no, si els individus defensen els recursos que hi al seu voltant o no, o si un individu passa la nit en una cavitat o entre les fulles, són totes opcions que decideixen els ocells per tal de maximitzar la probabilitat de supervivència immediata. Aquests comportaments es tradueixen en una millor capacitat per evitar els predadors o en millors perspectives d'adquisició d'aliment (Pulliam & Millikan 1982, Lima & Dill 1990, Senar 1994). Aquests factors podrien variar a curt termini, forçant d'aquesta manera la resposta dels individus que han de respondre a les noves condicions.

D'altra banda, les decisions preses durant l'estació no reproductora poden influir en gran mesura les futures perspectives de cria (Dhondt & Schillemans 1983, Lefebvre et al. 1992, Koivula et al. 1996). Els individus han d'assolir les millors posicions dins del sistema social per tal de començar la reproducció amb les màximes garanties d'èxit (Black 1996). Les limitacions indirectes imposades pel sistema social no impliquen necessàriament un augment de l'eficàcia biològica a curt termini, sino unes probabilitats més elevades d'èxit de cria o de futura supervivència de la descendència. La formació de vincles estables de parella (Orell et al. 1994, Black 1996, Delastrade 1999), la sedentarietat (Kaufman 1983, Lefebvre et al. 1992), o les estratègies d'espera o cua per tal d'incrementar la dominància en la jerarquia (Ekman 1989a, Koivula 1999), poden millorar l'eficàcia biològica dels ocells en una perspectiva a llarg termini, especialment en espècies o poblacions residents (Woolfenden & Fitzpatrick 1978, Greenwood and Harvey 1982, Smith 1978, 1984, Matthysen et al. 1992). El comportament present com a causa d'avantatges en el futur pot ser difícil d'identificar i d'emplaçar en el context correcte. I a primer cop d'ull, en alguns casos pot semblar fins i tot antiadaptatiu (Pulliam & Millikan 1982, Koivula 1999).

L'organització hivernal d'una població, o espècie resulta de la combinació de comportaments que maximitzen, d'una banda, la probabilitat immediata de supervivència, i de l'altra la futura esperança reproductora dels individus. Diferents individus es troben sotmesos a diferents pressions de selecció, i per tant, els condicionants socials dependrà de les característiques de cada un d'ells. Només un anàlisi detallat de l'organització social permetrà desemmascarar les complexes interrelacions que els éssers vius estableixen amb el medi mitjançant el comportament. Un marc especialment adequat per l'estudi d'aquest tipus de problemes l'ofereixen els ocells passeriformes que viuen en grups durant el període no reproductor (Pulliam & Caraco 1984, Senar 1994). El grup dels pàrids (*Paridae*) sembla oferir bones oportunitats per obtenir una major comprensió de la variació que s'observa en l'organització social dels ocells. A través d'un estudi detallat d'aquesta variació en diferents espècies o poblacions es poden identificar patrons generals i els factors que els determinen a diferents nivells.

Totes les espècies de mallerengues estudiades fins al moment viuen en grups socials durant l'estació no reproductora (Ekman 1989a, Matthysen 1990). Els sistema de costos i beneficis associat a la vida social ha estat estudiat en profunditat utilitzant algunes espècies de mallerengues com a models (Ekman 1989a, Matthysen 1990). Els beneficis de la vida social es relacionen bàsicament amb un increment en l'eficiència dels comportaments antipredadors (Inman & Krebs 1987, Hogstad 1988a, 1988b) i amb un increment de l'eficiència alimentària. Aquesta resulta de la transferència d'informació dins del grup (Krebs 1977, Mönkkönen & Koivula 1993), de la probabilitat augmentada de trobar fonts d'aliment (Hogstad 1988b), i del temps estalviat en la detecció de predadors producte de l'increment de la mida del grup (Inman & Krebs 1987, Hogstad 1988b). De tota manera, els costos de competència entre individus imposen un limit en la mida d'un grup (Ekman 1989b). A més, les relacions de dominància entre els membres fan que els beneficis que n'obté cada un siguin depenents de la seva posició en la jerarquia local (Koivula 1999). La dominància és una propietat inherent al sistemes socials. Els individus no tenen les mateixes habilitats competitives, fet que origina diferències en la capacitat d'acumulació i control dels recursos (Piper 1998). Els dominants monopolitzen els recursos però ho paguen amb els costos energètics que suposa de mantenir-se a la part alta de les jerarquies (Roskaft et al. 1986, Hogstad 1987). Per altra banda, els subordinats obtenen els beneficis de la vida en grup però es veuen forçats a utilitzar els llocs més pobres o perillosos degut a la competència amb els dominants (Scheneider 1984, Ekman 1987, Koivula et al. 1994).

Patrons socials en els pàrids

A més dels compromisos associats a la vida social, els pàrids semblen presentar un interessant patró de variació en l'estructura de l'espaiament i en la composició dels grups de diferents espècies (Ekman 1989a). Dos tipus principals d'organització han estat descrits fins al moment (Figura 1). En el primer cas, els ocells formen flocs territorials (ús exclusiu dels dominis vitals dels flocs), molt sedentaris i de composició constant. Aquests flocs semblen tenir una estructura interna, que, lluny de semblar atzarosa, està constituïda per una parella adulta i un número variable de joves, sovint també aparellats (Ekman 1979, Koivula & Orell 1988). En el segon cas, "sistema de floc bàsic" (Saitou 1988), els grups no són territorials i la pertinença als mateixos molt menys constant, donant lloc a grups de composició variable i grans agrupacions temporals de diversos grups d'ocells. De tota manera, també aquest tipus d'organització social sembla formar-se al voltant d'una parella, més o menys sedentària, d'ocells adults. En aquest cas, el número de joves pot variar profundament i els grups veïns es mesclen amb molta freqüència.

Els patrons estables d'organització social no sorgeixen d'una resposta directa a la maximització de la supervivència immediata dels individus, més aviat deuen la seva existència a estratègies concretes destinades a l'obtenció o manteniment de territori, i a la millora de les perspectives de cria futures. En el cas dels pàrids, la continuïtat en el temps d'associacions socials com les parelles (Dhondt & Schillemans 1983, Black 1996) o les estratègies d'establiment dels joves en l'estructura social existent (Ekman 1989a, Matthysen 1990) semblen els principals processos darrera dels patrons de variació observats. Ekman (1989a, 1989b) va suggerir que en poblacions tancades on les vacants són escasses i el gradient de qualitat d'hàbitat gran, restar amb els adults en petits grups territorials, seria la millor de pitjors opcions disponibles pels juvenils (Hogstad 1990). Esperar l'aparició d'un buit en el sistema podria ser l'única opció que possibilitaria als joves obtenir un territori per cria la següent estació reproductora (Koivula et al. 1996).

L'emmagatzemament i el seu possible paper en els sistemes socials durant l'estació no reproductora

El comportament d'emmagatzemament ha estat estudiat profundament en el pàrids (Haftorn 1956 a, b, Källander & Smith 1990, Brodin 1994 a, b, Sherry 1996, Lahti et al. 1998), i la seva presència ha estat detectada en quasi totes les espècies del grup estudiades fins el moment, amb la remarcable excepció de la Mallerenga carbonera (*Parus major*) i de la Mallerenga blava (*P. caeruleus*). Els individus de les espècies emmagatzemadores amaguen aliment en moments en que la seva disponibilitat és alta i el recuperen temps després per tal d'amortiguar possibles disminucions en la quantitat d'aliment disponible (Van der Wall 1990). Degut als beneficis que comporta, l'emmagatzemament ha estat citat com un factor clau darrera de l'estructura social dels pàrids (Ekman 1989a, Källander & Smith 1990). L'ús exclusiu de l'aliment emmagatzemat augmenta clarament els beneficis d'aquest comportament assegurant la recuperació del mateix. De fet, les dues úniques espècies no emmagatzemadores mencionades anteriorment, semblen organitzar-se en grups poc estables i no territorials durant l'hivern. Per tant, la dicotomia en l'organització social dels pàrids és sovint, atribuïda a una conseqüència de l'emmagatzemament de menjar (Ekman 1989a, Slikas et al. 1996). De tota manera, el paper de l'emmagatzemanet de menjar en la determinació dels patrons socials dels pàrids és encara un fet poc clar i lluny de ser inequívoc.

En un article recent, Smulders (1998) presenta un model dinàmic que suggereix que l'origen de l'hàbit de l'emmagatzemament es podria haver localitzat en una població no territorial d'una espècie de Pàrid ancestral sense la necessitat d'un sistema de memòria desenvolupat. La relació entre l'organització social i l'emmagatzemament mereix ser clarificada. En el marc actual de coneixement dels pàrids emmagatzemadors, sembla essencial un estudi detallat de poblacions de diferent estructura social per tal de clarificar les hipòtesis mencionades sobre l'aparició i posterior evolució del comportament d'emmagatzemament.

Figure 1. Representació dels diferents nivells d'organització social en dos espècies de pàrids. La Mallerenga capnegra, territorial en grups ; i la Mallerenga carbonera, representant dels sistema de floc bàsic. Els nivells d'organització són : (A) vincles individuals, (B) coherència dels grups, i (C) relacions entre els grups. A partir de Matthysen (1990).

Objectius de la tesi

El principal objectiu d'aquesta tesi és analitzar la variació en l'organització social dels pàrids durant l'època no reproductora i clarificar els factors més importants involucrats en aquest procés. Més concretament, s'estudià la relació i les possibles influències de l'emmagatzemament en aquesta organització. Realment és tan forta la dependència entre la territorialitat hivernal i l'emmagatzemament ?

L'estudi es centrà en l'organització social i l'emmagatzemament de dues espècies de mallerengues habitants de zones boreals i de boscos subalpins de muntanya : la Mallerenga capnegra (*Parus montanus,* marc 1) i la Mallerenga petita (*Parus ater,* marc 2) respectivament. El treball inclòs en aquesta tesi fa referència bàsicament a la Mallerenga petita. La Mallerenga capnegra ha estat estudiada amb detall per altres autors en la mateixa zona on l'estudi del capítol 5 va ser realitzat (marc 2). Així doncs moltes de les preguntes i problemes plantejats amb la Mallerenga petita ja han estat tractats en aquesta altra espècie.

Marc 1. La Mallerenga capnegra

La Mallerenga capnegra és un petit (pes 10-12 g) passeriforme resident tot l'any i habitant de la regió paleàrtica (Cramp and Perrins 1993). L'espècie és una de les més abundants als boscos boreals del nord d'Europa durant l'hivern. La Mallerenga capnegra passa l'hivern en petits grups de composició estable generalment d'entre quatre i sis individus (e.g. Ekman 1979a, Koivula & Orell 1988). A partir de l'establiment de finals d'estiu o de principis de tardor, els ocells són extremadament fidels a la mateixa àrea de cria durant la resta de les seves vides (Ekman 1979a). En els flocs, els individus exhibeixen una jerarquia de dominància lineal típica (Hostag 1987a, Koivula & Orell 1988; però veure Lahti et al. 1993). La sedentarietat i els grups de composició estable amb relacions de dominància no transitives, permeten l'estudi de l'efecte social sobre diverses variables de tipus ecològic, com l'èxit de reproducció o la supervivència (Koivula et al. 1996). És una espècie emmagatzemadora de menjar.

Marc 2. La Mallerenga petita

La Mallerenga petita és un petit passeriforme forestal (pes 9-10 g). És una espècie típica de boscos de coníferes, i està àmpliament distribuïda per tot el continent europeu i bona part d'Àsia. És una de les espècies reproductores més abundants dels boscos de coníferes de l'estatge subalpí i és l'espècie resident majoritària durant l'hivern. És també una espècie emmagatzemadora de menjar. L'organització social d'aquesta espècie és força desconeguda malgrat ser una de les espècies de mallerengues més comuns a tota Europa i haver estat estudia profundament durant l'època reproductora. Alguns estudis preliminars suggereixen que la Mallerenga petita escandinava podria tenir un sistema territorial de grups petits similar al de la Mallerenga petita (Ekman 1989a). D'altra banda, n'hi ha que no coincideixen amb aquesta visió i semblen haver trobat poblacions exhibint patrons socials molt més inestables lluny de ser territorials (Nakamura 1975). D'aquesta manera, tot i ser una espècie emmagatzemadora, l'organització social de la Mallerenga petita és força desconeguda. A més, en aquest punt semblen aparèixer variacions geogràfiques interessants.

Més concretament, primer s'estudià l'organització social de la Mallerenga petita durant l'època no reproductora al seu hàbitat òptim (i.e. bosc subalpí de coníferes) per tal de confirmar la no territorialitat suposada per aquesta població i aportar llum als mecanismes d'espaiament dels individus de la zona (Capítol 2). Tot seguit s'analitzà en detall i experimentalment el paper dels mecanismes de senyalització d'estatus en la determinació de les relacions de dominància entre individus de poblacions de muntanya de la Mallerenga petita (Capítol 3). Degut a la inestable organització social i a la gran mida dels grups de Mallerenga petita, la senyalització d'estatus podria ser d'especial importància a l'hora de determinar el resultat de les interaccions agonístiques entre individus amb poc o nul coneixement entre ells. D'aquesta manera el número d'interaccions violentes disminuiria, amb el corresponent estalvi en termes energètics i de reducció del risc de predació.

També s'estudià el comportament d'alimentació de les mallarengues sotmeses a períodes d'estrés o de reducció temporal en la disponibilitat d'aliment després de condicions climàtiques adverses (Capítols 4 i 5). En aquests capítols, l'objectiu principal va ser el determinar el paper que juguen aquests períodes de meteorologia adversa en l'ecologia, els patrons d'emmagatzemament i, indirectament, sobre l'organització social de les mallerengues.

L'emmagatzemament altera la distribució de l'aliment en el medi on habiten els ocells. Així doncs, si la distribució d'aliment determina d'alguna manera les estratègies d'alimentació dels individus, l'emmagatzemament esdevindrà un factor clau. Això doncs, s'estudiaren les relacions i possibles efectes dels patrons d'emmagatzemament en el comportament d'alimentació dels individus (Capítol 5). Més enllà, s'analitzaren també els usos més probables de l'emmagatzemament en poblacions i individus amb diferents condicionants socials i ambientals (Capítols 6 i 7).

La teoria sembla assenyalar que l'emmagatzemament és beneficiós per l'individu emmagatzemador quan aquest té major probabilitat de recuperar l'aliment que els individus veïns. En una població no territorial, la presència de grans associacions d'ocells comporta un alt perill potencial pels emmagatzemaments dels individus. S'estudiaren les estratègies que les mallerengues petites utilitzen en aquestes condicions per tal d'assegurar els beneficis associats amb la recuperació de l'aliment emmagatzemat i fer-lo compatible amb l'ús, no exclusiu, de les àrees de deambulació dels individus (Capítol 7).

Les limitacions imposades per un sistema d'organització social determinat durant l'època no reproductora poden arribar a ser d'especial importància a l'hora de definir els trets principals de la història evolutiva dels ocells. En espècies on l'establiment dels joves durant la tardor esta limitat pel temps degut a l'existència d'un sistema territorial tancat, la fecunditat podria estar limitada perquè una descendència tardana estaria en inferioritat competitiva respecte a la produïda amb anterioritat. Així doncs, es plantejaren els possibles efectes indirectes que l'organització social durant l'hivern pot tenir en les històries evolutives dels pàrids. En concret, es va testar la possible influència evolutiva de la territorialitat hivernal (com a exemple de sistema d'organització tancat on l'establiment dels joves està limitat pel temps) sobre la fecunditat de diverses espècies del pàrids (Capítol 8) i sobre l'hàbit eruptiu que algunes d'aquestes espècies presenten (Capítol 9).

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WINTER SPACING AND NON-BREEDING SOCIAL SYSTEM OF THE COAL TIT (*PARUS ATER*) IN A SUBALPINE FOREST [1]

Abstract : In the genus *Parus*, non-breeding social territoriality has often been attributed to the presence of food hoarding which by increasing the value of an area, is thought to favour the existence of exclusive territories. In order to study the validity of this statement, it is necessary to analyse the social structure of hoarding populations inhabiting different environments. I studied Coal tit spacing patterns and winter social systems in a colour-ringed hoarding population inhabiting a mountain coniferous forest in the Pyrenees. Using data on home range, range overlap and social coherence, the social system was found to be based on adult birds which had previously bred together and which occupied relatively small home ranges. Large home ranges of resident juveniles overlapped extensively with each other and those of adults. However, resident juveniles were re-sighted much closer to their ringing place than was expected at random, suggesting restricted floater ranges. Associations, composed mainly of juveniles, seemed to be rather large and loose, with low coherence values between individuals. No territorial defence by any group of birds was detected during the study. Therefore, the social organisation described for the present Coal tit population is similar to the loose, non-territorial basic flock system of non-hoarding species. Resident social patterns seemed to be primarily linked to the availability of breeding resources, probably leading to the high site fidelity of adults and the floater life of resident juveniles. On the other hand, short term survival chances may attract transients to a rich food supply and thus affect flocking strategies of birds. High availability of resources allowing a high population density seem to be the main proximate factor influencing the spacing patterns described.

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[1] Ibis, 142, in press (2000).

INTRODUCTION

Social organisation in gregarious birds during the non-breeding time has attracted considerable attention in the recent decades (Pulliam & Millikan 1982, Ekman 1989a, Matthysen 1990, Matthysen et al. 1992). In some species survival prospects of individuals depend on the possibility of attaining a position in socially structured groups (Smith 1984, Ekman 1987, Koivula & Orell 1988). Two kinds of factors, not mutually exclusive, are possible in determining the variability in social systems; 1) those which maximise immediate individual survival (Krebs & Davies 1995) and, 2) those which act in the long term and indirectly affect future reproductive success (Matthysen 1989, 1990, Lens & Wauters 1996). Studies conducted to date, show that both play a role in the winter sociality of birds (Pulliam & Millikan 1982). Increasing number of studies stress the importance of long term factors such as pair bond, site fidelity and prospects of future dominance or territory ownership, especially in resident species or populations (Woolfenden & Fitzpatrick 1978, Greenwood & Harvey 1982, Smith 1978, 1984, Matthysen et al. 1992).

A key factor determining the social structure of winter groups is the settlement strategy juveniles adopt for recruitment into the breeding population. Four strategies have been described (Smith 1984, Ekman 1989a, Lens & Wauters 1996) ; (1) establishing a new territory in an unoccupied area, (2) evicting a territory owner and taking over its territory, (3) joining adults in group territories and remaining as subordinates until the adult of the same sex disappears ('settler or hopeful dominant strategy'), or (4) surviving without a fixed territory and waiting for a vacancy to occur elsewhere ('floater strategy'). The strategy adopted seems to depend on the relative benefits that the it gives to the individual (Smith 1984, Ekman 1989b). As populations differ according to local environmental conditions, the optimal strategy adopted by juveniles varies with the environment (Lens & Wauters 1996). In parids, rapid establishment of juveniles in territorial winter groups after independence seems to be the most common rule (Nilsson & Smith 1988, Ekman 1989a). However, in the Great (*Parus major*) or the Blue tit *(P. caeruleus*), this is not always the case, and the groups formed are much more lax and heterogeneous (Hinde 1952, Saitou 1988). Groups of these species largely overlap and lack territorial structure with an exclusive use of home ranges. This difference in behaviour is usually attributed to food hoarding (Ekman 1989a, Slikas et al. 1996), which appears to increase the value of territories, and thus also the benefits of restricted ranges (Vander Wall 1990). Non-hoarding species would not be able to increase the value of their territories and benefit to the same degree from maintaining its exclusive use during the non-breeding season (Källander & Smith 1990, Matthysen 1990). However, the relationship between territoriality, flock cohesion and food hoarding is still unclear (Smulders 1998). Furthermore, studies on the possible co-evolution of these traits does not take the phylogeny into account (Ekman 1989a), nor the different strategies that food hoarding species may utilise to avoid cache robbery in non-territorial systems (Brodin 1994, Lahti & Rytkönen 1996, Sherry & Duff 1996). In order to test the validity of the stated relation between the food hoarding habit and the variation in non-breeding social systems it is necessary to collect information about the variation in the social structure of hoarding species inhabiting different environments.

The Coal tit (*P. ater)* is a common and widely studied species living mainly in temperate coniferous forests (Cramp & Perrins 1993). It is a hoarding species (Haftorn 1956), and despite some preliminary research (Nakamura 1975, Ekman 1989a), no detailed studies of its social organisation during winter have been undertaken on a colour-ringed population. Given its hoarding habit, the social system of the Coal tit has been assumed to be flock territorial (Matthysen 1990, Ekman 1989a). This is far from clear and previous studies suggest a more flexible social behaviour comparable with that of the Great tit (Nakamura 1975, Brotons & Haftorn 1999). Here, I studied the non-breeding social organisation of a Coal tit population in a mountain area. The area is occupied by birds all year around, and it reaches high densities of up to 1 pair per hectare. Both, adult and juvenile individuals hoard food actively during autumn and winter (Brotons & Haftorn 1999, unpubl. manuscript). The hoarding hypothesis predicts a close, territorial social system in this population. The aim of this paper is to analyse the spacing patterns and the social organisation of the Coal tit in this environment and compare the results with the current knowledge of the winter social strategies of the genus *Parus*.

STUDY AREA AND METHODS

I studied Coal tit social organisation and spacing patterns in a 150 ha coniferous forest located in the 'Cadí-Moixeró' Natural Park (Eastern Pyrenees, Spain) at an altitude of 1800-2100 m. Mountain Pine (*Pinus uncinata*) dominates the study area, with the Scots Pine (*Pinus sylvestris*) predominant on southern slopes and at lower altitudes. The understory is scarce, dominated by the Juniper (*Juniperus communis*) and grasses. Further details about the vegetation can be found in Vigo (1976). Until recently, the forest has been exploited resulting in stands of different ages. The area has a relatively cold climate during winter, with the mean monthly temperatures from December to February falling below zero and the permanent snow cover lasting from December to early April (data from La Molina ski station, 10 km from the study area, same altitude).

The study was carried out during the winters 1996-97 (December-February) and 1997-98 (November-January). Colour-ringed adults were captured at the nest during the breeding season (52 adults in 1996, and 58 in 1997). This constitutes about 30 % of the monitored breeding population of the study area for each year. Juveniles were attracted with tape-lures and then mist-netted from December 1996 to January 1997 (203 individuals) and from October 1997 to December 1997 (85 individuals). Birds were individually colour-ringed, weighed and measured according to Svensson (1992). An index of subcutaneous fat accumulation was estimated according to Kaiser (1993). In order to obtain more accurate data on range overlap of Coal tits, during the second winter, ringing and re-sighting efforts were concentrated in two plots of the study area (hereafter plots A and B, 1 km apart and of approximately 20 ha each). This had the effect of reducing the number of total juvenile captures in that winter. No extra food was offered to the birds since the presence of feeding tables is known to affect non-breeding social patterns in birds (Jansson et al. 1981, Brittingham & Temple 1988).

During periodic field visits throughout the winter (390 h of field work conducted over 36 days, 1996-97, and 28 days, 1997-98), I checked the study area intensively. When a group containing a colour-ringed individual was found, I recorded the identities of all possible colour-ringed birds in the flock. The location of the flock was registered on a 50x50m grid map. I also recorded the number of birds present as the minimum estimate of the size of the group. Given the difficulties involved in recording all the birds present in large flocks, the estimates should be considered as minimum values. However, group sizes (i.e. number of birds of a foraging flock which were in contact either visual or auditive) could often be calculated more accurately as groups crossed roads or a forest clear. Observations on one focal bird were considered independent of each other if at least 10 minutes had elapsed or the bird had moved at least 100m (see Matthysen et al. 1992 for similar methods). Home ranges of individuals were mapped using all observations and trapping data and their accuracy was assessed using incremental area plot analyses. In this way, it is possible to determine whether home range size increases with sample size or reaches an asymptote after a number of data points. Home range sizes were calculated using the Kernel method (KER) and minimum convex polygons (MCP) containing 100 %, 90% and 75 % of the observations. The latter estimates (75 %) will, hereafter, be referred to as the core areas of individuals and could be only calculated on data from resident adult birds. If not otherwise stated, in overlap analyses I used MCP containing 100 % of the observations. I used Jacobs' index (Jacobs 1974) in order to test whether observations of a given individual were closer to a given location in the study area (i.e. breeding site in adults and ringing site in juveniles) than randomly expected. Jacob's values range from 0, resulting from the observations located at random around the selected focal point, to 1 resulting from observations being distributed closer to the focal point than expected by chance, and -1 when observations are located further away than expected at random. Location data analyses were performed with RangesV program (R. Kenward & K.H. Hodder, Institute of Terrestrial Ecology, Wareham, U.K.).

Transient or non-resident birds were defined as individuals observed in the area for a short time only (<10 days, typically only during the ringing date). Resident birds were those individuals that were re-sighted within the study area at least once 10 or more days after the ringing date. In spite of the number of birds that were ringed most of the visual contacts were with un-ringed birds, indicating either a high bird density or a high turnover rate in the population. The fact that even shortly after ringing it was already difficult to re-sight colour-ringed juveniles (though not adults), suggests that the later is true, and juveniles have a high movement capacity (see also Ekman 1979b). Analyses of juvenile spacing patterns were conducted on colour-ringed individuals which constitute only a proportion of the total population of juveniles. I followed or re-sighted a total of 132 resident birds (36 adults and 44 juveniles during the first winter, and 30 adults and 30 juveniles the second), with a total of 1004 and 853 observations of individual birds in each winter respectively (172 and 107 groups). During field visits, I recorded also agonistic interactions within flocks. Most of the observed interactions between individuals involved contests for resources such as pine cones or needle clumps containing food, as the winner remained feeding on the food source. Often interactions ended with the retreat of the defeated bird. When possible, the identity of the birds involved in the contest was noted. In the case of repeated interactions, I included only the final dominance outcome for that pair of individuals. From the end of January onwards, as spring and breeding approach, territorial contests involving repeated chases and fights and often more than two individuals, also occur. These interactions were not included in the current data set. From the end of autumn and during winter, I recorded no further interactions involving colour-ringed individuals which could be related to territorial defence.

RESULTS

Home range and spacing of adults

Adults appeared to have constant and stable home ranges. They were re-sighted in restricted, well defined areas. According to the incremental area plot analyses (Figure 1a), I was able to calculate unbiased estimates of adult home range size for 38 individuals. These birds had core areas of around half the size of total home range estimates (paired t-test, t_{25}=6.4, p<0.0001, Table 1) indicating that most of the observations were distributed over a reduced area. Neither home range nor core area sizes differed significantly between adult males and females (home range, t-test, t_{37}= -0.9, N.S., core area, t_{37}= 0.2, N.S.). I restricted overlap analyses with neighbours to those adults re-sighted during the second winter in plots A and B. Home ranges overlapped with those of several neighbouring ranges (home range including 100 % of observations, Plot A, 0"SE= 6.8 " 0.4 individuals, N=13 ; Plot B, 0"SE= 5.0 " 0.4 individuals, N=13).

	Adults n=38	Juveniles n=22	
MCP analyses	0"SE	0"SE	t-test
100 %	3.3"0.2	8.5"1.4	4.9 ***
90 %	2.6"0.1	4.9"1.2	2.3 *
75 %	1.6"0.1	3.6"0.8	2.6 **
Kernel analyses			
100 %	3.4"0.2	10.7"3.8	2.9 **
90 %	2.3"0.2	4.8"1.1	2.8 **
75 %	1.2"0.1	2.7"1.0	2.9 **

Table 1. Mean home range sizes (ha) for resident adult and juvenile birds. Juvenile estimates correspond to birds for which at least 10 observations were obtained. * p<0.05, **p<0.01, ***p<0.001. MCP stands for minimum convex polygons method.

Furthermore, being of smaller size (table 1), core areas showed still some overlap with adjacent cores (Core area including 75 % of observations; Plot A, 0"SE= 3.0 " 0.5 individuals, N =13; Plot B, 0"SE= 3.0 " 0.5 individuals, N =13; Figure 2). The number of adult ranges with which each home range overlapped did not differ between the two plots (t-test, t_{25}=1.9, N.S). The ranges of the two mates from known breeding pairs overlapped extensively (0"SE= 86.5 " 3.6 %, N =9). I often observed groups of juveniles moving within adult home ranges, indicating that sedentary adults did not have an exclusive spatial use of their territories (see below). Adults showed a remarkable site fidelity to previous breeding territories with 85% of individual Jacob's values being higher than 0.75 (0"SE=0.85 " 0.03, N =38), which significantly differs from a random expectation (t_{38}= 22.4, p<0.001). The data suggest that once a bird has bred in a given area, it does not move far from it. This is further supported by the finding that adult home ranges in two consecutive winters overlapped to a very high degree (0"SE=72.1 " 5.9 %, N =16).

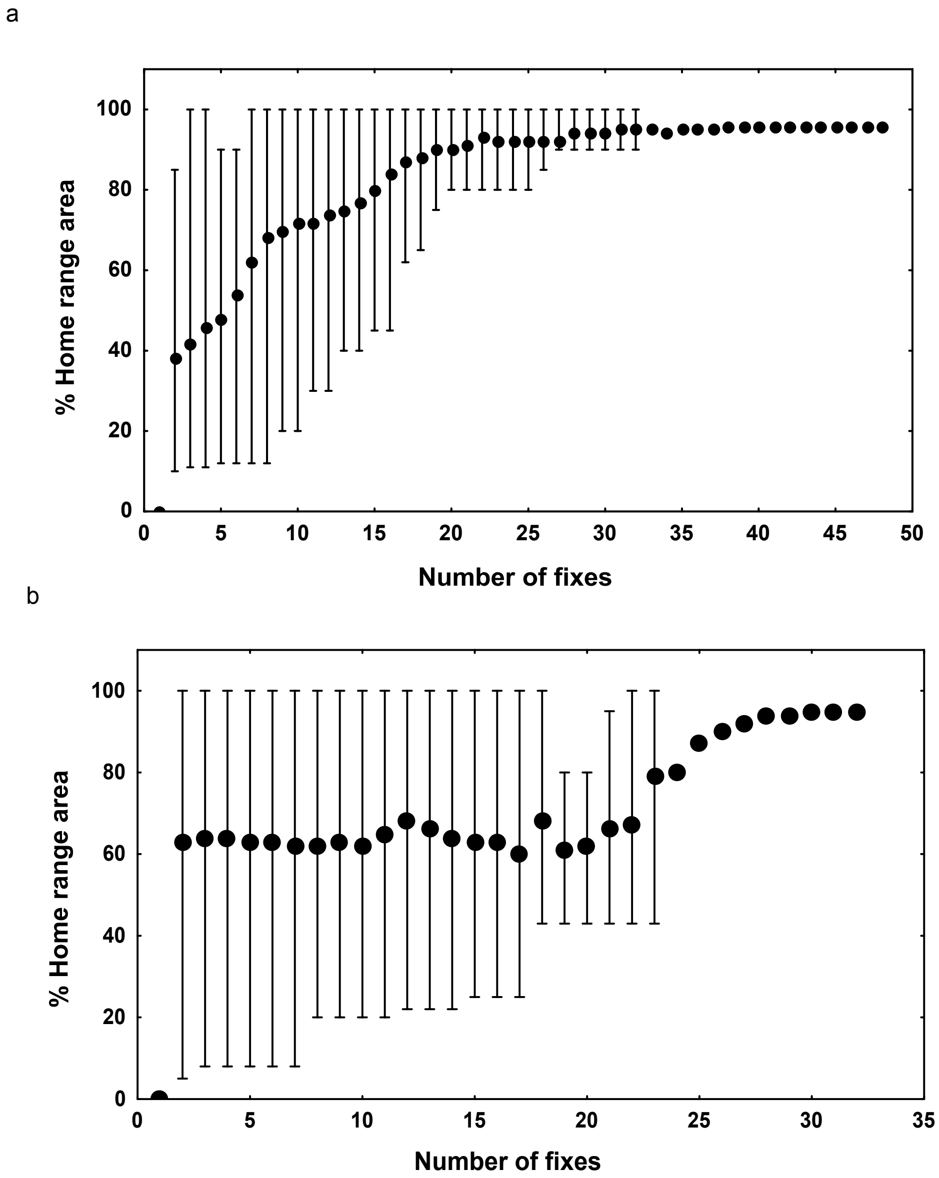

Figure 1. a. Incremental area plot based on winter home ranges of 66 adults birds. After 19 observations, home range area estimates approach 90 % of the total value. b. Incremental area plot based on winter home ranges of 74 resident juvenile birds. No asymptote was reached with the number of observations obtained. Points represents means and bars 95 % confidence limits for utilisation distributions.

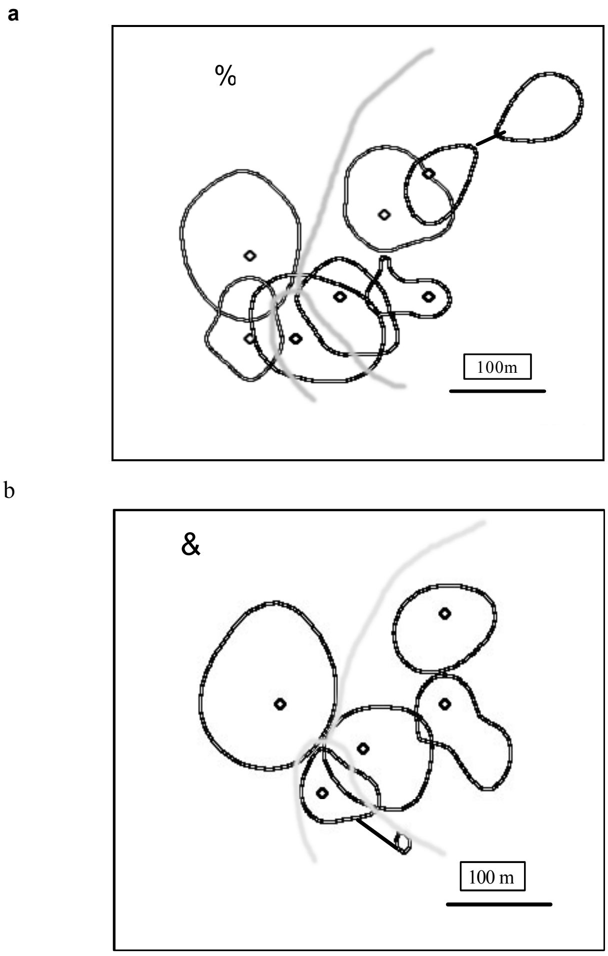

Figure 2. Core areas (Kernel method, minimum estimates containing 75 % of the total home range area) of the 12 adults, 7 males (a) and 5 females (b), re-sighted in plot A during the winter 1997-98. Grey lines represent roads.

Home range and spacing of juveniles

Only 74 out of 288 colour-ringed juveniles (26.6 %) were resighted at least once after a 10 day period following ringing and were considered residents. No unbiased estimates of these ranges could be calculated as home range area increased with increasing sample size (Figure 1b). However, I could estimate the minimum home range sizes of 22 of the 78 resident juveniles for which I was able to obtain at least 10 observations (Table 1). Bearing in mind that home range estimates are based on a small representation of the more resident juveniles, these seemed to have much larger home ranges than adult birds (Table 1). Analyses performed on the Kernel estimates gave similar values (Table 1). However, high values of Jacob’s index (Figure 3) indicated that many resident juveniles tended to be re-sighted closer to the place where they were ringed than expected by chance. These data suggest that resident juveniles seemed to have large, but more or less restricted, ranges around a central area. I did not find any relation between Jacob’s indices and the number of days between the ringing date and the date of last re-sighting (Spearman, r=0.05, t_{66}=0.46, N.S.). I found birds with low Jacob´s indices (less resident) even long after ringing, stressing the point that residence was not an artefact of the sampling effort, and that spacing seemed to be unrelated to the period of time elapsed since the capture of the bird.

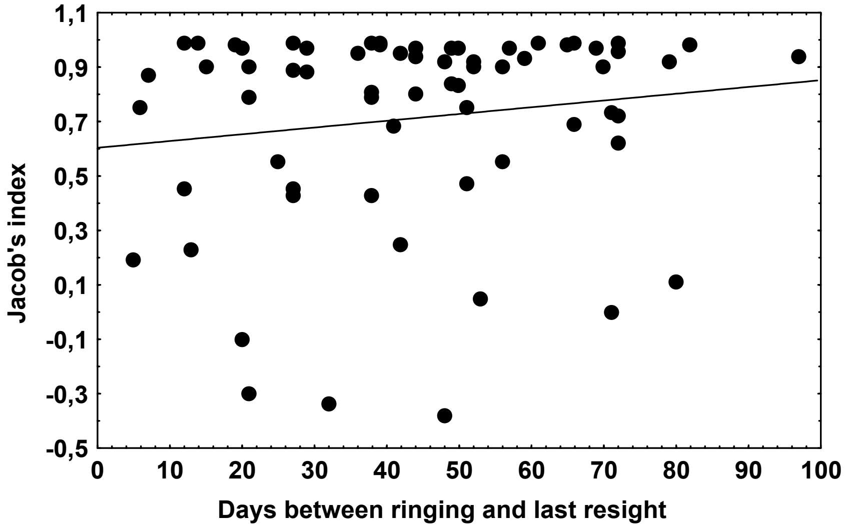

Figure 3. Scatter plot representing the relation between tendency to remain closer to the ringing site (given by Jacob's index) and the days between ringing data and date of last re-sight of resident juvenile birds.

Home range overlap in resident juveniles

The home range of resident juveniles re-sighted in plots A and B overlapped at least to some degree with almost all resident adults present in each plot (0"SE =10.7 " 0.5 adults, N =15 resident juveniles in plot A; 0"SE = 7.2 " 0.6 adults, N =10 resident juveniles in plot B). No extensive movements of more resident juveniles existed between distant areas (plots A and B), and only two re-sighted birds changed locations once during the study period. Home ranges of juveniles overlapped extensively without a clear pattern emerging. Resident juveniles shared home ranges on the average with 16 resident juveniles, the average overlap of the ranges being 24 % of the total surface (N=44). Given the small number of juveniles re-sighted this is a very conservative estimate. Thus, the home range overlap of juveniles either with the other juveniles or the adults is likely to be much greater than described here.

Group coherence and flocking behaviour

The very high coherence indices (Ekman 1979a) (0"SE = 0.73 "0.03, N =9) suggest strong pair bonding of adults having bred together in the area the previous summer. Adults were seen also with other juveniles, but except for three individuals associations showed a final value of 0 due to the scarcity of simultaneous re-sights. Another association recorded between adults and juveniles resulted from juveniles pairing with an already settled adult (i.e. one that possibly had lost its mate). In such cases, new associations began to behave as if both birds were mated and coherence indices were very high (coherence index, 0"SE =0.78"0.06, N =3).

From all the possible combinations of two juveniles ringed together at the same place, only 20 pairs were re-sighted afterwards. On only 2 occasions were the two birds re-sighted more than once together. Thus, no homogeneous sets of juveniles could be detected in this study. However, although the association within juvenile groups seemed to be very loose, most of the pairs re-sighted after the ringing (90 %) involved resident juveniles captured at the same study plot. This may indicate some kind of loose relationship between resident juveniles sharing a given area. Overall, the results obtained for juvenile group members were interpreted as a low, if any, degree of cohesion within juvenile aggregations.

Adults travelled alone or in pairs more frequently than juveniles did (X^2_4= 29.83, p<0.0001, Figure 4). Furthermore, mean size of groups containing adults was smaller than that of groups where colour-ringed juveniles were sighted (Mann-Whitney U-test, Z=5.09, n_1=72, n_2=107, p<0.0001). However, adults joined juvenile groups on several occasions. This behaviour seemed to be actively performed by adults, because on some occasions (N=8), I observed an adult in its core area joining a group of juveniles when they appeared. After a few minutes, the adult bird had returned to its core area while the juveniles flew elsewhere. Juveniles were, but on few occasions (i.e. juveniles mated with an adult), re-sighted in company of several other individuals. These groups were often quite large (>10 individuals, 45% of records, figure 4), easily up to 50 individuals, reaching on one occasion up to 100 individuals, including birds of other species such as Crested tits (*P. cristatus*), Goldcrests (*Regulus regulus*) and Short-toed treecreepers (*Certhia brachydactyla*).

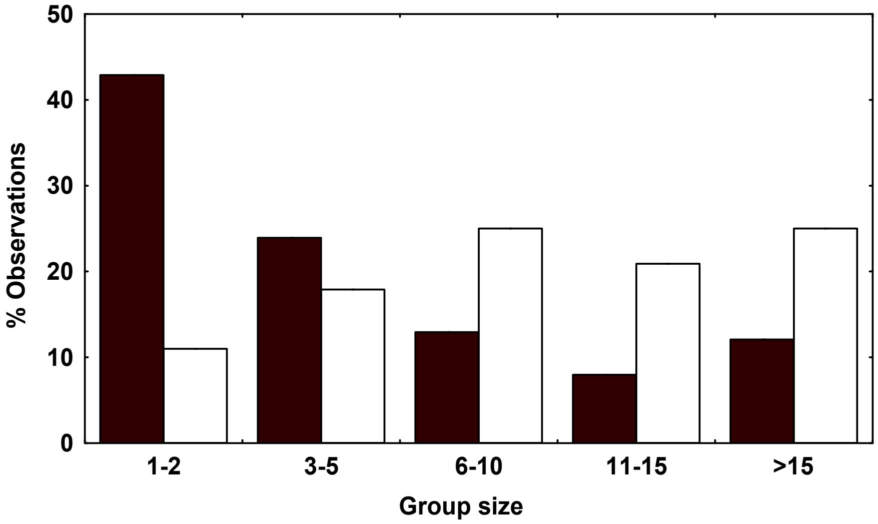

Figure 4. Distribution of group sizes estimated from flocks where colour-ringed individuals were re-sighted. Black columns include groups were adults or adults and juveniles were seen, where white columns include groups were only colour-ringed juveniles but not adults were re-sighted. Range of group sizes 1-100 individuals.

Temperature variation seemed to affect flocking behaviour of groups involving both adult or mainly juvenile individuals. Groups with adult presence tended to be of larger size as maximum daily temperature decreased (Spearman rank correlation, r_s=0.33, t_{105}=-3.65, p<0.001, Figure 5a). The same negative relation between group size and maximum daily temperature decreased (Spearman rank correlation, r_s=-0.43, t_{70}=-4.04, p<0.0001, Figure 5b) was found in groups where only juveniles were detected.

Dominance relationships

Most of the observed interactions between individuals involved contests for resources such as pine cones or needle clumps. Often interactions ended with the retreat of the defeated bird. Resident adults won almost all the interactions that took place in the core areas of their home ranges (38 won Vs. 1 lost, Sign-test, Z_{39}=5.7, p<0.001). The relative lack of interactions involving adults away from their core areas (3 won Vs. 6 lost, Sign test, Z_9=0.7, N.S.) showed that they were less clearly dominant here than in their own home ranges, mostly due to losses with local neighbouring adults (38 won Vs. 1 lost within home range, and 3 won Vs. 6 lost far from it, Fisher's exact test, p<0.001). The interactions observed seldom involved resident juveniles. However, these fights (3 won Vs. 1 lost) suggest that they might be dominant over other un-ringed individuals which were most probably juveniles also.

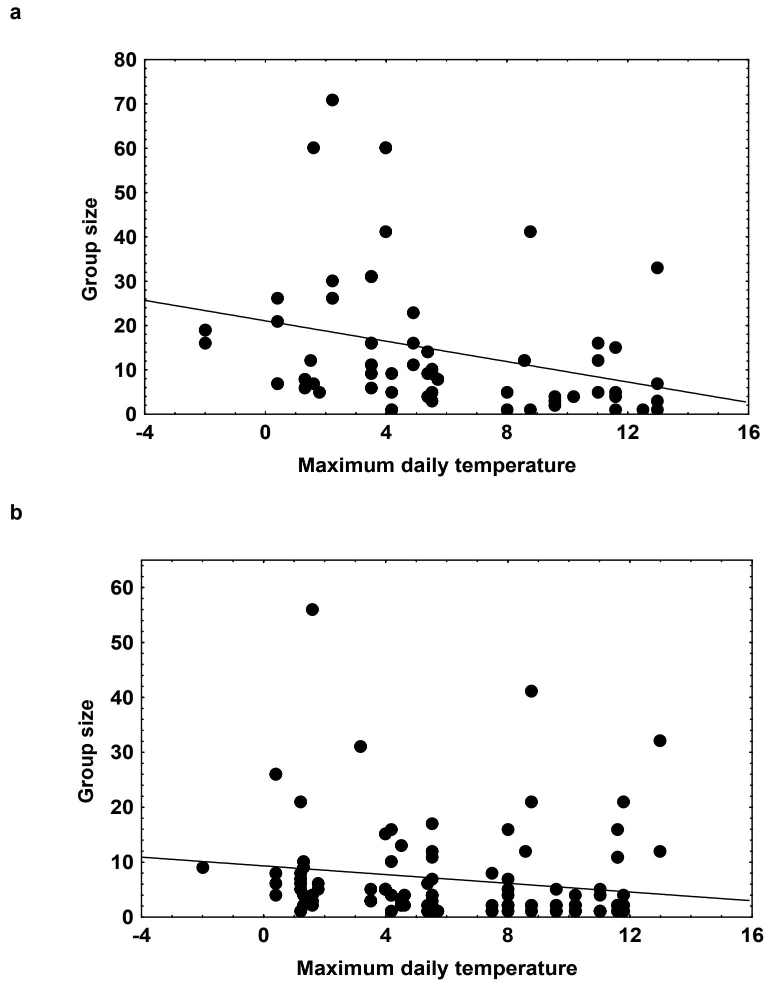

Figure 5. Group size of Coal tit flocks in relation to maximum daily temperature. a. Groups were colour-ringed adults were sighted. b. Groups were only colour-ringed juveniles but not adults were sighted.

Body size and condition of juvenile birds

Resident and transient juveniles did not differ in wing or tail-length (wing-length, residents 0"SE = 62.9"1.6, transients 0"SE = 62.7"1.5; t_{282}=1.5, N.S.; tail-length, residents 0"SE = 47.4"1.6, transients 0"SE = 47.1"1.5; t_{278}=1.6, N.S.). Wing and tail-length are sex dependent in the Coal tit, with males often having longer wing and tail-length than females (own unpubl. data). Therefore, I used wing-length as a covariate when analysing tarsus length variation in order to account for body size variation and indirectly for the sex of individuals. After overall size component was removed, the analyses showed that transient juveniles had shorter tarsi than resident individuals (tarsus length, residents 0"SE = 16.8"0.5, transients 0"SE = 17.0"0.5; ANCOVA, wing length as a covariate, $F_{1,278}$= 11.2, p<0.001). No differences were detected in the number of un-moulted great-coverts (known to be related to nestling fledging date, Christmas et al. 1989) between the two groups of juveniles (Number of un-moulted great coverts, residents 0"SE = 3.7"1.5, transients 0"SE = 3.7"1.5; U-Mann-Whitney, N_1=207, N_2=65, Z= 0.3, N.S.). Resident juveniles were found to have lower levels of subcutaneous fat reserves than transient birds (Fatness index, residents 0"SE = 1.7"0.7, transients 0"SE = 2.0"0.8; ANCOVA, hour as a covariate, $F_{1,270}$=7.0, p<0.01). Since the fatness index used in this study is unrelated to body size (Kaiser 1993), no bias in relation to sex is expected to be related to the difference detected.

DISCUSSION

In this study population, Coal tits did not maintain or defend territories, nor did they form stable coherent flocks during the non-breeding time. Adults tended to travel alone or in pairs and showed a high degree of fidelity to previous breeding areas, without territorial defence. They also maintained breeding territories as the core of their winter home ranges and were dominant within them (i.e. site-related dominance, De Laet 1984). Neighbouring adults flocked together occasionally, but ranges were easily differentiated.

The social organisation of juveniles was not so clear. Most juveniles can be regarded as transients, since they were not re-sighted within the study area after ringing (Hinde 1952). They usually moved in large flocks of rather unstable composition and had a large home range. However, the most resident juveniles seemed to have restricted ranges, overlapping with those of several adult pairs. As in adults, there was no territorial behaviour involving spatial defence. Juvenile residents can be considered as floaters (sensu Smith 1984, Hogstad 1990), with varying size of the roaming areas. Based on their coherence indices with a resident adult pair, only three individuals seemed to be permanent members of a resident flock (sensu Ekman 1979a). However, in order to distinguish real flock members from juveniles established with widowed adults, a more intensive monitoring of these juvenile individuals is required in a restricted area from early autumn onwards. The morphological differences and differing fattening strategies of transients and resident juveniles point that the two strategies are qualitatively different rather than just variation in a continuum range of possible behaviours.

Social systems in the *Paridae*

This social pattern in the Coal tit is similar to the basic flock system found in some populations of non-hoarding species such as the Great or the Blue tit (Saitou 1988, see also a review in Ekman 1989a, Matthysen 1990). However, unlike the Great and the Blue tit, this Pyrenean population of Coal tits are large scale food hoarders in autumn and winter (Brotons 1998). Both juvenile and adult residents hoard food actively, and so do transient birds likely at lower rates (own unpubl. data). Thus, hoarding alone does not seem to account for a discrete territorial social system in parids, although it may partially account for the high degree of residency of part of the population. Storing may be compatible with a non-territorial basic flock system because individuals can adopt different methods to avoid cache robbery (Brodin 1994, Lahti & Rytkönen 1996). Winter social organisation is perhaps more closely dependent on local population characteristics such as population density, availability of breeding resources, and proportion of year-round residents (Smith & Van Buskirk 1988). Previous studies (Smith & Van Buskirk 1988, Matthysen et al.1992) have argued that the absence of a coherent social system and non-breeding territoriality would be attributable to the absence of resident individuals in a given area. As in such populations, birds are not searching for a future breeding position in the area, short term factors shape social systems and can lead to a loose territorial attachment and therefore, plasticity in social structure. In the population studied here, sedentary year round residents were abundant. In spite of this, territoriality was absent, both in adults and juveniles, resulting in loosely aggregated groups.

What are the reasons for the larger home ranges of juvenile Coal tits? Given that ultimately in parids social patterns during the non-breeding season are largely dependent on the establishment strategies used of juveniles (Greenwood & Harvey 1982, Nilsson & Smith 1988, Matthysen 1990), a deeper analysis of the options available to juveniles during that period will clarify the role of different factors affecting sociality. In my study population, most resident juveniles clearly behaved as floater individuals without clear home range areas (sensu Smith 1984). In a review on winter social patterns of tits, Ekman (1989a) predicted that when survival rates of floater juveniles approach that of territorial juveniles, the benefits from enhanced future chances of vacancy acquisition may overcome costs of floater life. In these conditions, juveniles would benefit from inspecting a restricted, but high number of established pairs and wait for a vacancy to occur among them. Furthermore, when the costs of inspection of new groups is low because of the small distance between established pairs (Brotons unpubl.), floaters are likely to further benefit from the searching of possible vacancies elsewhere. More northern populations of Coal tits seem to be more territorial (Ekman 1989a). In harsher environmental conditions, the survival costs of reduced hoarding opportunities can impose so high costs to floater life that juveniles would favour establishment in territorial flocks as early as possible in order to increase the benefits of storing food for future use (Brodin & Ekman1994).

Proximate constraints on territoriality

Previous studies of the winter social organisation in loosely territorial species such as the Great or the Blue tit (Hinde 1952, Saitou 1988), suggest that the high movement rate of juveniles might be linked to rich, heterogeneous and clumped distribution of food sources. In such cases, floater life would be more adaptive than a territorial and sedentary way of life. In my study area pine seeds are one of the main food sources of Coal tits after the onset of cone opening in October and throughout the winter (Brotons 1997). Mountain pines are characterised by a large and heterogenously distributed cone crop production which is often more constant among years than in other well known conifers (Génard & Lescourret 1987). Coal tits use pine seeds flexibly during the winter (Brotons 1997). So, presumably they are not forced to abandon the area, rather the contrary, as judged from the high number of transients birds recorded in this study. If so, the costs of sharing resources would be less than the cost of defending a territory against intruders (Davies & Houston 1984). This pattern would offer a proximate explanation for the absence of territoriality in the present Coal tit population (Matthysen 1990). On the other hand, the short term benefits of group living (i.e. predator defence and local enhancement, Lima & Dill 1990) would promote temporary associations of juveniles and adults depending on the prevailing environmental conditions, leading occasionally to large group sizes. The negative association found in this study between group size and ambient temperature supports the predicted role of short term climatic variation on the flocking behaviour of Coal tits.

In the present conditions, floater life may be the best choice for juveniles in order to achieve a position in the future breeding population and to enhance short term survival probability. However, reliable survival estimates of resident and transient juveniles would be required in order to test the proposed link between favourable environmental conditions and enhanced floater survival in mountain coniferous forests.

Non-territoriality, food hoarding and sedentarity

In this context, the non-significant role of hoarding on determining territoriality in this population, could come from the main use that individuals seem to give to hoarded items. Hoarded food is probably mainly used to bridge bad weather days, therefore, favouring sedentarity. Hoarding would not affect territoriality because pine seeds, which are costly to defend by means of a territory, would be readily available naturally throughout the winter (Brotons and Haftorn 1999). Although territoriality was not detected, site fidelity was extremely high in adult birds. In spite of large home ranges, resident juveniles also seemed to be sedentary during the study period. Sedentary individuals commonly dominate transient ones (De Laet 1984, Sandell & Smith 1991), which facilitates their priority to resources in case of sudden food shortages. Sedentary habit facilitates the recovery of stored food, and more important, it seems to favour breeding prospects through queuing and chances of getting a good position in the breeding population (Nilsson 1990). Therefore, winter sedentary birds might assure, or increase breeding prospects the following season, whereas transients will have to wait for future vacancies within a closed system, or move to empty areas to establish breeding territories there. These new areas are of presumably lower quality than those already occupied.

Origin of transient birds

The fact that transient juveniles had shorter tarsi and higher fat reserves than juvenile residents suggests a lower competitive ability (Sandell & Smith 1991). Tarsi are already full grown once the fledglings abandon their nests. Therefore, once corrected by overall body size, differences in tarsus length could be related to differential competitive abilities of individuals due to differences in growth rate during the nestling stage. Higher levels of subcutaneous fat reserves in transient juveniles may allow such individuals to hedge the increased variability in food supply associated with the transient life (Ekman & Lilliendahl 1993). Thus, I suggest that in my population, transient birds comprise juveniles of a low competitive ability that are temporarily attracted to the study area by its rich food resources (i.e. rich and regular pine seed crop, Génard & Lescourret 1987). Spacing patterns of transient juveniles might be mainly driven by the short-term benefits of transient life and group living rather than by the long-term benefits of territory acquisition (Senar et al. 1990). Knowledge of the movement, origin and settlement of transient individuals would help to clarify the understanding of the population dynamics of the Coal tit in mountain areas. Two further questions remained unsolved. The first is whether transients are recruited to the breeding population with the same success as residents juveniles. The second is whether transient birds have chosen transient life by themselves or are forced to adopt this strategy by residents due to the superior competitive ability of the latter.

I have shown that, 1) contrary to certain suggestions based on the hoarding habit of the Coal tit (Ekman 1989, Matthysen 1990) a population of this species in the Pyrenees does not form territorial coherent flocks during winter in a habitat I judge to be productive. And, 2) that the spacing patterns of resident and transient juveniles seemed to be dependent on different factors. Social structure of resident birds may be linked to the availability of future breeding territories, probably leading to the high site fidelity of adults and the floater life of resident juveniles. On the other hand, short term factors may attract transients to a rich area and shape temporary association of birds. In the case of the Coal tit in the Pyrenees, hoarding behaviour does not lead to a territorial flock based system. Storing behaviour may favour sedentary habit in existing established pairs. Other factors, such as the abundance of a clumped pine seed crop or a high density population can favour floater life in juveniles. Even within species, social behaviour is predicted as being plastic and to have evolved in response to the prevailing conditions (Krebs & Davies 1995). Therefore, coherent and territorial flocks, and the basic flock system might be the two ends on a continuum of possible social organisations for a range of environments (Matthysen 1989).

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STATUS SIGNALLING IN THE COAL TIT (*PARUS ATER*): THE ROLE OF PREVIOUS KNOWLEDGE OF INDIVIDUALS[2]

Abstract : In social species, the existence of signals associated with the social status of individuals might help to reduce the intensity and the number of the agonistic interactions produced between group members. This paper analyses the importance of plumage badges on the determination of dominance relationships between Coal tits (Parus ater). First, I determined dominance relationships within three groups of 6 juveniles males of similar body size that had lived together for two weeks in outdoor aviaries. Dominance hierarchies among individuals were not associated to bib size. Second, experimentally, I manipulated the bib size of some of the birds. The result of encounters between manipulated and control individuals without prior knowledge of each other, showed that individuals with larger bib sizes were more often dominant than unmanipulated ones. Therefore, badge size had no impact on the outcome of conflicts among companions within groups of stable composition, but the impact was significant when knowledge was lacking.

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[2] Etología, 6 :49-52 (1998)

INTRODUCTION

Within non-breeding flocks of group living species individuals compete for priority of access to resources such as food or shelter. Competition through agonistic interactions is energetically costly (Hogstad 1987). Thus, any individual which possessed attributes facilitating a reduction in the number or in the intensity of interactions would be presumably at an advantage. The status signalling hypothesis states that variations in plumage colour are used to signal differences in individual capabilities to win agonistic contests (Rohwer 1975, 1977). Potential badges signalling status of individuals have been proposed in a number of species (Järvi & Bakken 1984, Pöysa 1988, Moller 1987, Studd & Robertson 1985, Senar & Camerino 1998, Senar 1999 for a review). However, often the evidence of a given badge signalling status is contradictory, raising the need to identify the situations where the signal may or may not work in a dominance framework. Prior knowledge of individuals might reduce advantages of a signalling system because other factors might override the dominance ability cues provide by plumage variation. Therefore, status signalling would be particularly beneficial if flocks are unstable with regard to membership, since it would reduce the cost of asserting status each time a new flock was joined (Lemel & Wallin 1993).

Natural variation in character is a prerequisite for a plumage badge to function as a signal, being the second requirement the correlation of this variation with dominance. In the genus Parus, the bib of Willow tits (Hogstad & Kroglund 1993) and the breast stripe of Great tit (Järvi & Bakken 1984, Whitfield 1987) seem to function as signals of resource-holding potential accomplishing these two requisites. The objective of this study was to assess the role as signal of the bib size in Coal tits (*Parus ater*) living in flocks during the non-breeding season. Particularly, the main point was to identify the importance of the bib size in contest outcome between individuals with and without prior knowledge of each other.

METHODS

I captured 18 Coal tits from three different locations in the Eastern Pyrenees. The three sites were separated by at least 10 km, in order to minimise the probability that captured individuals in different places had previous knowledge of the others. All individuals were juvenile males according to Svensson (1992) and unpublished data on sexual size dimorphism of individuals in the study populations. Individuals captured at the same site (n=6) were kept together in separate outdoor aviaries (2x 1.5x 1 m) without visual contact. The individuals were colour ringed and the number of non moulted great covers, tarsus, tail and wing length were measured. The three bib size measures taken were: maximum width and height of the bib and width of the bib at half the value of the measured height. A relative index based on bib shape measures gave a good estimation of overall bib size in a sample of museum skins (n=32, r=0.86, p<0.001). Exact bib sizes of museum skins was calculated by drawing on paper real bib sizes of a sample museum skins and weighting them on a precision balance.

Coal tits were fed ad libbitum with pine seeds, sun flower seeds and tenebrionidae larvae. Vitamins were added twice a week. After two weeks, the dominance hierarchies were determined in each flock after 3 hours of food deprivation. Dominance was estimated from entrance order to the feeder and from interaction outcomes. We assessed the importance of bib size and other morphological measures on dominance rank which was log transformed, (see Lemel & Wallin 1993) using a backward multiple linear regression analysis.

In the next part of the experiment, from each group, I choose five birds. The top ranking individual of each group was excluded because of size asymmetries in relation to the other individuals. Two of these five birds were chosen from every second position in the hierarchy in order to enlarge their bib size. With a black marker, bib size was enlarged on a strip 5 mm wide following its original contour. The other three individuals were painted on their original bib contours.

All birds were maintained in the experimental cage (50x 50 x 50 cm) for at least 24 hours prior to the experimental trials which took place a maximum of four days later. Therefore, no bias in the prior knowledge of the experimental cage existed. Since birds with enlarged bibs were tested pair-wise against control birds from the other two flocks, the contestants had no prior information of their opponents fighting ability. Some of the birds were used in different dyads but never against the same opponent. Experimental confrontation lasted 35 minutes. The experimental cage was supplied with a piece of pine seed (4 mm long) every fifth minute. We recorded the following variables from a hide nearby the cage: the number of times each individual had access to a food item, the total number of agonistic interactions won by each individual of the dyad; the number of direct interactions such as attacks, robberies of food items, supplants, won by each individual; and the number of indirect interactions such as waitings and non-forced withdraws.

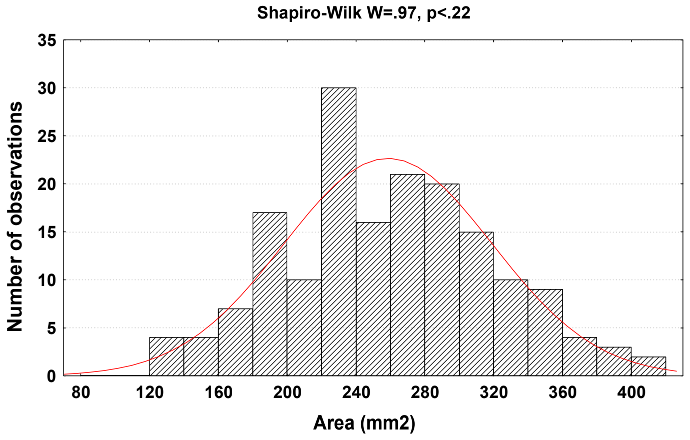
Individuals with enlarged bibs were selected in order to avoid dominance and size biases. Dyads did not differ in size in more than 0.75 mm. In order to check further for any possible bias with respect to body size for either individuals with enlarged bibs or controls, we tested whether contest outcome was somehow influenced by this variable. I could not include the individuals of one group in the dominance analyses due to the escape of some of its members.

RESULTS

Bib size variation in natural conditions

Bib size distribution in natural conditions followed a normal distribution both in juvenile and adult birds (Figure 1). When age classes were grouped together, bib size still fitted significantly a normal distribution (Shapiro-Wilk W=0.975, n=222, N.S.). Bib size was significantly correlated to wing length in both adults and juveniles (Wing length, r=0.53, t_{219}=8.96, p<0.0001 ; age, r=-0.06, t_{219}=-1.06, N.S.). Furthermore, I did not detect any difference in bib size among age classes ($F_{1,219}$=1.14, N.S., Figure 1).

a



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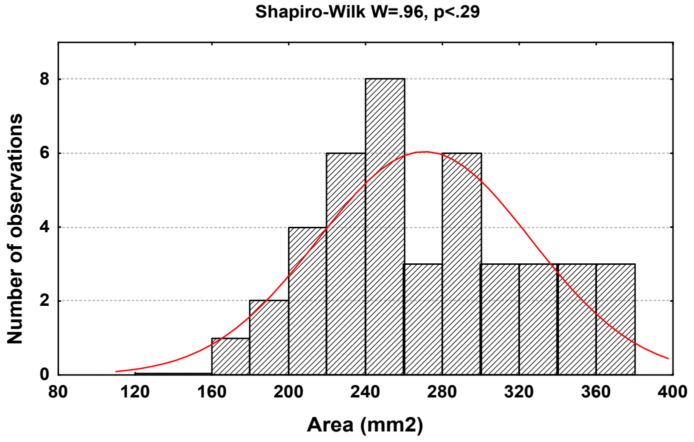

Figure 1. Range of bib size (mm^2) in a natural population of Coal tits in the Pyrenees A. Juveniles (n=172 individuals). B. Adults (n=50 individuals).

Dominance and prior experience about rivals

Results of a backward multiple linear regression performed on the two groups, showed that only wing length was related to the rank achieved by individuals in the dominance hierarchy (table 1, figure 2). The results were consistent among experimental groups after using them as a dummy variable in the multiple regression model (table 1). Therefore, taking into account the variation explained by the variable wing length, bib size did not seem to add any significant explanation to dominance hierarchy among individuals with previous knowledge (table 1).

	Beta	t value	P
Wing length	-0.73	-3.41	0.006
Tail length	-0.32	-1.17	0.27
Tarsus length	-0.13	0.54	0.59
Bib size	-0.24	0.81	0.43
Number of unmoulted great covers	-0.05	-0.23	0.81
Experimental group	-0.17	-0.77	0.46

Table 1. Linear regression model with the number of unmoulted great covers, bib size, tarsus, tail and wing length, combined with the position in the hierarchy as the dependent variable (corresponding 1 to the top dominant and 6 most subordinate bird).

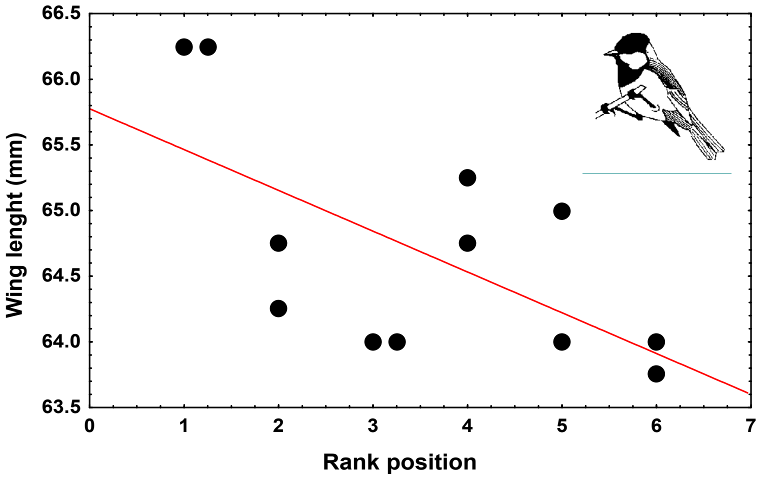

Figure 2. Linear relationship between dominance rank (corresponding 1 to the top dominant and 6 most subordinate bird) and wing length within flocks of Coal tits with stable membership. Spearman rank, n=12, r=-0.61, p<0.05.

Dominance and lack of experience about rivals

Each manipulated individual, with the bib enlarged, was confronted with unfamiliar unmanipulated individuals from the other two flocks. In total we performed 18 experimental trials, and 12 of them could be included into the analyses because birds interacted long enough to record dominance outcomes. Birds with enlarged bib sizes were more often dominants than unmanipulated ones. Out of 12 encounters, 10 ended with the manipulated individuals beating the bird with the smaller bib (Sign test, Z=2.02, p=0.04). Furthermore, owing to their dominant status, manipulated individuals took and consumed a larger number of food items than unmanipulated ones (Wilcoxon test, n=12, Z=3.3, p=0.0008).

Manipulated and unmanipulated individuals did not differ in the number of direct agonistic interactions they were engaged in and won by them (Wilcoxon test, n= 12, Z=1.5, p=0.14, figure 3). However, manipulated birds won more indirect interactions than unmanipulated ones (Wilcoxon test, n=12, Z=2.7, p=0.007, figure 4). That is, birds with smaller bib sizes carried out more waitings and non-forced displacements than bib enlarged birds.

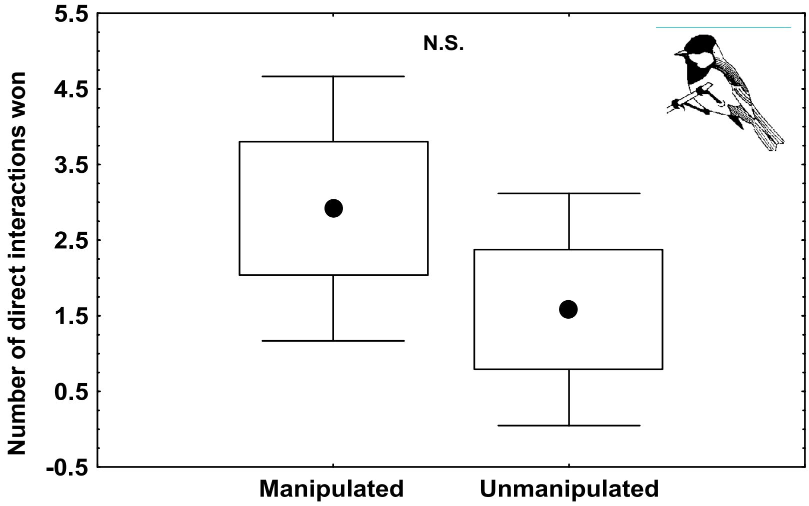

Figure 3. Number of direct interactions such as attacks, robberies of food items and supplants, won by each individual of the dyad during the experimental trials. Bars represent standard deviations and boxes standard errors.

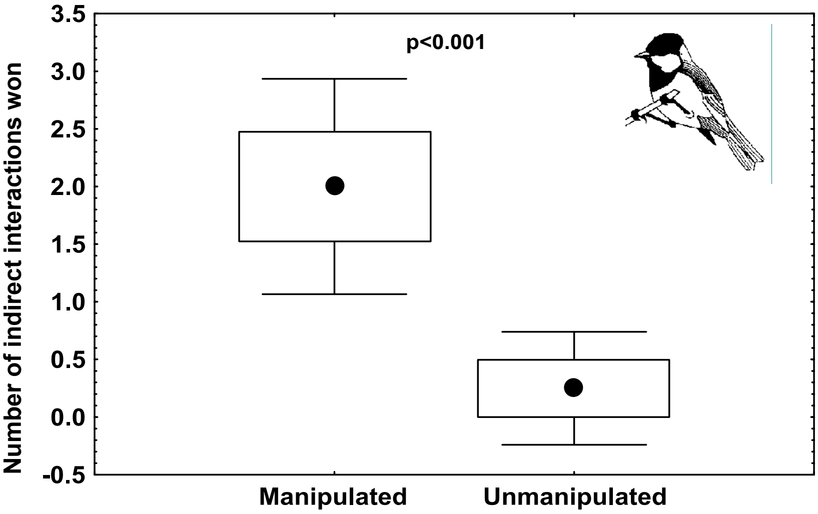

Figure 4. Number of indirect interactions such as waitings and non-forced withdraws won by each individual during the experimental trials. Bars represent standard deviations and boxes standard errors.

DISCUSSION

Bib size did not seem to influence dominance relationships among individuals with prior knowledge of each other. Among stable groups only wing length, as the main estimator of body size, seemed to be related to dominance. On the other hand, among strangers, individuals with enlarged bibs were more likely to win encounters, mostly due to the active behaviour of unmanipulated birds which seemed avoid large badged individuals withdrawing as soon as they approached with no mediated aggression, or waiting until food was available. Unmanipulated individuals seemed to perceived the large bib sizes of rivals and reacted accordingly by reducing the intensity of the interactions in which they were subordinates. Therefore, the bib size of the Coal tit seems to function as a signal of status, and supports the status signalling hypotheses (Senar 1999), at least in unfamiliar flocks. The fact that the badge system for status signalling in the Coal tit may fail to work within groups of stable composition may be because the relevance of variation in badge size may shift from a signalling system into a recognition system when individuals become familiar (Lemel & Wallin 1993). In unstable flocking conditions, individuals unaware of the resource-holding potential of an opponent may use badge size to estimate dominance. In other bird species, status signalling has also been demonstrated when contestants lacked information about the fighting ability of the antagonist (Rohwer 1985, Roskaft & Rohwer 1987, Lemel & Wallin 1993). My findings, with regard to the high frequency of indirect interactions lost by unmanipulated birds, lends additional support to the status signalling hypotheses.

During autumn and winter, juvenile Coal tits live in social groups of large size. These large groups appear to be of rather unstable composition (Brotons 1997). Therefore, a status signalling system might be of importance in the Coal tit at least in two particular points of their life when stranger individuals have higher probabilities to meet. First, during juvenile dispersal, when juveniles disperse from parental territories and individuals from different areas mix, and consequently lack experience about each other's resource-holding potential (Lemel & Wallin 1993). And second, during winter time, in encounters between transient winter flocks (Brotons 1997, Senar 1999).

Given that in the Coal tit status signalling system seems to work when prior experience about the rival is lacking, its importance in front of other asymmetries determining social dominance should be analysed (Arcese & Smith 1985, Koivula et al. 1993). More concretely, the interactions between prior residence and status signalling, on unknown individuals appears of special interest in this context (Sandell & Smith 1991). Status signalling has been shown to be an important mechanism in relation with dominance. The new questions posed by the studies so far conducted, merit without any doubt further insights in the topic.

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CHANGES IN THE FORAGING BEHAVIOUR OF THE COAL TIT (*PARUS ATER*) DUE TO SNOW COVER[3]

Abstract : This paper studies the foraging behaviour of the Coal Tit (*Parus ater*), a small passerine wintering in mountain coniferous forests in the Pyrenees. I compared tree site use and the foraging techniques of birds, (1) under snowy conditions, when snow covered the outer substrates of pines, and (2) under snow-free conditions. Under snowy conditions, birds foraged in the lower and inner parts of trees, using trunks and thick branches as their main foraging substrate. During normal, snow-free conditions, birds used upper and outer parts of trees feeding mainly on pine cones and needles. Movement patterns of individuals differed from one condition to the other. During snow free conditions, birds used more costly energy methods, mainly flight and hanging position, while in snowy conditions they used lower energy consuming methods, mainly hopping. The results support Norberg's hypothesis (1977) that when the prospects of obtaining prey increase, foraging methods requiring higher energy consumption can be used.

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[3] Ardea, 85 :249-257 (1997).

INTRODUCTION

Weather conditions are a significant factor in determining the way in which birds interact with their environment. It is well known that climate and weather play an important role in shaping the migratory patterns of birds (Baker 1978, Elkins 1983) and also influence many aspects of bird behaviour and ecology, such as foraging or reproductive patterns (Grubb 1979, Spencer 1982, Elkins 1983).

In winter, birds living in northern environments or at high altitudes suffer the greatest pressures from a harsh climate. Small forest passerines are especially vulnerable to bad weather because they need to forage almost continuously during the short winter days in order to meet their minimum energy requirements (Spencer 1982). Weather conditions have been shown to influence the foraging behaviour of certain forest passerines in such a way that birds tend to reduce their energy expenditure (Grubb 1979, Carrascal 1988, Lens 1996, Wachob 1996) and maximise prey intake profitability (Pyke 1984, Stephens & Krebs 1986). Although bird survival may be strongly influenced by changes in behaviour (Jansson et al. 1981, Ekman 1984), the processes and proximate factors associated with weather-induced shifts in foraging behaviour are not completely understood.

An example of such changes are the short-lasting modifications which occur as the available foraging surface is decreased or altered in some way. As snow accumulates on tree surfaces, snowfalls seem to have a negative impact on bird foraging behaviour, by making the search for prey more difficult (Spencer 1982, Macarrone 1987, Smith 1991). When the available foraging surface decreases, birds must adapt foraging techniques and use of space to the new conditions. The working hypothesis, following Norberg (1977), is that in order to optimise their energy balance, individuals foraging in surface-reduced conditions will use energetically cheaper searching methods due to the decreased profitability of prey exploited in these substrates.

Therefore, this study seeks to clarify the effect of tree snow cover on the foraging behaviour of the Coal Tit, in a mountain coniferous forest. The specific questions raised are:

-Does the snow accumulated on trees produce a shift in tree use?

-Do birds change their prey searching techniques after a snowfall?

-If so, what are the main characteristics of the searching techniques used in differing conditions, and could they be related to preference of substrate used?

STUDY AREA AND METHODS

The study area of about 150 ha is located in the eastern Pyrenees, in the north-east the of Iberian Peninsula, at an altitude between 1800-2100 m. Mountain Pine (*Pinus uncinata*) dominates the study area with Scots Pine (*Pinus sylvestris*) predominant in southern slopes and in lower altitudes. Understory is scarce, dominated by *Juniperus communis* and grass, more information about the vegetation can be found in Vigo (1976). The forest has been exploited until recently on a long-term cycle, resulting in tree stands of different ages in the area. The annual precipitation is approximately 1100 cm, around 35 % falling as snow during winter months. Snow remains on the ground from December to April. Usually about five to six times a year, a precipitation of more than 10 cm of snow occurs, leaving snow on trees for three to four days depending on temperature and wind speed. The winter of 1996 was especially snowy, with 16 days on which precipitation of more than 10 cm of snow fell.

The Coal Tit is a small forest passerine (body weight x=9.22 g, S.E.=0.51, n=255, unpubl. data). In the Pyrenees, during winter it lives in flocks of up to 70 individuals often with up to three Crested Tits, up to three Goldcrests, and solitary Treecreepers (unpubl. data). Therefore, in our study area flocks were clearly dominated in numbers by the Coal Tit and, frequently, this species was their only component.

METHODS

Foraging behaviour was monitored between January and March 1996. During this period, two conditions were distinguished according to the amount of snow accumulated on the trees. During snowy conditions (1), a snow layer of more than 5 cm covered most outer parts of pines, whereas under snow-free conditions (2) no snow at all was noticed on tree surfaces and birds could freely choose foraging substrates. Days on which data were collected were chosen so as to avoid intermediate amounts of snow on trees. Thus situations were clearly differentiated, and assignment of observations to study conditions could be conducted without ambiguity.

During data collection days, I walked systematically throughout the study area searching for tit flocks. When a flock was located I used two techniques to describe the birds' foraging behaviour. Tree site and substrate use were described by instantaneous sampling of the birds' position (Carrascal 1983, Morrison 1984), whereas searching techniques were recorded by the continuous following of focal individuals (Robinson and Holmes 1982).

Instantaneous sampling describing the position of Coal Tits on trees was initiated five seconds after a bird was located (to avoid the recording of conspicuous behaviour). Whenever possible, consecutive observations with a 20 s delay were taken with no more than four consecutive samples per individual to assure statistical independence (Carrascal 1983). Space use was measured with a range of variables using rank scales (derived from Carrascal 1983), relative height (in the tree, 1 to 4, from the bottom to the top), distance from the trunk (1 to 4, from the trunk to the periphery). Also the substrate (trunk, thick branch >1cm, twig < 1cm, needle, cone and others) and the individual activities (foraging, bill pointing downwards; or vigilance, bill pointing above the horizontal) were recorded

Unfortunately, I obtained an insufficient amount of data on colour-ringed individuals to perform analysis on an individual basis. However, it is very unlikely that there was a systematic difference between the birds sampled under the two conditions. Some unbanded transient birds may have been sampled twice on different days of the study, but never on the same day because I changed groups after the observation of unbanded birds. In such cases the time elapsed between observations and the movement of individuals suggest that possible pseudoreplication of the data was not a problem (see also Leger & Didrichsons 1994). Observations were taken between 8.00 a.m. and 14.00 p.m. by the same observer so as to avoid possible bias resulting from different interpretations of each variable and under similar temperature and wind speed conditions, since these factors can influence space use in forest passerines (Grubb 1979). In total, 95 observations were taken during three different periods of snow (four sampling days), and 121 observations were taken during snow free conditions (nine sampling days).

Continuous sampling of focal individuals started 5 seconds after the bird was located on the tree. Searching movement was defined as any change in position made by a bird that was searching for prey. Number of hops, short flights (<20 cm), medium distance flights (20 cm -1 m) and long flights (>1m) were recorded as searching movements. Also the number of pecks (i.e. head movements directed to capture prey), hovers, hanging positions, number of times the bird switched from one tree to another and height of visited trees were carefully registered. Each sequence ended when the bird was lost from sight. The foraging sequences of the individuals were dictated to a tape recorder and transcribed later. Analyses only included those foraging sequences longer than 25 s (x=61 s, S.E.=5.6). I pooled sequences of the same individual collected during a given sampling period, therefore only independent observations on different individuals, mostly one sequence per individual, were included in the analyses. In total, 24 of such sequences were registered under snow-free conditions and 16 under snowy conditions.

In order to identify the prey available for Coal Tits on trunks and thick branches, the number of arthropods was measured on these substrates. From six trees where Coal Tits had been seen feeding under snowy conditions, I examined 40x40 cm surface of trunk and thick branches at a height of 1.5 m. Samples were taken by gently cleaning the bark surface with a brush, and by letting the resulting material fall into a plastic bag. Later the samples were examined in the laboratory and all arthropods bigger than 1 mm were counted. Coal Tits foraging on outer canopies fed mainly on pine seeds in our study area (see results), and secondarily on medium-size arthropods, as confirmed for many other populations of Coal Tits (Haftorn 1956, Gibb 1960, Obeso 1987, Cramp and Perrins 1993, Suhonen 1991). Hence no prey samples from the outer parts of trees were collected in this study.

Shannon's diversity index corrected for sample size (Bowman et al. 1971) was used as a measure of niche breadth in the distribution of positions and substrate use in trees. Statistical analyses were performed according to Sokal & Rohlf (1981).

RESULTS

Instantaneous sampling of birds showed that when snow covered the outer tree surfaces, individuals used the lower and inner parts of the trees more frequently than when trees were free of snow (height, X^2_3= 39.41, p<0.001; distance from trunk, X^2_3= 80.92, P<0.001, figure 1).

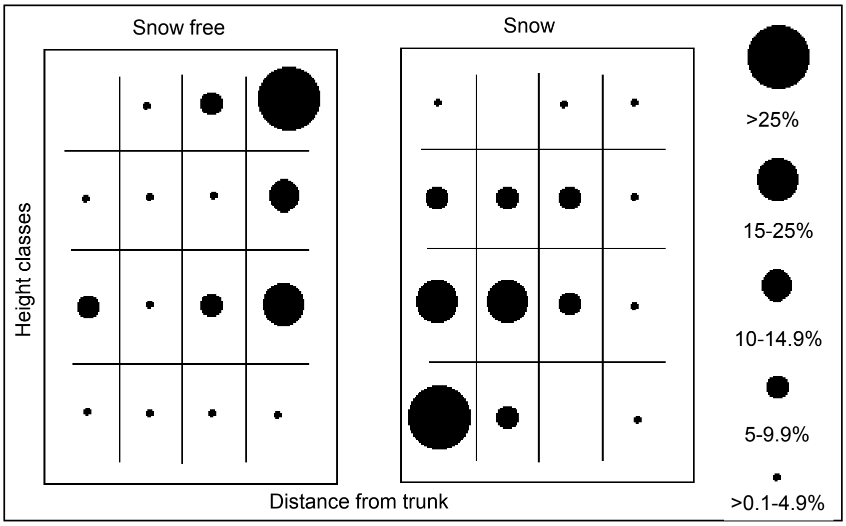

Figure 1. Frequency use for each of the 16 foliage regions delineated by relative height and distance from trunk. Horizontal axis represents distance from the trunk (from left to right, on a scale of 1 to 4, trunk to periphery), and the vertical axis relative height (increasing from bottom to top).

Pine cones and needles were the most frequently visited substrates during snow free conditions, with birds using other substrates infrequently, mainly branches, to consume pine seeds taken from cones (figure 2). In snowy conditions, Coal Tits used trunk and thick branches as their main foraging substrates (X^2_5=92.75, P<0.001, figure 2). Nevertheless, I did not find significant variation in niche breadth between conditions (i.e. diversity of 16 parts of the tree exploited during foraging, table 1). Niche breadth in substrate use did decrease in snowy conditions, thus when snow was present, birds concentrated their foraging on fewer substrates than they did when trees were free of snow (table 1).

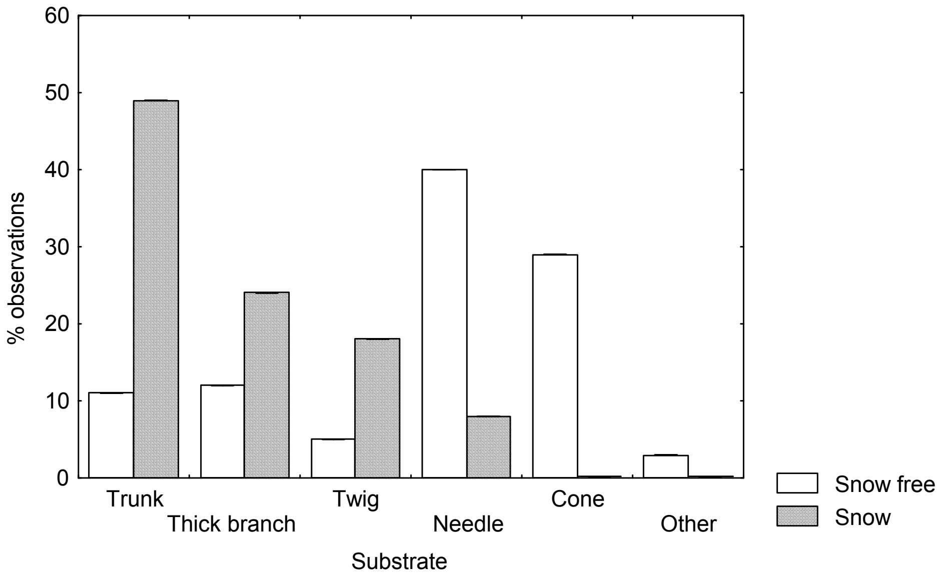

Figure 2. Substrate use by birds in snow-free and snowy conditions.

Continuous focal sampling of individuals showed that the total number of searching movements did not differ between snowy and snow free conditions (table 2). However, the proportion of different movement types differed greatly between both conditions. The frequency of short and medium distance flights was greater in birds foraging on snow-free surfaces, whereas the difference in long-flight frequency remained non-significant (table 2). Although the number of hops did not differ between conditions, the number of hops made per flight undertaken was greater under snowy conditions (table 2). As a result, birds spend more time moving and moved over greater distances in snow-free conditions as usually flight takes more time and implies travelling greater distances than when hopping.

	Conditions					
	Snowy		Snow free			
	Diversity	S.D.	Diversity	S.D.	t-test (1)	d.f.
Tree site	2.20	0.032	2.17	0.046	0.017 (N.S.)	162
Substrate	1.14	0.084	1.40	0.033	1.972 *	194

(1)p<0.05 (*).

Table 1. Substrate use and tree site diversity of foraging niches under snow and snow free conditions. Values are the Shannon diversity index for the distribution. S.D. are standard deviations.

The number of hanging positions and pine cones visited by the birds was higher under snow free conditions. In addition, the number of pecks increased when birds foraged on snow covered trees (table 2). Coal Tits seldom used hovering as a searching technique and its frequency of use did not differ between conditions. No differences were found in the height of trees exploited by birds between conditions (t-test=2.06, d.f.=36, N.S.).

In order to obtain a better interpretation of movement patterns and foraging data and to show potential associations between the variables measured, a principal component analyses (PCA, Battacharyya 1981) was conducted. Out of nine initial variables, four independent factors were extracted to explain 78 % of the variance contained in the data set (table 3).

	Snow free conditions (N=24)		Snowy conditions (n=16)		
	Mean	SE	Mean	SE	t-test (1)
Pecks (no/min)	18.12	1.72	27.49	3.50	2.66 **(2)
Short flights (no/min)	7.43	0.88	4.35	0.83	2.38 *
Medium flights (no/min)	2.09	0.43	0.44	0.17	2.94 **
Long flights (no/min)	1.22	0.31	0.67	0.23	1.25 N.S.
Hops (no/min)	8.33	0.81	11.09	1.49	1.76 N.S.
Hovers (no/min)	0.50	0.24	1.13	0.52	1.24 N.S.
Hangings (no/min)	3.62	0.52	1.53	0.51	2.72 **
Pine cones (no/min)	3.17	0.54	0.09	0.09	4.46 ***
Tree changes (no/min)	1.53	0.31	0.87	0.25	1.52 N.S:
Total number of movements (no/min)	19.14	1.41	17.1	1.91	0.85 N.S.
Number of hops per flight	0.88	0.13	2.59	0.57	3.54 **

(1)T-test corrected for different variance estimates when necessary.
(2)p<0.05 (*), p<0.01(**), p<0.001(***).

Table 2. Movements and activity of Coal Tits recorded under snowy and snow free conditions. S.E. are standard errors. Total number of movements (all types of flights plus hops), number of hops per flight (number of hops divided by total number of all types of flights).

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Pecks (no/min)	-0.83			
Short flights (no/min)	0.52	0.62		
Medium flights (no/min)	0.73			
Long flights (no/min)			0.96	
Hops (no/min)		-0.87		
Hovers (no/min)				0.80
Hangings (no/min)		0.33		-0.79
Pine cones (no/min)	0.33	0.61		0,38
Tree changes (no/min)	0.60		0.59	
Explained variance (%)	24	20	18	17
T-test of factors between conditions	p<0.01	p<0.05	N.S.	N.S.

Table 3. Factor loadings resulting from PCA analyses of movement patterns of Coal Tits under snowy and snow-free conditions. Differences between both conditions are shown in the last row. Only coefficients higher than 0.30 are shown in the table.

The first factor determines a negative association between the number of pecks and number of short and medium distance flights undertaken by birds, therefore an increase in the pecking rate is correlated with a decrease in the number of short and medium distance flights (i.e. snowy conditions). The second factor is strongly related to movement techniques used by birds, showing a negative association between the number of hops and the number of short flights and cones visited, thus contrasting flightless with aerial techniques related to pine cone use. The third factor relates the number of long flights to change of tree, indicating that while foraging, birds used this movement when switching from one tree to the next. The fourth factor relates use of hovers negatively with use of hanging position, but the little use birds made of hovers detracts from the importance of this factor. Because patterns of change between trees (i.e. factor 3, table 3) did not differ between conditions, but factors describing searching techniques within trees did (i.e. factors 1,2, table 3). It seems that according to snow cover, Coal Tits modified searching patterns when moving within a given tree but not when switching from one tree to the next. In order to relate substrate use to searching techniques it is important to know the main food sources in the different parts of a tree, and so to know the main items taken by birds in different conditions. In snow-free conditions, the pecking rate was significantly associated with the number of cones visited ($R^2=0.35$, n=16, $P<0.05$). This seems to reinforce the idea that in winter Coal Tits fed mainly on pine seeds when foraging on the outer and higher parts of pines. On inner tree surfaces (i.e. trunks and thick branches), the potential invertebrate prey consisted nearly exclusively of springtails (*Collembola*, family *Entomobrya)*, other groups such as spiders, were almost absent from samples taken. Springtails were present at a very high density on inner tree surfaces (x=18 individuals/dm^2, S.E.=3.22, n=6). Mean size of individuals was 1.7 mm (S.E.= 0.23, n=45).

DISCUSSION

In snow free conditions, Coal Tits foraged in the outer and upper parts of pines, mainly on cones and needles as has been shown in other studies (see Cramp & Perrins 1993). Moreover, in these conditions they used hanging position and short and medium distance flights as their main searching movements. These techniques seemed clearly related to movements between cones on outer canopies and exploitation of pine seeds (i.e. hanging positions). When outer canopies were not available for birds due to snow cover, individuals restricted their foraging activities to trunks and low thick branches, resulting in a smaller diversity of substrates used. Under these conditions, birds reduced the number of flights. At the same time birds increased pecking rates suggesting a change in prey use supported by results of arthropod availability on inner tree surfaces. Hence, under snowy conditions Coal Tits seemed to concentrate their search effort on small but abundant prey by reducing overall movement rates.

Optimal foraging models, based on the premise that animals collect food in a way which maximises their net rate of food intake, have been quite successful in predicting the decision rules by predators in a number of previous studies (Royama 1971, Krebs et al. 1978, Pyke 1984, Stephens & Krebs 1986). Some of these studies carried out on tits have demonstrated that birds distribute their search effort in relation to spatial differences in the profitability of feeding sites (Smith & Sweatman 1974, Krebs et al. 1978). Thus, more profitable and, hence, preferred sites will be those exploited under normal conditions when birds are able to choose freely between substrates. As the available foraging surface decreases, birds would be expected to shift to less-preferred sites containing less-rewarding prey. In this study I have shown that when forced by transient snow cover of outer tree canopies, Coal Tits changed substrate use and so prey choice. According to the morphology of species, different substrate selection for foraging often requires different locomotion types (Norberg 1979, Robinson & Holmes 1982, Moreno et al. 1988, Gustafsson 1988). In fact niche shifts recorded in our study were linked to a change in the searching techniques used by birds.

Since short flights and hanging positions are energetically very costly for small passerines (Alatalo 1982a, Laurent 1986, Tatner & Bryant 1986, Carlsson & Moreno 1992), movement patterns employed by Coal Tits during snowy conditions are in agreement with Norberg´s hypotheses (1977) that when the prospects of achieving prey decrease (i.e. preference decreases) lower energy consuming searching methods will be used.

Furthermore, in snowy conditions a decrease in movement and flying rates and the use of the inner parts of trees could help birds to avoid falling snow from higher canopies. Falling snow at high temperatures or under strong wind might be harmful to birds, by affecting their flying performance or directly resulting in physical damage if struck directly (unpubl. data).

Carrascal (1988) found that some forest species shifted towards tree trunks after snow storms. His results raised the role of inner tree surfaces in softening the smoothing negative consequences of harsh temporary weather conditions. Our study clearly gives support to this view for the Coal Tit. Mature forests, containing higher proportions of inner tree substrates, may allow Coal Tits to withstand snowy winter climate better than young pine stands where small trees stay snow covered longer than older ones. Because hoarding tits, such as the Coal tit, store food mostly in the crevices of inner parts of trees, the presence of the hoarding habit reinforces the idea of tree trunks and thick branches as reserves of food in transitory adverse weather conditions (Lens et al. 1994, unpubl. data).

In conclusion, when conditions become more difficult for birds due to a decrease in foraging surface, Coal Tits used available substrates, preyed on secondary, less-preferred prey and used energetically cheaper techniques. Behavioural plasticity in foraging may become important, allowing birds to withstand adverse temporary conditions derived from a harsh climate. Deeper understanding of the proximate factors affecting the foraging of birds under climatic stress is needed.

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COSTS AND BENEFITS OF AGE-RELATED MICROHABITAT SEGREGATION IN WILLOW TIT WINTER FLOCKS[4]

Abstract : It is expected that through phenotypic flexibility, flock living birds respond to asymmetries in resource access by shaping behavioural strategies to minimise mortality risk. We analysed the habitat use of the Willow tit in winter flocks, and assessed the possible factors involved in shaping habitat segregation between adults and juveniles in differing temperature regimes. When foraging in mild conditions (ambient temperature >0ºC), flocks divided into sub-groups and adults foraged in inner parts of trees more often than juveniles but no differences were recorded in the vertical position occupied in trees. At lower temperatures (< -4ºC), flocks re-united and juveniles moved to outer parts of trees increasing horizontal segregation between age classes. In mild conditions, vigilance behaviour was not related to the position of birds in trees. When temperature decreased, scanning frequency was higher in outer parts of trees. In mild weather, juvenile position in trees was associated with body size and mass. This relationship was not observed in adults or in either group in cold climatic conditions. The age-related foraging microhabitat segregation detected in cold conditions fits the caching distribution previously studied in the same population. This supports the hypothesis of the importance of previously hoarded food in determining future foraging habitat use. The adult preference for safer or richer inner parts of trees as foraging sites during adverse weather seems to determine the habitat segregation between adults and juveniles. Furthermore, in mild weather when juveniles are free to choose foraging sites, individuals seem to balance the costs of using a potentially dangerous microhabitat with the benefits of building energetically cheap and large food reserves there through hoarding. We suggest that if predation costs are low, this balance should progressively shift from the use of a safer microhabitat towards the energy saving benefits of more efficient food caching and foraging patterns.

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INTRODUCTION

In group living birds, individuals have different access to resources according to their position in the social hierarchy (Drews 1993). In the winter groups of parids, several studies have demonstrated habitat segregation between dominant and subordinate individuals (Ekman & Askenmo 1984 ; Hogstad 1988 ; Desrochers & Hannon 1989 ; Suhonen 1993; Krams 1996). This difference in habitat use seems to be the result of the active choice of the most preferred sites by dominant birds, which forces subordinate juveniles to occupy food-poor or more exposed sites.

The degree of habitat segregation and the kind of division it takes, depends on the relative costs and benefits for different dominance classes. Predation risk is avoided by foraging in protected microhabitats (Ekman & Askenmo 1984 ; Hogstad 1988). Food distribution is the second factor involved in microhabitat selection within tit flocks. In most species parids, this distribution is actively transformed by food hoarding. Through the later use of the stored food, individuals can increase their food availability (Brodin 1994). Lens & Dhondt (1994) found that juvenile Crested tits (*Parus cristatus*) stored food in outer, exposed parts of trees in autumn. Later, on cold days they were forced to forage in these parts when adults were present. Similar shifts in foraging microhabitat sites have been described for the Willow tit (*P. montanus*) when the degree of cohesion within established groups increased with decreasing air temperature (Hogstad 1988). Lahti et al. (1997) found that subordinate Willow tits hoarded in outer parts of trees more often than dominant ones in autumn. No segregation in the hoarding height among dominance classes was recorded. Therefore, if food distribution modifies the microhabitat use of distinct dominance classes in this population during winter, juveniles are expected to forage in more outer parts of trees than adults but no differences in foraging height should be observed. This expected pattern deviates from the habitat use pattern frequently described for other Willow tit populations (Ekman & Askenmo 1984 ; Hogstad 1988). Morphology is also known to be associated with microhabitat use in tits (Gustafsson 1988 ; Moreno & Carrascal 1993). Certain morphological combinations are adaptive in certain substrates therefore favouring the use of certain sites by individuals. Therefore, flexible responses to varying risk factors can be constrained and modified by morphological adaptations.

The objective of the present field study was to investigate the validity of the predictions above in the same Willow tit population studied by Lahti et al (1997). Furthermore, we compared our results with previous studies on parids, in order to identify the role of alternative factors such as predation risk and morphology on possible age-related differences in the use of the microhabitat.

METHODS

The study was conducted near Oulu, northern Finland (65°N, 25°30'E). The study area covers 22 km^2 of a variety of typical boreal forest habitats. Prior to the field work, all Willow tit flocks of the study area were individually colour banded, sexed according to behaviour (Koivula et al. 1994) and aged (Laaksonen & Lehikoinen 1976). Territorial flocks generally consist of two adults and two to four non-kin juveniles born in the previous breeding season (Ekman 1979 ; Koivula & Orell 1988). The flocks included in our study were chosen from zones of the study area which are mainly covered by the Scots pine (*Pinus sylvestris*) and secondarily by the Norway spruce (*Picea abies*).

Foraging behaviour was observed between 10:00 and 16:00 h during both, autumn and winter time (October-November 1996 and in February-March 1998). When a group was located, we randomly chose one of the individuals as the focal bird. To avoid initial disturbances, the bird was followed after a 5 minutes delay. The behaviour of each bird was recorded in 15 s intervals (foraging, scanning, hoarding). For each foraging bout (bill pointing downwards) the following variables were also recorded (see Lahti et al. 1998 for similar methods) : (1) the relative height (four classes), and (2) the horizontal position in the tree (four classes) : trunk, the first third of the branch (inner part) or the two outermost thirds of the branch (outer part). The bird was classified as 'scanning' if its bill pointed upwards (i.e. above the eye) and 'hoarding' if it had food in the bill and it was caching it. We also recorded the presence (and identity and relative position if possible) of conspecifics.

To reduce statistical dependence between the observations, only one record was made per individual per tree. Up to 5 observations were taken from the same individual in a day. All observations were dictated into a tape-recorder and transcribed afterwards. To further ensure sufficient replication we used medians of each individual in the analyses. The data set includes averages of 8.3 and 12.1 observations per individual in mild and cold conditions respectively. We were able to follow ten winter flocks in both cold (20 juveniles and 23 adults, total of 356 observations) and mild conditions (21 juveniles and 17 adults, total of 424 observations).

We divided the observations into two groups according to the temperature regimes under which they were collected. Mild conditions were obtained mainly during autumn when the ambient temperatures ranged between 0°C and +9°C (median= 5.1ºC). Cold conditions were assigned to the winter days when the temperature ranged from -4°C to -20°C (median=-10.3ºC).

Adult birds dominate juveniles and males over females (Koivula & Orell 1988). However, in monogamous birds such as tits, space use by males and females may be affected by the long-term benefits of a pair so that dominant males can protect females by allowing them to use richer or more protected sites in spite of their lower rank positions (Hogstad 1988, Ekman 1990). Therefore, we used only age as a reliable measure of dominance.

Statistics

In within-flock comparisons, age class medians for each flock were calculated prior to statistical analyses. A paired non-parametric design, with the flock as the basic unit, was used when we analysing the differences in microhabitat use differences between age classes in similar weather conditions (Wilcoxon-signed rank test, Sokal & Rohlf 1981). Because some birds disappeared during a given season, and part of the data came from two separate winters, the paired tests could not be based on the observations of the same individuals. Instead, the sampling was based on pairs of flocks inhabiting territories with similar habitat structure. For most of the territories, we were able to collect data in mild and cold weather, but the individuals included in the analyses were different depending on conditions.

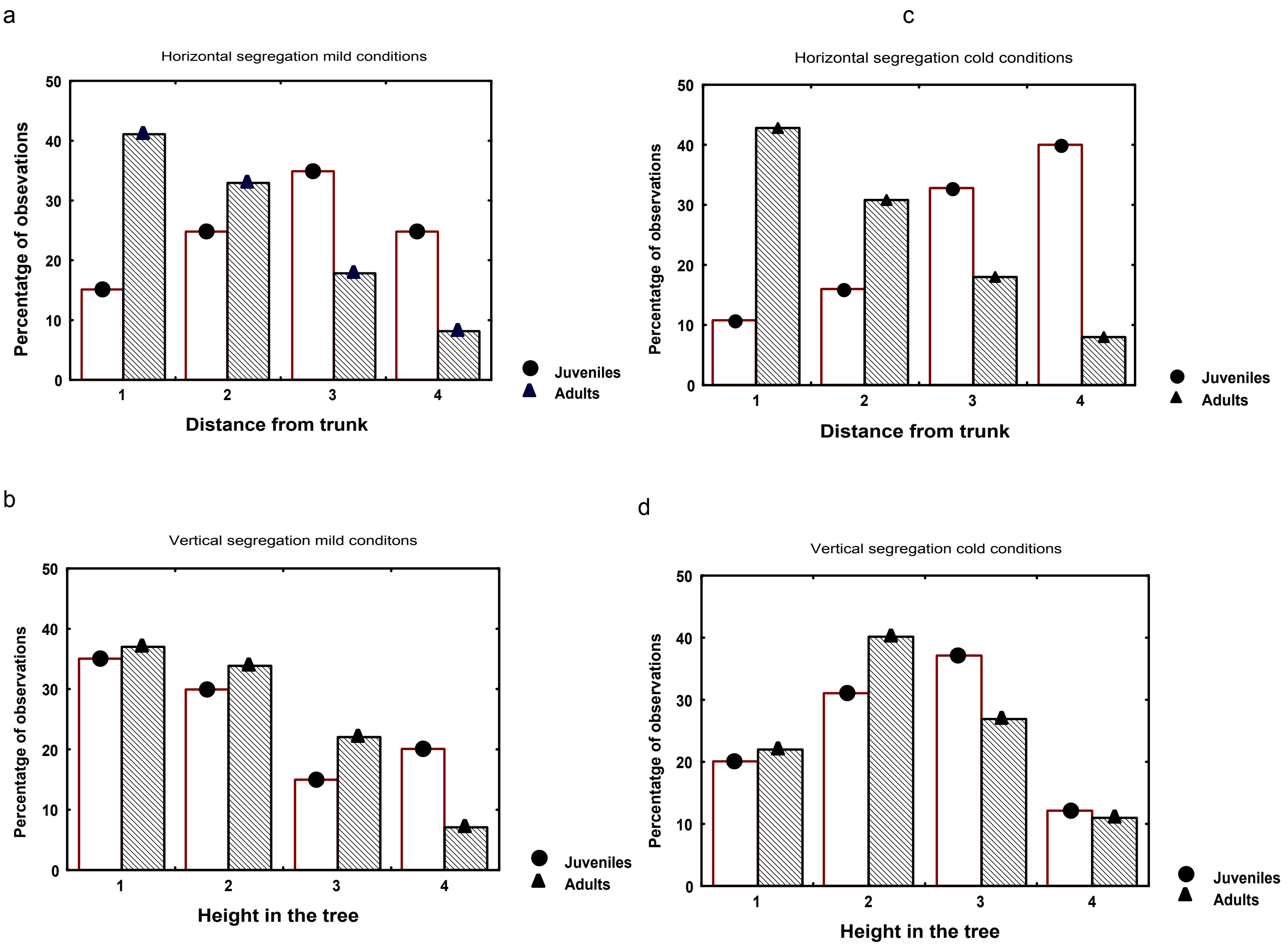
In order to detect predators, birds can not rely on the results of previous scanning (Lima & Dill 1990) activities. Therefore, we analysed scanning frequencies including each observation taken per individual per tree as the basic sampling unit in the analyses. We used X^2 statistics to test for possible differences in the scanning frequencies in differing environmental conditions.

In the ecomorphology analyses, the individual was taken as the basic sampling unit. Spearman rank correlation coefficient was used to test the possible relation between body size and horizontal and vertical positions of birds in trees.

RESULTS

Site selection by adults and juveniles

In mild weather, Willow tit flocks often segregated into age-specific subflocks. Consequently, only in 16% of the observations were individuals observed foraging with more than one companion in the same tree. In cold conditions, individuals of the flock reunited, foraging more often in the same tree with other flock mates (16% v.s. 54 %, X^2_1=29.9, p<0.0001). When foraging in mild conditions mainly in age-specific subflocks, there were no differences between adult and juvenile birds in the vertical position occupied in trees (Wilcoxon signed-rank test, n=10, Z=1.4, ns). However, adults used inner parts of trees more often than juveniles (Wilcoxon signed-rank test, n=10, Z=2.4, p<0.05, Figure 1). In cold conditions, birds reunited in coherent flocks, but patterns of foraging locations within trees did not change. Again, no differences were detected between adult and juvenile birds in the foraging height (Wilcoxon signed-rank test, n=10, Z=1.5, ns, Figure 1). Adults still used inner parts of canopy more often than juveniles (Wilcoxon signed-rank test, n=10, Z=2.7, p<0.01, Figure 1). We also analysed possible changes in the position occupied in trees within each age class in both cold and mild conditions. In cold weather, juveniles foraged in outer parts of conifers more often than in mild weather conditions, but no significant shifts in the foraging height was detected (Wilcoxon signed-rank test, vertical distribution, n=10, Z=1.4, ns, horizontal distribution n=10, Z=-2.1, p<0.05). Adults foraged preferably in inner parts of trees (Wilcoxon signed-rank test, n=10, Z=1.15, ns) but they partially shifted to the upper parts in cold conditions (Wilcoxon signed-rank test, n=10, Z=-2.1, p<0.05, Figure 1).


a Horizontal segregation mild conditions

c Horizontal segregation cold conditions

b Vertical segregation mild conditons

d Vertical segregation cold conditions

Figure 1. Percentage distribution of foraging records for adult and juvenile Willow tits within trees for various temperature regimes. a, horizontal and b, vertical segregation regimes in mild conditions. c, horizontal and d, vertical segregation regimes in cold conditions.

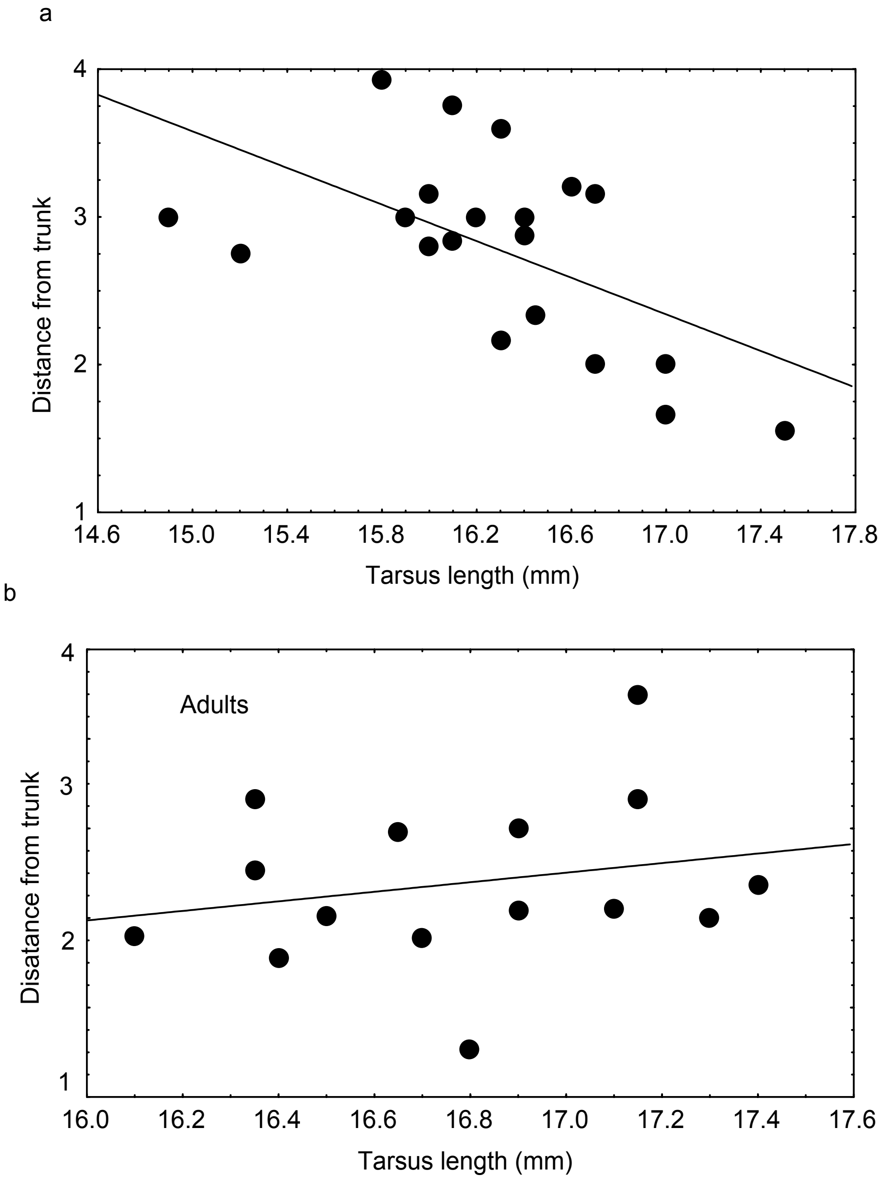


Figure 2. Tarsus length plotted against average horizontal position within trees for juvenile, a) and adult, b) Willow tits in mild conditions. Regression line only represents linear association between the two variables.

Vigilance behaviour

In mild conditions, the frequency of head lifts did not differ in the distinct microhabitats within trees (Horizontal component, X^2_3=3.98, ns, Vertical component, X^2_3= 5.46, ns). However, in cold conditions, our results indicated a higher frequency of head lifts in outer parts of conifers (Horizontal component, X^2_3=11.72, $p<0.01$). No significant differences were detected in vigilance behaviour at different heights (Vertical component, X^2_3= 4.2, ns).

Morphology and site selection

During mild conditions, the habitat use of juvenile birds was correlated with body size. Birds with short tarsi foraged more often in outer parts of trees than individuals with longer tarsi (Horizontal position, Spearman rank correlation, r_s=-0.48, n=20, $p<0.05$, figure 2a). Larger birds also tended to forage higher up in trees (Vertical position, Spearman rank correlation, r_s=-0.41, n=20, p=0.07). In cold conditions this association was not observed (Horizontal position, Spearman rank correlation, r_s=0.18, n=21, ns ; Vertical, Spearman rank correlation, r_s=-0.30, n=20, ns). Body mass followed a similar pattern, with heavier birds tending to occupy inner sectors of trees

(Horizontal position, Spearman rank correlation, r_s=-0.54, n=15, p<0.05) but not in cold conditions (Horizontal position, Spearman rank correlation, r_s=-0.24, n=13, ns). Habitat use by adults was not related to tarsus length neither in mild (Horizontal position, Spearman rank correlation, r_s=0.20, n=15, ns ; Vertical, Spearman rank correlation, r_s=-0.05, n=15, ns, figure 2b) or cold conditions (Horizontal position, Spearman rank correlation, r_s=-0.14, n=14, ns ; Vertical, Spearman rank correlation, r_s=-0.26, n=14, ns).

DISCUSSION

Our results show that hoarding patterns in autumn (Lahti et al. 1998) are reliable predictors of niche segregation among adult and juvenile Willow tits in winter. Horizontal segregation resulted from adults foraging more than juveniles in inner parts of trees, whereas there was no difference in foraging heights. Previous studies on other tit populations have shown evidence of a high overlap between foraging sites and hoarding niches in adverse conditions. This overlap facilitates the recovery of hoarded food during high energy requirement periods (Brodin 1994a ; Lens et al. 1994). Furthermore, matching of microhabitat foraging segregation with storing locations may decrease cache robbery and therefore, increase benefits of the hoarded food (Brodin 1994a).

During adverse weather conditions, Willow tit flocks move around in tight groups, with individuals of the group commonly occupying the same or adjacent trees. In such conditions, intraspecific competition for optimum foraging sites arises (Lens & Dhondt 1992). Dominant individuals (i.e. adults) are assumed to have preference in the use of better foraging sites, whereas subordinates seem to be relegated to poorer or more dangerous ones (Ekman & Askenmo 1984 ; Suhonen 1993). The benefits of juveniles foraging with adult dominant birds may be balanced against the costs of foraging in a preferred microhabitat with an absence of adults. Although juveniles are forced to forage in less optimum sites (i.e. outer parts of tree canopies), flocking seems to be the best option for them. They benefit from the foraging experience of adults via neophobia (Mönkkönen & Koivula 1993), from the enhanced predator detection associated with increased group sizes (Hogstad 1988b) and from food resources from hoarding, which may later reduce the costs of using more dangerous areas (Lens and Dhondt 1994).

Ekman & Askenmo (1984) and Hogstad (1988a) explained the age-related vertical segregation of Willow tits in cold conditions, stating that adults had the active choice of the upper halves of trees, which were seemingly less risky areas in terms of owl predation (Kullberg 1995). At a microhabitat level, monopolisation of safe sites by adults has also been found in other studies. Desrochers (1989) found that adult Black-Capped Chickadees (*P.atricapillus*) used upper and inner parts of trees known to be less exposed to predation by Shrikes (*Lanius spp*.). In contrast, in another population of chickadees, adults used more frequently lower parts of trees, which were safer from hawk attacks (Glase 1973). Differential vertical segregation patterns between dominance classes have also been found to depend on vegetation structure which determines hunting strategies of predators and therefore, dangerous sites (Krams 1996).

Contrary to Ekman & Askenmo (1984), and Hogstad (1988a), who found adult Willow tits monopolising upper parts of the canopy, we detected only horizontal segregation between age classes. Higher scanning rates recorded in the outer parts of trees in more stressful cold conditions, supports the widely accepted idea that those sectors are more risky to predation than the inner parts of trees (Suhonen 1993a, Kullberg 1995, 1998). However, in cold conditions, in spite of the lack of vertical segregation between adults and juveniles, adults increased the use of higher parts of trees. Under stress conditions, adults may benefit to some degree from being higher up in trees, presumably because they are less exposed to owl predation (Ekman 1986). Further increases in predation pressure might increase vertical segregation among dominance classes as found by Ekman & Askenmo (1984) and Hogstad (1988a).

However, the overall results of this study suggest that predation is not the only factor governing site selection by Willow tits. In certain conditions, other factors may balance the importance of predation risk in site selection strategies. In cold temperatures, adult birds foraged in inner parts of trees more than juveniles, but adults already occupied such sectors of trees in mild weather conditions when individuals are under reduced energetic stress. Hogstad (1988a) found that in mild conditions, adults used all available canopy areas with the same frequency. He suggested that if birds find more food in certain parts of trees, then adults would be expected to use such parts regardless of ambient temperatures, as our results suggest. Although some studies have found arthropod fauna to be evenly distributed all over the trees (Furunes 1978), or more abundant in higher sectors (Suhonen et al. 1992), none of these studies have taken into account the surface over which this fauna is distributed. Furthermore, hoarding species alter food distribution within trees. Since hoarding is dominance dependent (Brodin 1994a), then food available for individuals also differs in various parts of trees. Thus, reliable comparisons on the true availability and profitability of food items between inner and outer parts of trees is still lacking (Hutto 1990). Furthermore, inner parts of trees are more protected from energetically expensive wind (Lens 1996) and low temperatures (Wachob 1996) and are less likely to be covered by snow than outer parts (Brotons 1997). Therefore, adults primarily due to their lower predation risk, but also because of food availability and favoured microclimatic conditions could choose inner parts of trees.

If inner parts of trees are the preferred sites of adults in our study area, why don’t juveniles use these same sites in mild conditions when they are freer to choose their foraging site? This shift has been found in other populations of Willow and Crested tits (Hogstad 1988). In a Crested tit population, Lens et al. (1994) found that juveniles using inner parts of trees in mild conditions had to make an additional effort in terms of flight (Carlsson & Moreno 1992) in order to locate stores in the outer parts of trees where they foraged later on. However, Lahti et al. (1998b) found that the hoarding microhabitat of juvenile Willow tits did not change after the experimental removal of adults. They concluded that juvenile Willow tits might store food supplies having a future foraging niche in mind. Therefore, Willow tits probably do not benefit from altering hoarding behaviour when facing a temporary absence of adults. In harsh conditions, juveniles have to use foraging sites other than the preferred. Thus, when storing in mild conditions, they have to make a decision based on the relative costs of transporting stores to outer parts of trees, and the benefits of using presumably safer or richer sites close to the trunk. As juvenile birds used outer parts of trees more than adults in mild conditions, this suggests that energy saving from reducing the distance between foraging and hoarding locations can be beneficial enough for juveniles to withstand the possible costs of outer exposed foraging locations (Lens et al. 1994). An increased hoarding effort through energy saving mechanisms may allow juvenile Willow tits to built up large food reserves, which can be used later in cold conditions when these resources are decisive for their survival (Brodin 1994b, Lahti et al. 1998).

In mild conditions, the importance of energy budget and ecomorphological aspects of foraging site selection in juveniles is further stressed by the link detected between size of individuals and their position within trees. Gustafsson (1988) found that heavier Coal tits (*P.ater*) with longer tarsi tended to occupy inner parts of trees. Long tarsi are more suitable for walking and jumping and short tarsi for foraging in a hanging position below twigs (Norberg 1979; Moreno & Carrascal 1993). Small, light birds are more efficient on thin twigs and among needles where slow flight, hanging and hovering are essential foraging techniques. Heavy birds suffer from higher energy costs when moving because of their greater body mass (Norberg 1979). Therefore, our results support the idea of a strong relation between morphology, foraging efficiency and microhabitat choice in trees. The importance of ecomorphology further stresses the possible use of energy saving mechanisms utilised by juveniles in order to built up food reserves economically.

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GEOGRAPHIC VARIATION OF THE STORING BEHAVIOUR IN THE COAL TIT *PARUS ATER* : THE ROLE OF WINTER RESIDENCY AND ENVIRONMENTAL CONDITIONS [5]

Abstract: Foraging and hoarding behaviour of the Coal Tit *Parus ater* were studied in two distant populations, in the Pyrenees and in Norway. The two populations differed in their degree of winter residence and environmental pressures. Location of foraging and hoarding sites were described in the Pyrenees during winter, and during autumn in Norway where no hoarding takes place during winter. Significant differences in the hoarding behaviour of Coal Tits between these areas were observed. In the Pyrenees, birds hoarded on inner and lower parts of the trees, using trunks and thick branches as caching sites, which are the substrates most heavily used in conditions of winter environmental stress. In Norway, birds hoarded items on outer and higher parts of the trees, mainly among needled twigs, which were those substrates used in normal foraging. The Norwegian population hoarded animal food more frequently. Our results show that hoarding behaviour varies among populations and suggest that the differences recorded may be related to differences in competitive pressures and the prevailing environmental conditions. Furthermore, the absence of a safe long-term hoarding niche in the Norwegian population due to interspecific competition, would make a strong sedentary habit difficult, offering a functional explanation to the differences observed in the degree of winter residence between Norwegian and Pyrenean Coal Tits.

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[5] With Svein Haftorn (Norwegian University of Science and Technology, Norway). Ibis, 141 :587-595.

INTRODUCTION

Food hoarding is suggested to be an advantage to individuals which face periods of high food abundance followed by periods of food shortage. That is, as an alternative to the build-up of internal body reserves, external storing of food items allow individuals which live in variable environments to smooth changes in food supply (McNamara et al. 1990). Some theoretical models have suggested that food may be hoarded over the short or the long term. Data from the field, both observational and experimental, provide support for tits retrieving food after both short and long time periods (Källander & Smith 1990, Brodin & Ekman 1994). Field studies of naturally hoarding tits indicate a pronounced long-term hoarding of winter supplies throughout the autumn (Haftorn 1956 a, b, Pravosudov 1985, Hitchcock & Sherry 1990, Brodin & Ekman 1994,). Estimates based on observations of foraging Willow Tits *Parus montanus* suggest that more than 50% (Haftorn 1956b) and as much as 70% (Nakamura & Wako 1988) of the winter diet may be of food hoarded in the autumn. Another type of long term storing may be used as emergency food during periods when foraging is precluded for various reasons such as snow blizzards (Vander Wall 1990). However, memory in hoarding parids does not seem always to last long enough for caches to be retrieved after several weeks or months (Källander & Smith 1990). Some studies have shown that individuals use stores within hours or a few days after these have been made (Cowie et al. 1981, Sherry 1982, Stevens & Krebs 1986, Brodin 1992). This type of hoarding is thought to act as external short-term reserves which may be useful to postpone weight increase towards late afternoon (McNamara et al. 1990). In this way, birds might avoid accumulation of internal fat reserves which are known to increase predation risk through a loss in flying performance (Metcalfe & Ure 1995, but see Haftorn 1992).

Because a prerequisite to recover hoarded food is to stay in the same place where the food has been hidden, movements of birds during hoarding and recovering periods, and the degree of residency, are predicted to affect hoarding behaviour (Källander & Smith 1990). That is, long-term hoarding is expected to be favoured when social and environmental conditions allow easy recovering of caches stored by a given bird (Tomback 1978, Brodin & Ekman 1994). On the other hand, short-term hoarding does not impose so many restrictions because caches may be remembered by the birds and chances of being lost during short periods of time are small. Thus even transient birds may potentially gain benefits from using this behaviour (Källander & Smith 1990, Vander Wall 1990). Therefore, we predict that differences in the degree of winter residence may influence the birds' storing and recovering behaviour.

Few studies have dealt with geographic variation of hoarding behaviour within a single species. Some of these studies have found latitudinal variations in hoarding intensity (Brodin et al. 1994, but see Brodin et al. 1996), but hoarding site variations among different populations within a single species have, so far, received little attention (Petit et al. 1989). Because environmental factors often change geographically and hoarding is known to increase the fitness value of individuals, hoarding behaviour is predicted to be plastic and variable among populations with different environmental conditions.

Here we studied foraging and hoarding behaviour in two geographically separated populations of the Coal Tit living under different environmental conditions and differing in degree of winter residency.

STUDY AREA AND SPECIES

Foraging and storing behaviour of Coal Tits were surveyed in two different locations: (1), in the Pyrenees and, (2), in Southern Norway. The first area, of about 1.5 km^2 is located in the 'Cadí-Moixeró' Natural Park in the eastern Pyrenees (north-east of the Iberian Peninsula), ranging from 1800 to 2100 m a.s.l. Mountain Pine *Pinus uncinata* dominates the study area with Scots Pine *Pinus sylvestris* predominant in southern slopes and in lower altitudes. Understory is scarce, dominated by Juniper *Juniperus communis* and grasses; more information about the vegetation can be found in Vigo (1976). The forest has been exploited until recently on a long-term cycle, resulting in tree stands of different ages in the area. The annual precipitation is approximately 1100 cm, around 35 % falling as snow during the winter months. Snow remains on the ground from December to about April. The second area, at Drammen, is located in southern Norway. The area is covered by coniferous forests, mainly by Spruce *Picea abies* and Scots Pine *Pinus sylvestris*. The main characteristics of the area are described in more detail in Haftorn (1954).

The Coal Tit is a small forest passerine (mean body mass is 9.22 g, se=0.51, N=255, unpubl. data). In the Pyrenees, Coal Tits are very common throughout the winter and form flocks of up to 70 individuals, often with few Crested Tits *P. cristatus*, few Goldcrests *Regulus spp*. and solitary Treecreepers *Certhia spp*. (Brotons unpubl. data). Therefore, in the Pyrenees, winter flocks were clearly dominated in numbers by the Coal Tit and, frequently, this species was their only component.

In the Norwegian study area, the Coal Tit is very abundant in autumn, but its numbers decrease sharply through the winter because of migratory and eruptive movements (Haftorn 1956a). As a result, during winter, tit groups are dominated by Willow and Crested Tits, which were the most abundant tit species in the area during the study period. Therefore, degree of winter residence of the Coal Tits in a given area, understood as the degree of individual presence, clearly differs between the Pyrenees and Norway.

METHODS

In the Pyrenean study site, foraging behaviour in Coal tits was monitored between January and March 1996 and 1997. During this period, two environmental conditions were distinguished according to the amount of snow accumulated on the trees. During snowy conditions (1), a snow layer of more than 5 cm covered the outer parts of the pines, whereas under snow-free conditions (2) snow was never noticed on tree surfaces and birds could freely choose foraging substrates (Brotons 1997b). Days on which data were collected were chosen so as to avoid intermediate amounts of snow on the trees. Thus, situations were clearly differentiated, and assignment of observations to study conditions could be conducted without ambiguity.

During data collection days, the first author walked systematically throughout the study area searching for tit flocks. When a flock was located, he described individual tree site, and substrate use was described by instantaneous sampling of the bird’s position (Carrascal 1983, Morrison 1984). Instantaneous sampling of Coal Tits was initiated 5 s after a bird was located (to avoid the recording of conspicuous behaviour). Consecutive observations with a 20 s delay were taken with no more than four consecutive samples per individual to assure statistical independence (Carrascal 1983). Space use was measured with a range of variables using rank scales, relative height (in the tree, 1 to 4, from the bottom to the top), distance from the trunk (two categories, inner and outer parts of trees from the trunk to the periphery) and the substrate used (trunk, thick branch >1cm, twig < 1cm, needle, cone and others).

Unfortunately, data on colour-ringed individuals were insufficient to perform the analyses at an individual level. Although a part of the resident population is colour-ringed, some unringed birds, both residents and transients, might have been sampled twice on different days of the study, but never on the same day because groups were changed after the observation of unringed birds. In such cases, the time lapse between observations and the movement of individuals suggest that possible pseudoreplication of the data was not a problem (see also Leger & Didrichsons 1994). Observations were taken between 8.00 a.m. and 4.00 p.m. by the same observer to avoid possible bias resulting from different interpretations of relevant variables and under similar temperature and wind speed conditions, since these factors can influence space use in forest passerines (Grubb 1979). In total, 131 observations were taken during three different periods of snow, and 153 observations were taken during snow free conditions.

In the Pyrenees, data on hoarding behaviour were collected from December 1996 to March 1997. The act of storing is very conspicuous and was observed throughout the winter on days without snow cover present on trees. Foraging Coal Tits were followed and when a storing action was noticed, cache position in the tree and type of substrate used were recorded in the same manner as with foraging behaviour. Moreover, the type of food and the position of the stored item on a given substrate was recorded, top (25%), side (50 %) or bottom (25%). As with foraging data, hoarding behaviour was recorded mainly on unringed individuals. Because birds often flew back to the original source of food to gather another item, a new caching bout was initiated and this was evidently not constrained by the previous caching site. However, after a maximum of four storing actions of the same bird the recording stopped and the sampling was switched to another group. In total, 102 hoarding actions were included in the analyses.

Foraging and hoarding data from Norway were taken as a subset of the data from Haftorn (1956a), and come from a population of unringed Coal Tits. Methods are fully described in the cited paper and were very similar to those used for data collection in the Pyrenees. Foraging was only described under normal weather conditions in autumn (September to December of years 1949, 1950 and 1952, in total 352 observations). Hoarding behaviour was only studied during autumn (August to November of the years 1949, 1950 and 1952, in total 221 observations) because during winter relatively few Coal Tits remained in the area, and data suggested that no hoarding took place (Haftorn 1956a).

Shannon's diversity index was used as a measure of niche breadth in the distribution of positions in the tree and substrate use. We used the estimation described by Bowman et al. (1971) that allows us to compare the index obtained in different conditions irrespective of sample size. Finally, as a measure of niche overlap between conditions we used Morisita's index (Morisita 1959). We included height classes and substrates as resources. We selected this index because it presents the smallest bias in response to variation in sample size (Smith & Zaret 1982). Unfortunately, it is not possible to obtain accurate confidence intervals for this overlap index, therefore, estimates should be interpreted with caution.

RESULTS

Birds used different storing places in Norway and the Pyrenees. In the Pyrenees, birds used mainly inner and lower parts of the trees, whereas in Norway hoarding individuals stored items mainly on the outer and higher parts of trees (horizontal, X^2_1=182.1, P<0.001, height, X^2_3=170.5, P<0.001, Figs. 1 and 2). Furthermore, in Norway storing took place almost exclusively in needled twigs, but in the Pyrenees birds used inner substrates of the trees, mainly the trunk and thick branches (X^2_4=261.4, P<0.001, Fig. 3). As a result, overlap values for storing height and storing substrate between areas were very low (Table 1).

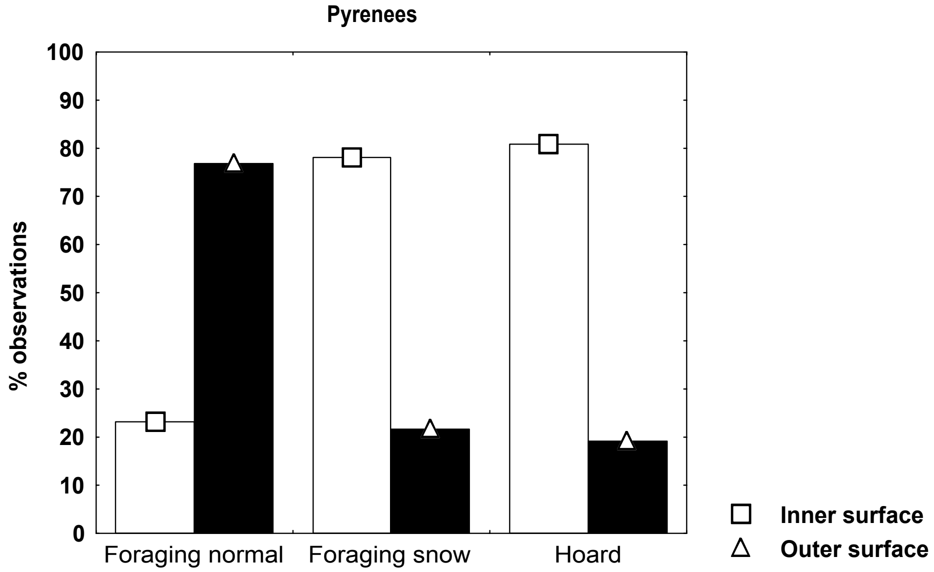
		Norway		Pyrenees		
	Overlap values Height classes Substrates	Foraging normal	Hoarding	Foraging normal	Foraging snow	Hoarding
Norway	Foraging normal	1	0.78 0.62	0.86 0.91	0.47 0.27	
	Hoarding		1			0.32 0.14
Pyrenees	Foraging normal			1	0.49 0.28	0.51 0.34
	Foraging snow				1	0.82 0.71
	Hoarding					1

Table 1. Overlap values in height classes and substrates distributions between birds in Norway and the Pyrenees. Overlap values were not calculated in case of crossed conditions (hoarding in one of the study areas and foraging in the other).

		Height		Substrate		
		Diversity	S.D.	Diversity	S.D.	
Norway	Foraging normal	1.101	0.042	1.052	0.072	*
	Hoarding	0.997	0.033	0.401	0.057	
Pyrenees	Foraging normal	1.305	0.062	1.357	0.084	*
	Foraging snow	1.177	0.045	1.140	0.034	*
	Hoarding	0.989	0.067	0.956	0.082	

Table 2. Substrate use and vertical width of foraging and hoarding niches in the Pyrenees and in Norway. Values are the Shannon index of diversity of the distribution. S.D. are standard deviations. Asterisks (*) at the side of foraging data, indicate significant differences between the diversity of the foraging and the hoarding sites used within each study area (t-tests p<0.05, Bonferroni correction applied to the Pyrenees mean data).

a



b

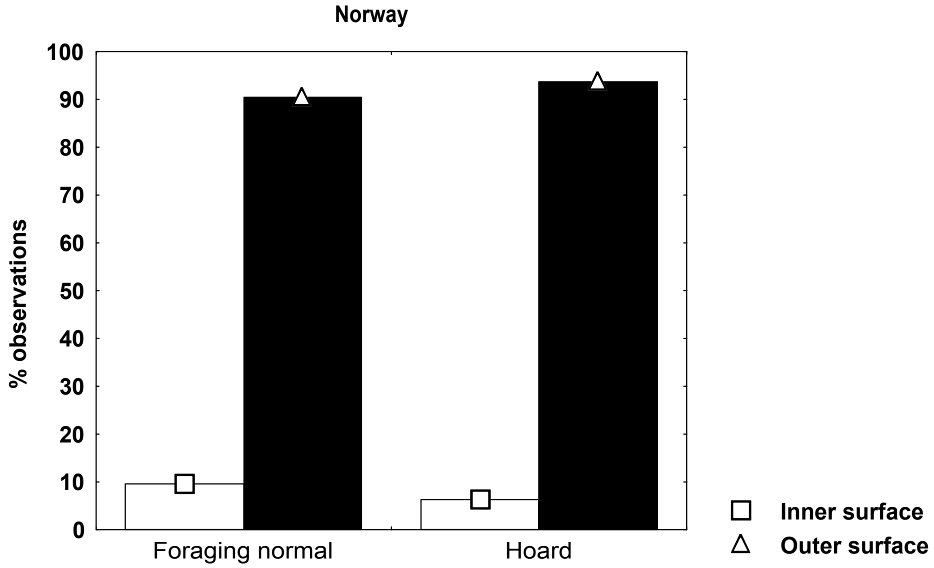


Figure 1. Foraging and hoarding distributions of the horizontal parts of trees used by the Coal Tits in the Pyrenees (a) and Norway (b).

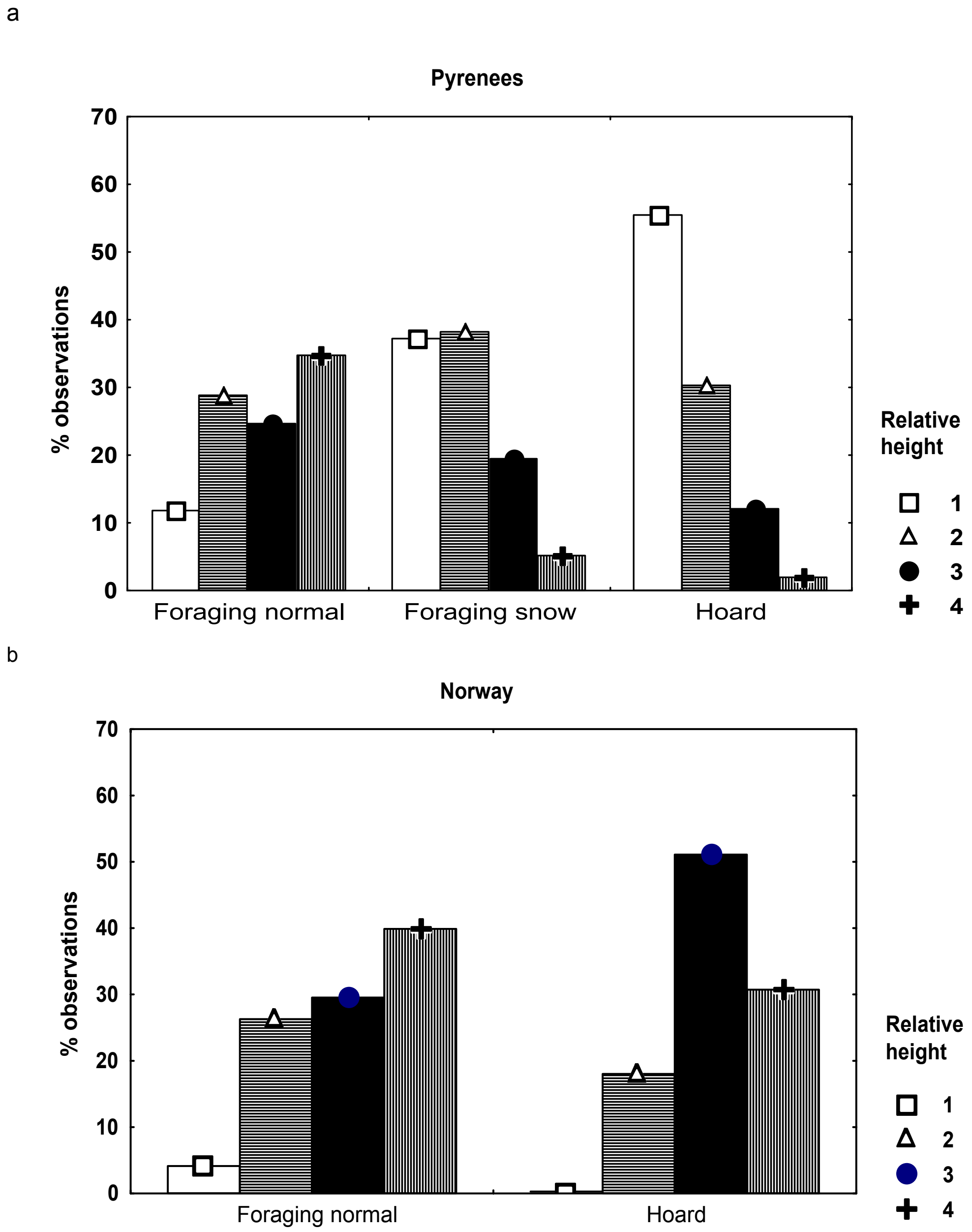


Figure 2. Foraging and hoarding distributions of the vertical parts of trees used by the Coal Tits in the Pyrenees (a) and Norway (b).

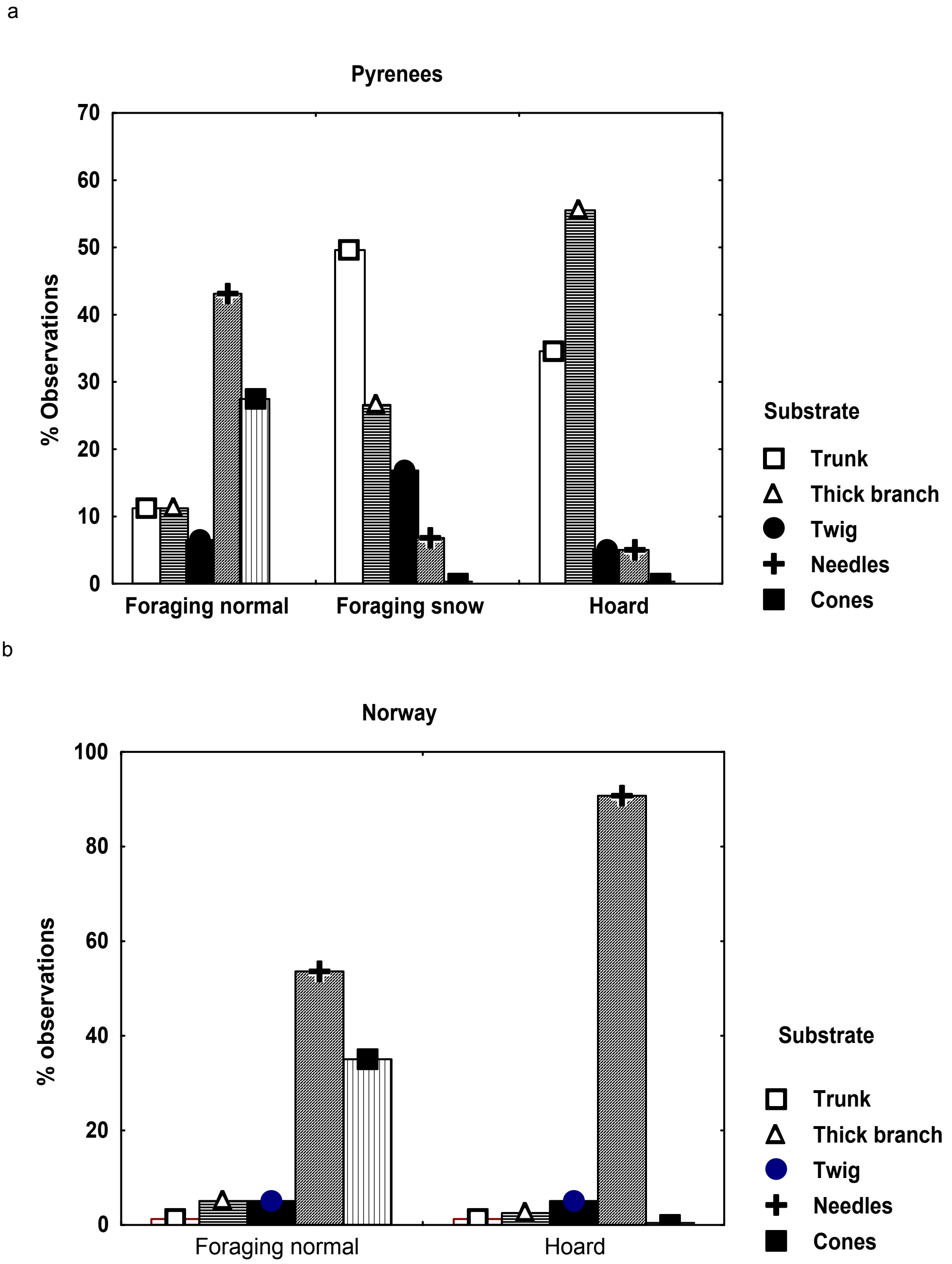


Figure 3. Foraging and hoarding distributions of the substrates used by the Coal Tits in the Pyrenees (a) and Norway (b).

In Norway, foraging takes place mainly on outer and higher parts of trees, with needles and cones (when seeds are available) as the main substrates used (Figs. 1, 2 and 3). Therefore, storing sites were very similar to foraging sites, although a significant difference between the height of foraging and hoarding sites was detected (horizontal, X^2_1= 1.66, ns, height, X^2_3=23.7, $P<0.01$), as a result, overlap index was quite high and reached values of about 65 % (Table 1). Taking into account that cones are never used as storing sites this result indicates a great coincidence between sites where items are stored and sites which are used for foraging (Table 1).

In the Pyrenees, under normal conditions, birds used similar foraging sites to those used in Norway (horizontal, X^2_1= 12.0, $P<0.01$, height, X^2_3=7.0, ns., Figs. 1 and 2). Despite this significant difference in horizontal location of foraging sites, overlap values in height classes and substrate were extremely high (Table 1), suggesting that under normal conditions Coal Tits foraged in similar locations in both areas. In the Pyrenees, sites and substrates used for normal foraging were radically different from those used for storing (horizontal, X^2_1= 78.2, P<0.001, height, X^2_3=15.6, P<0.001, substrate, X^2_4= 122.3, P<0.001, Figs. 1, 2 and 3). On the other hand, hoarding sites and substrates coincided to a high degree with sites and substrates used by birds after a snowfall, when outer surfaces were covered with snow (horizontal, X^2_1= 0.17, ns., height, X^2_3=3.7, ns, Figs. 1,2 and 3, Table 1).

In both areas, niche diversity was lower in the hoarding distribution than in the foraging distribution (Table 2), which indicates that birds concentrated on a reduced diversity of sites and substrates when storing than when foraging.

Even though the main stored items in both areas were coniferous seeds, conspicuous differences arose in the type of food cached. In Norway, birds stored spruce seeds when these were available. However, animal food was also used, and was almost the only type of food stored during years with poor seed crop. During the winter, Coal Tits in the Pyrenees stored only pine seeds, not making use of animal food for this purpose, in spite of the fact that, at least to some degree (obs. pers.) insect food was also available at that time (Table 3). In the Pyrenees, Coal Tits did not locate their stores at random, but rather they used protected locations on branches (i.e. bottom parts and sides) much more often than expected (Table 4). When birds store on outer branches or among needled twigs, protection against harsh weather is not likely to differ between orientation of storing sites. Therefore, in Norway, data on storing location on branches was not collected nor analysed.

Food items	Norway % (n=268)*	Pyrenees (%) (n=101)
Vegetal food	27	99
Animal food	73	1

*Data from Norway comes from three years. In 1950 birds stored almost exclusively pine seeds, whereas in 1949 and 1952 birds stored only animal food.

Table 3. The food items most frequently stored by the Coal Tits in Norway and the Pyrenees.

Branch side	Expected %	Observed % (n=38)
Bottom	25	50
Sides	50	45
Top	25	5
	X^2_1	41.5
	P	<0.0001

Table 4. Comparison of expected (random) use with observed use of side of branches for location of stores for the Coal Tits in the Pyrenees.

DISCUSSION

In this study, we have clearly demonstrated that hoarding behaviour varies and may show important differences among populations of a single species. In Norway, birds stored during autumn, not in winter time, and used outer and higher parts of trees both for feeding and storing. In the Pyrenees, birds stored throughout the winter using inner and lower parts of trees as main storing substrates, i.e. those most heavily used for foraging in winter during snowy conditions.

What are the main causes of these differences between populations? As stated by others (Källander & Smith 1990, Vander Wall 1990), the degree of residence is a key factor determining the way animals hoard food and later on recover it. The degree of residence of the two populations studied differed.

In the Pyrenees, the Coal Tit is very common during the whole winter, being, by far, the most common forest dwelling passerine during this period of the year. Although some juvenile individuals show complicated movement patterns as floaters (Matthysen 1990, Brotons 1997a), most of the birds (adults and some juveniles) remain in a restricted range during most of the winter, which would allow birds to forage in the same areas where they have stored food. The high overlap values between hoarding and foraging sites under snowy conditions, strongly suggests that stored food might be used under conditions of decreased foraging surface when birds are forced to change to less rewarding foraging sites (Brotons 1997b). Under normal weather conditions (i.e. on days without snow and wind), Coal Tits used outer and higher parts of trees where they fed mainly on pine seeds. Because under such conditions, location of foraging sites was very different from hoarding sites, Coal Tits did not seem to make use of caches then. Therefore, hoarded food might be used in a medium or long-term perspective to compensate for bad foraging conditions derived from a harsh climate. Storing sites are in the most protected parts of trees, where they are most likely to be available in case of heavy snowfall (Haftorn 1974, Vander Wall & Smith 1987). Moreover, caches are located in the most protected parts within substrates (i.e. lower parts of branches). Both the fact that food stored was almost exclusively composed of pine seeds (i.e. less perishable food types, Brodin 1994) and the protected location of stores, reinforce the view that individuals used stored items during periods of adverse weather to improve foraging conditions (Carrascal 1988). A few visual observations (n= 5) of individuals recovering pine seeds from trunk and thick branches under snowy conditions, add further evidence to the possible use of stored items in the Pyrenees.

In Fennoscandia, the Coal Tit is a partially migratory, eruptive species (e.g. Haftorn 1956a, Ulfstrand 1963), implying that the winter population varies heavily over the years, as for example shown by the Swedish register of the winter avifauna (Svensson 1993). Irregularly, great emigrations take place in the autumn, evidently resulting in a marked drop in the winter population. The key factors causing such eruptive movements are still poorly known, but the production of coniferous seeds is believed to play an important role (e.g. Löhrl 1974 and references therein). One might predict that emigrations largely coincide with a relatively high autumn population of Coal Tits combined with failing seed production. Available evidence supports this view (Svensson 1979). In contrast, in years with a rich seed crop many Coal Tits are expected to spend the winter within the breeding area. Much field work is required, however, to clarify population fluctuation in tits.

When coniferous seeds are abundant Norwegian Coal Tits store seeds *en masse*. Although the Coal Tits in Norway store on the exposed outer part of branches, some items hidden in bud capsules and between needles should nonetheless be accessible to the tits despite heavy snow on the upper surface of the branches. Therefore, scarce wintering Coal Tits might be able to utilise, at least to some degree, stored food as a way to increase the pool of food available to them during winter. However, clear evidence is still lacking. In default of seeds, Coal Tits in Norway frequently store insects, especially aphids and larvae. Insects are assumed to be a very short lasting type of food that should be used within a short time (Gendron & Reichman 1995). We emphasise, however, that very little is known about the durability of stored insects as adequate food for tits. Do they utilise stored insects after they have become dry, even in winter time? Obviously, this point needs further investigation. At present, we consider insects to be stored on a short term basis without excluding the possibility of a long-term ingredient.

Short-term hoarding may be evolutionarily stable when individuals have a high probability of recovering their own stores and they benefit from the use of external reserves, (Andersson & Krebs 1978, McNamara et al. 1990). Thus, the fact that during autumn, Norwegian birds used foraging locations highly similar to storing sites, suggest that individuals were able to recover stores on a short-term basis. Few opportunities to recover stores later on due to the exposed locations of caches, type of stored food, and the low degree of winter residency also point in this direction. Outer parts of trees do not sound very feasible as storing sites for long-term usage. If the Coal Tit’s habit of storing on these tree parts limits food availability severely during northern winters with much snow, the advantages of long-term storing would be reduced and partial migration to better areas would be adaptive. Still in these conditions, short-term hoarding would be advantageous to Coal Tits during autumn.

But, why then, should not birds in the Norwegian population use more protected caching sites and thereby develop a long term food source and thus have more chances of becoming sedentary? Competition between closely related species is likely to have played a role in shaping hoarding behaviour in the Coal Tit. In the study area in Norway, the Coal Tit co-exists with two other hoarding species, the Crested and the Willow Tit. These latter species are very common during winter, and they mainly use inner and lower, more protected, parts of trees for foraging and storing (Haftorn 1954, 1956b, Suhonen & Alatalo 1991, Lens et al. 1994). Therefore, Coal Tits using these substrates as hoarding locations would most probably incur on a high additional cost from kleptoparasitism if hoarded food was only to be used in days of adverse conditions (Moreno et al. 1981). The absence of a safe long-term hoarding niche, due to interspecific competition, would constrain the evolution of long-term hoarding in Norwegian Coal Tits. Also, direct competition for foraging and hoarding sites would probably result in high costs for the Coal Tits (Alerstam et al. 1974, Sorensen 1997). Differences in the competitive pressures encountered by Coal Tits in the two populations of the present study, would offer a functional explanation for the differences found in the hoarding niche of the two populations. Moreover, the difficulties faced by Coal Tits in building up long term stores due to competition with other tits, together with the harsher climatic conditions of the Norwegian area, are likely explanations leading to the typical irruptive-type movements of Coal Tit populations in northern Europe.

The picture is rather different in the Pyrenees, because only the Crested Tit is present and in very low numbers in comparison to the Coal Tit, which clearly would reduce the degree of kleptoparasitism and/or competition for hoarding and foraging sites. As a result, the cost of building up long-term reserves is predicted to be much lower than in the presence of competitive species.

In Norway, a variable seed crop may render the development of long-term hoarding in the Coal Tit even more difficult, because in years with poor seed crops birds may not be able to withstand the winter and thus may be forced to migrate. However, as other species of tits do build up long term reserves under such conditions, a variable seed crop does not seem enough by itself to obstruct the development of a long-term hoarding in Norwegian Coal Tits. In the Pyrenees, Coal Tits fed mainly on seeds of Mountain Pine. Seed crops in these areas are very abundant and rather regular across years, in contrast to crops in spruce forests (Génard & Lescourret 1986, 1987). Rich seed crops might allow the Coal Tits in the Pyrenees to store food throughout the winter in order to ensure a food supply in adverse weather (Brodin & Clark 1997). During normal weather conditions, a rich seed crop assures an abundant food source all winter. Thus, sedentary birds may benefit from stored food during the stages of decreased foraging surface due to harsh weather (Brotons 1997b)

Furthermore, the storing pattern described for the Coal Tit in the Pyrenees offers an alternative way by which birds may protect caches against conspecifics (Moreno et al. 1981, Brodin 1994). The fact that foraging and storing locations only coincide under adverse weather conditions, implies that possible conspecific cache pilferers are not likely to find stored items during normal weather conditions, thus assuring that caches last long enough to be recovered when needed. This may allow, for instance, the Coal Tits to congregate in groups of up to 70 individuals during normal conditions. Further investigations on the processes involved in cache protection and recovering in populations differing in social structure are needed to shed more light on the evolution and adaptive value of hoarding behaviour.

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INDIVIDUAL FOOD HOARDING DECISITIONS IN A NON-TERRITORIAL COAL TIT (*PARUS ATER*)

POPULATION : THE ROLE OF THE SOCIAL CONTEXT[6]

Abstract

Among the *Paridae* a strong association has been hypothesised to exist between food hoarding and the exclusive use of territories by winter groups. However, a recent hypothesis locates the origin of hoarding in a non-territorial ancient species. Data on hoarding from populations showing loose social systems is very scarce. Here, I studied hoarding behaviour in a non-territorial, high density Coal tit population in a subalpine forest in order to identify the mechanisms underlying individual storing decisions. Coal tits hoarded food intensively, showing a clear peak in late autumn. The presence of close neighbours (<5m) had the strongest, negative influence on caching probability, whereas distant neighbours (>5 m) foraging in the same flock did not affect the probability of caching. Adults concentrated their stores around the centre of their home ranges. Juvenile residents hoarded at similar rates to those of adults, showing the same tendency to avoid close conspecifics. Caching intensity but not caching location was unaffected by the time of day. Caches located in the inner parts of trees took longer to store and were located further away than those in outer parts of trees. Furthermore, resident adults stored in inner, safer caching locations, more often than juvenile residents and transients did. Differences in hoarding effort according to the storing substrate and the bimodal daily storing location found in juvenile residents and transients suggest that stores have a different future use depending on where they are made. Individuals may benefit from the use of hoards in the short term (i.e. juveniles using outer parts of trees) as an alternative to internal fat reserves; or as a food deposit (i.e. inner locations) for long term use during adverse weather conditions, favouring sedentarity. Therefore, my results show that hoarding is compatible with a non-territorial, non-breeding social system, offering a frame on which hoarding could have originated in an ancient, non-territorial but sedentary tit species.

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[6] Submitted

INTRODUCTION

Hoarding behaviour has evolved in different groups of birds as an adaptation which allow individuals to ensure or increase food supply in moments of shortage or increased energy demand (Vander Wall 1990). Among the *Parida*e, several social species hoard food intensively during autumn and winter (Sherry 1989). Andersson & Krebs (1978), stated that any hoarding animal must have an advantage over non-hoarding individuals in his group in retrieving the item it has hoarded. If not, the non-hoarding animals would enjoy the same benefits without the costs involved in hoarding. Some behavioural studies and recent neuroanatonomical data suggest that, in fact, individuals do employ several mechanisms (see review in Sherry & Duff 1996) that ensure the enjoyment of the hoarded food (Brodin & Ekman 1994). Territorial behaviour is a major behavioural strategy by which birds protect stores and safeguard their future exclusive use (Vander Wall 1990). By limiting the use of a given area to competitive individuals, territoriality favours the exclusive retrieval of stores through a reduced probability of robbery. To date, detailed studies of food hoarding in Parids have been mainly restricted to territorial, coherent winter flocking species (Cowie et al. 1981, Moreno et al. 1981, Haftorn 1974, Pravosudov 1985, Petit et al. 1989, Lens et al. 1994, Brodin 1994a,b). Group size in such associations is small, often limited to 6-8 individuals (Matthyseen 1990). Few studies have been conducted on the hoarding behaviour of partially non-territorial species (Haftorn 1956). However, Smulders (1998) hypothesised that the origins of the hoarding habit could be traced to a non-territorial species of an ancient Parid that did not have the need for a specialised memory system. Possible storing mechanisms and the use of stores in a hypothetical original non-territorial species are unknown. Therefore, by conducting behavioural analyses of non-territorial hoarding populations of parids, we might shed new light on the evolutionary origin of the hoarding behaviour in this group of passerines.

In this study, I report the hoarding behaviour of a high density (25-40 birds /10 ha during autumn and winter, own unpubl. data), non-territorial Coal tit population inhabiting a coniferous mountain forest in the Pyrenees. Specifically, I studied the hoarding intensity of individuals during autumn and early winter with the objective of comparing these results with those obtained in territorial populations of other hoarding species. Second, I studied the behavioural decisions that individuals made at the time of hoarding food items. Specifically, I wanted to identify the behavioural mechanisms used by hoarding individuals when deciding to store a food item, taking into account, that in a non-territorial population, birds do not have exclusive use of their territories and furthermore, they often move in large groups. Finally, I studied hoarding effort in relation to the location of stored food items. This was analysed in order to determine the possible differential uses that birds might assign to caches according to their residence status.

METHODS

The hoarding behaviour of Coal Tits was surveyed from September 1997 to January 1998 in the Pyrenees mountain range. The study area of about 150 ha is located in the 'Cadí-Moixeró' Natural Park in the eastern Pyrenees (north-east of the Iberian Peninsula), ranging from 1800 to 2100 m a.s.l. Mountain Pine *Pinus uncinata* dominates the study area with Scots Pine *P. sylvestris* predominant on southern slopes and at lower altitudes. Understory is scarce, dominated by Juniper *Juniperus communis* and grasses. More information about the vegetation can be found in Vigo (1976). The forest has been exploited until recently on a long-term cycle, resulting in tree stands of different ages in the area. The annual precipitation is approximately 1100 cm, around 35 % of which falls as snow during the winter months. Snow remains on the ground from December the beginning of April.

The Coal Tit is a small forest passerine (body mass, 0"SE= 9.22 "0.25, N=255, Brotons unpubl. data). In the Pyrenees, Coal Tits are very common throughout the winter and form flocks of up to 100 individuals, often with a few Crested Tits *P. cristatus*, Goldcrests *Regulus spp*. and solitary Treecreepers *Certhia spp*. (Brotons unpubl. data). Therefore, winter flocks are clearly dominated in numbers by the Coal Tit and frequently this species is their only component.

Prior to the study, the birds were individually colour-banded and aged. Adults were sexed according to breeding behaviour following Svensson (1992). During the same period, colour-ringed individuals from two plots within the study area (Chapter 1) were followed intensively in order to determine their spacing patterns. Using resights of colour-ringed individuals, home ranges and core areas (defined as minimum convex polygons containing 100 % and 75% of observations) of adult resident birds were established (home range, 0"SE=3.3" 0.2 ha, core area, 0"SE=1.6" 0.1 ha, N=24). I could not, however, determine the exact home range sizes of resident juveniles because these were much bigger than those of adults, and their estimates did not stabilise with the number of observations obtained (home range minimum estimate, 0"SE=8.5 " 1.4 ha, N=12). Transients were numerous in the study area, and only 26 % of the 85 juveniles colour-ringed during the winter were resighted at least 10 days after first captured and thus, considered juvenile residents. Un-ringed individuals were common during the whole of the winter, suggesting a high turnover rate in the transient population of Coal tits. Home ranges were not of exclusive use, but rather were used by neighbouring adult pairs, resident juveniles and numerous transients (Brotons in press). Therefore, classical Parid territoriality, defined as the exclusive use of a home range by resident individuals, was absent in the present study population. A typical Coal tit flock was rather heterogeneous and composed by a high number of juveniles (normally more than 10 individuals), both transient and residents, roaming over a large area and often joined actively by the resident adult pair of the range that the flock was crossing (Brotons in press). In such trips, resident adults used temporarily the home ranges of neighbouring resident pairs before returning to their own.

Sampling of the hoarding behaviour

Hoarding behaviour was studied in wild flocks of Coal tits during autumn and winter. After the location of one flock, 5 min period was allowed to pass before the observation was started. This was done to allow the birds to become accustomed to the presence of the observer. Each observation consisted in the observation of a focal, colour-ringed individual and the recording of the following behavioural descriptors: First, I recorded whether the individual stored food or not during the observation period and the number of stores it cached. Second, I noted whether there were other individuals near the focal individual. This last recording was divided into two different variables. Presence/absence of individuals closer than 5m (close neighbours), and presence/absence of conspecifics further than 5 m but closer than 20 m from the focal bird (distant neighbours). I chose 20 m as longer distances are increasingly difficult to observe. It was very difficult to recognise colour-marked conspecifics roaming near the bird and, therefore, the effect of social dominance could not be tested. The act of hoarding typically includes finding the food (e.g. commonly a single food item such as a pine seed) and transporting it to the cache which is located from tenths of centimetres to tenths of metres from the finding place. When the bird stored an item, an additional set of variables was taken in order to describe storing site and effort. I also noted the distance travelled between the finding place and the final cache location (storing trip), the time taken to complete the storing trip, the storing substrate (i.e. trunk, thick branch, twigs or needles) and the exact location of the item within the tree (see Brotons and Haftorn 1999 for further description of the methods). The observation period was terminated by the loss of the focal bird from sight. If the same bird was found again, a new record was taken only after at least 2 min to avoid serial correlation (Brodin et al. 1996). The final data set included hoarding observations from 34 adults and 18 resident juveniles. Because I was not able to follow intensively all individuals the whole of the study period, sample sizes may differ in different statistical analyses.

Hoarding Seasonality and Frequency

I studied hoarding seasonality and frequency in 12 adults (8 males and 4 females) from which I was able to obtain at least 3 observations during each month of the study. Mean length of the observation periods pooled for a given individual was 304 s (S.E.= 42 s). Mean values per individual and month were used as monthly hoarding frequency estimates. Then, hoarding frequency was analysed by a repeated measures ANOVA in which the month was the within-subject factor and the sex was the between-subject factor. The same statistical method was used in the analysis of juvenile hoarding seasonality. However, due to the scarcity of observations obtained from resident juveniles (n= 8), repeated measures analysis involving these individuals were carried out by pooling the monthly data into three periods of two months (except for November for which the data was not clumped). Hoarding frequency was log-transformed prior to the analyses in order to achieve homogeneity of variances and normality of error distribution.

Analyses of the Hoarding Decision

In order to assess the importance of various social-related factors on the hoarding decision (i.e. when and how the birds decided to store an item), I performed a logistic regression analysis with the presence or absence of hoarding in each observation period as the dependent variable. In this analysis, I used individual based observations of 60 s period as the sampling unit. When the observation period was longer, only the first 60 s were taken into account. The independent factors included in the model were: presence of close or distant neighbours around the focal individual (two level factors each), the distance of the focal bird to the core of its territory (categorised according to whether the observation was made within the core area of the individual or beyond) and the time of day (i.e. morning, from sunset to 11:00 hours, midday, from 11:01 to 14:00 hours, and afternoon, from 14:01 till dawn). First, a full model was fitted including all factors. Then, a stepwise backward elimination of the non-significant ($p>0.10$) factors was employed to select a final model containing only significant variables (minimal adequate model). The effect of each factor was studied by removing the least significant term remaining in the current maximal model (Crawley 1993).

In the first data set, I included 34 adult individuals (mean number of observations per individual = 9.48). Individuals do not have fixed hoarding behaviours and pooling different hoarding observations in order to obtained an individual mean could discard interesting information just for the sake of statistical dependence. Instead, I adjusted the degrees of freedom to account for the repeated use of a given individual: the weight of a particular hoarding observation was divided by a constant such that the sum of weights of all hoarding observations was equal to the number of individuals analysed (Desrochers 1992). This method had both, the advantages of preserving the information on individual variation on hoarding behaviour, and of counting each individual as only one observation in the statistical sense.

A second model including also juvenile residents (N=18 individuals, mean number of observations per individual = 3.8) allowed to assess the effect of age on the studied factors. This model included the age of birds (i.e. adults and first year juveniles), time of day (three levels, see above) and close and distant neighbours (two levels, see above) as explanatory variables. Model selection also followed a backward stepwise procedure identical to that used in the first model selection. The data were analysed using logit models in Statistica and GLIM 4 for PC statistical programs (Crawley 1993).

Analyses of the Hoarding Effort and Location

Hoarding effort was considered to be related to the distance and the time spent in a given storing event. Both variables were significantly and positively correlated (Pearson, $r=0.45$, $F_{1,57}=11.8$, $p<0.001$). Therefore, I used only one measure of hoarding effort (i.e. hoarding distance) in most of the analyses. In detail, I studied the variation in the storing effort according to the location of the cached item within the tree. This was analysed through a four-factor ANOVA, with month, time of day, substrate and residence status as fixed factors, using each individual as the independent statistical unit (i.e. the storing trips to hoard an individual food item, Petit et al. 1989, were weighted according to the total number of observations per individual, see above). The storing trip distance was square root and time taken to complete the storing trip was log-transformed prior to the analyses.

In the study plots where the observations were made, ringing effort had been especially high (Brotons in press). Therefore, most of the resident birds, both adults and juveniles were colour-ringed. However, a high number of unringed, most likely transient birds, were frequently sighted in the area. In order to compare the hoarding effort of resident individuals and more transient Coal tits, I compared hoarding data from colour-ringed individuals (number of stores per individual = 2.2, N=14 resident juveniles; number of stores per individual = 6.3, N= 34 adult residents) with data obtained from unringed birds. Since by definition, transients spend a short time in a given area I could not collect storing data from transient colour-ringed individuals. Therefore, I assumed that most of the unringed birds sighted within the study plots were transient individuals, and given the sedentarity of adults, most probably juveniles. Storing data for unringed birds was collected in the same way to that for colour-ringed birds, but hoarding frequencies could not be estimated as individuals were impossible to identify in different days. Thus, transient individuals were not included in frequency or hoarding decision analyses. When I had different consecutive storing events of an unringed individual, they were weighted according to their total number (mean number of stores per individual = 1.4, N=67 transients). High mobility of transient individuals made re-sampling of unringed birds on different days very unlikely. Differences in the hoarding locations of adult and juvenile residents, and transients birds were assessed using logistic regressions on weighted individual based observations. In this analysis, substrate classes that varied from trunk to needles according to their distance from the trunk itself, were classified as inner (0) and outer substrates (1), and referred to as substrate index. Height was similarly analysed, using lower (0) and higher (1) locations within trees as categories for the dependent variable. The independent factors included in the analyses were residence status (resident adult, resident juveniles and transients) and time of the day (see above).

RESULTS

Hoarding Intensity and Seasonality

Mean hoarding intensities per individual during the whole study period were 2.3 stores/10 min (S.E.=0.3). However, storing intensity varied significantly by month. The frequency increased from September to November, when it peaked, and fell again as the winter advanced (month, $F_{4,40}$=4.7, p<0.01, Fig. 1). Among adults, sex did not affect hoarding intensities (sex, $F_{1,10}$=0.5, N.S.), which remained similar in both sexes during the five months of the study (interaction, $F_{4,40}$=0.6, N.S.). The data did not show any significant differences in hoarding intensities

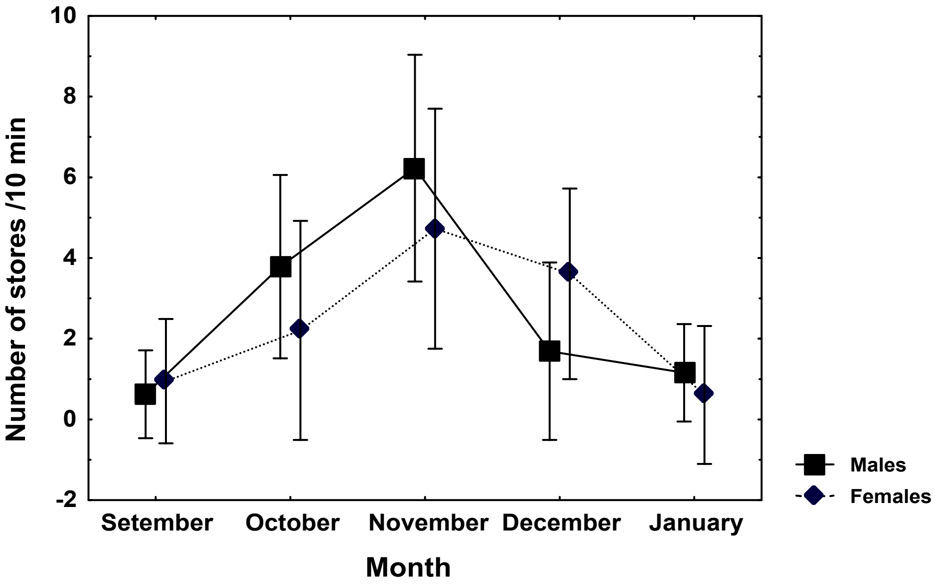


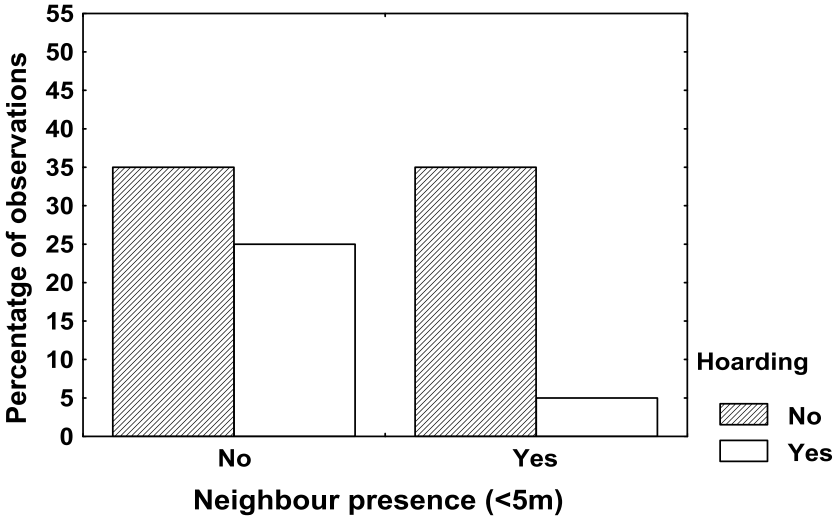
Figure 1. Hoarding intensities of male and female adult Coal tits, based on 8 males and 4 females followed during the five month of the study. Bars represent standard deviations and lines are only meant to facilitate the reading of overall tendencies.

between juvenile and adult birds (age, $F_{1,16}$=0.6, N.S.), while juveniles also showed significant seasonality with hoarding intensity peaking in late autumn (month, $F_{2,8}$=5.8, p<0.05).

Hoarding Decisions

Close neighbours reduced significantly, by a factor of more than 4 (log odds ratio=$e^{-1.40}$) the hoarding probability, making this the main determining factor (Fig. 2). Distant neighbours from the same flock but foraging more than 5 m away from the focal bird did not seem to influence hoarding probability (Table 1). Adults concentrated stores around the core areas of their home ranges, and hoarding frequency decreased sharply as the birds were observed further from the centre of their home ranges (Fig. 2, Table 1). The likelihood of an individual caching within its core area was about 2.5 (log odds ratio = $e^{-0.95}$) times that of the individual caching outside it. Coal tits did not seem to hoard more intensively at any particular time of day, and so this factor was not included in the final model.

A.



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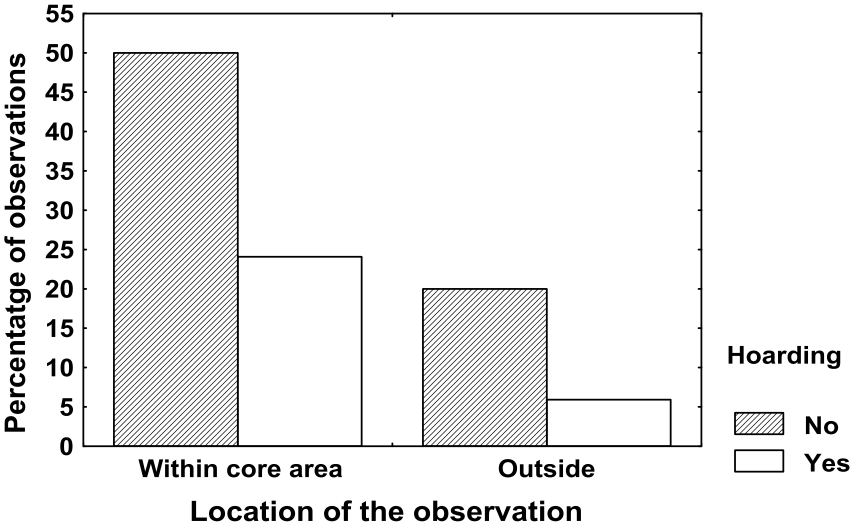


Figure 2. Adult hoarding frequencies during 60 s periods and A. presence of closer conspecifics (<5m, N=373 observations), B. distance from the main core area of individual home range (N=313 observations).

	Change X^2	Change *df*	P	Estimate
Time of the day	0.16	2	N.S.	
Distant neighbours	0.35	1	N.S.	
Distance from core area	3.13	1	=0.07	-0.95
Close neighbours	4.62	1	<0.05	-1.40

Table 1. Logit model selecting factors that best explain the probability that an adult resident stores at least a food item during a 60 s observation (N=34).The factors were tested with a step-wise backward procedure calculating the change in deviance (Change X^2) and in degrees of freedom (Change df) when a variable was excluded from the full model. See text for details.

In the second model, the only factor which was finally included was again the presence of closer neighbours (Change X^2=10.85, Change *df*=1, P<0.001). This indicates that neither the age of birds (Change X^2=0.92, Change *df*=1, N.S.), the time of day (Change X^2=0.42, Change *df*=2, N.S.) nor the interaction of the two (Change X^2=0.40, Change *df*=3, N.S.) had any effect on the hoarding intensity of individuals in the study population.

Hoarding Effort and Location According to Residence Status

Hoarding effort varied depending on where an item was cached. Items stored in inner parts of trees, such as the trunk and thick branches, took longer to store and were located further from the origin than items stored in outer parts of trees (storing distance, substrate, $F_{3,73}$=9.80, p<0.001, Fig. 3; storing time, substrate, $F_{3,31}$=6.81, p<0.001). The difference in hoarding effort according to the storing location was consistent independently of whether the storing individual was resident or transient in the area (Storing distance, residence status, $F_{3,73}$=0.50, N.S., storing time, residence status, $F_{3,31}$=0.23, N.S.), of the month when the storing took place (Storing distance, month, $F_{12,73}$=0.53, N.S.) and of the time of day (Storing distance, time of day, $F_{6,73}$=0.38, N.S.)

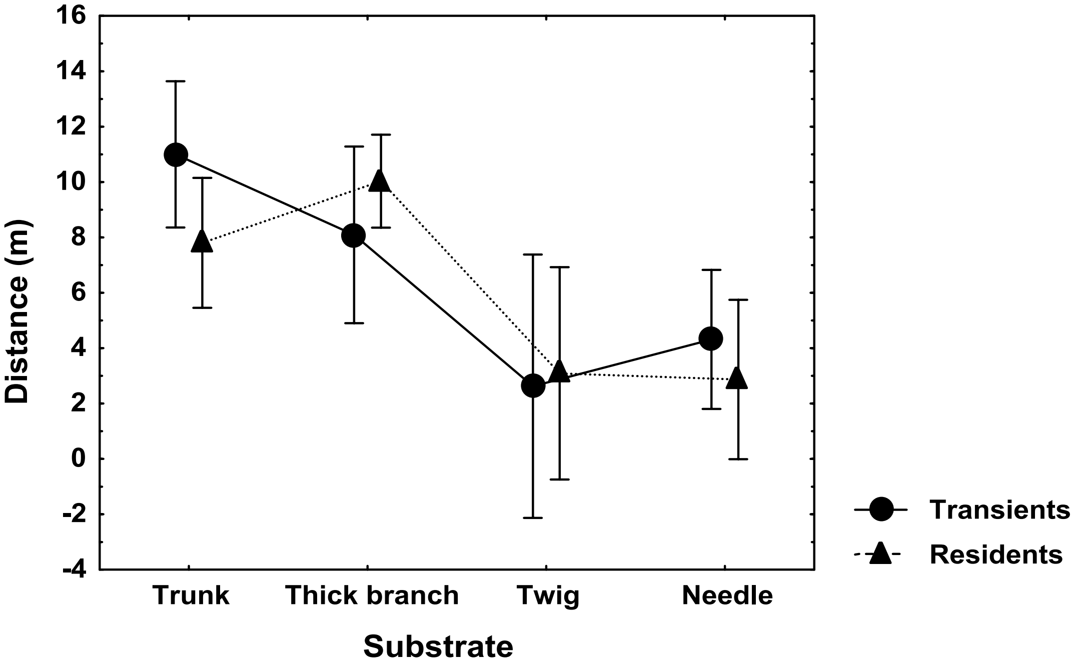


Figure 3. Storing effort, measured as the distance travelled by the bird before storing a food item, in relation to the cache location within the tree. Bars represent standard deviations and lines are only meant to facilitate the reading of overall tendencies.

Juvenile residents and transients did not differ in the frequency of use of inner substrates such as trunks and thick branches (group, Change X^2=0.45, Change *df*=1, N.S., Fig. 4). However, there was a highly significant effect of time of day on the choice of storing locations by individuals (time of day, Change X ^{2}=15.23, Change *df*=2, P<0.001). More concretely, both, resident juveniles and transients stored consistently more often in outer substrates in the morning and afternoon periods, compared to the hours around noon (interaction group*time of day, Change X ^{2}=1.00, Change *df*=2, N.S., Fig. 5). On the other hand, adult residents hoarded in the inner part of trees independently of the period of the day considered (time of day, Change X ^{2}=0.34, Change *df*=2, N.S., Fig. 5). Therefore, resident juvenile storage behaviour was more like that of transient birds, whereas resident adults stored more often in inner tree substrates that the former group (group, Change X ^{2}=15.23, Change *df*=2, P<0.001, Fig. 5). The interaction between time of day and group was also significant (Change X ^{2}=5,68, Change *df*=2, P<0.05) suggesting a different role of time of day on the hoarding patterns between adults and juvenile residents and transients.

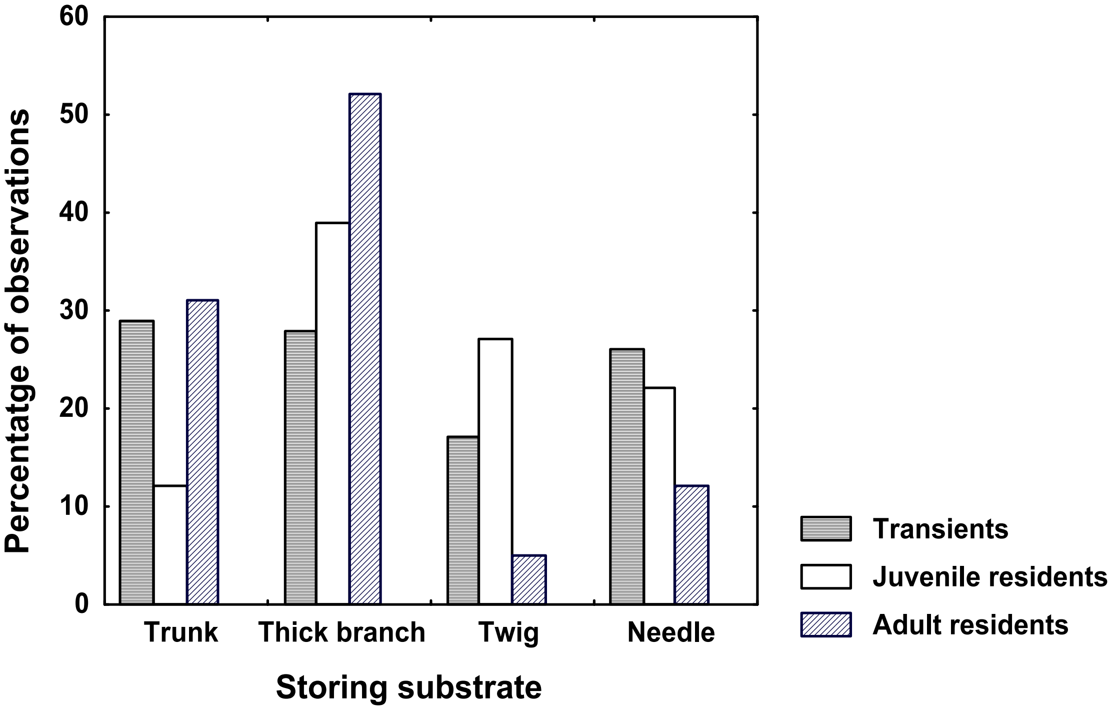
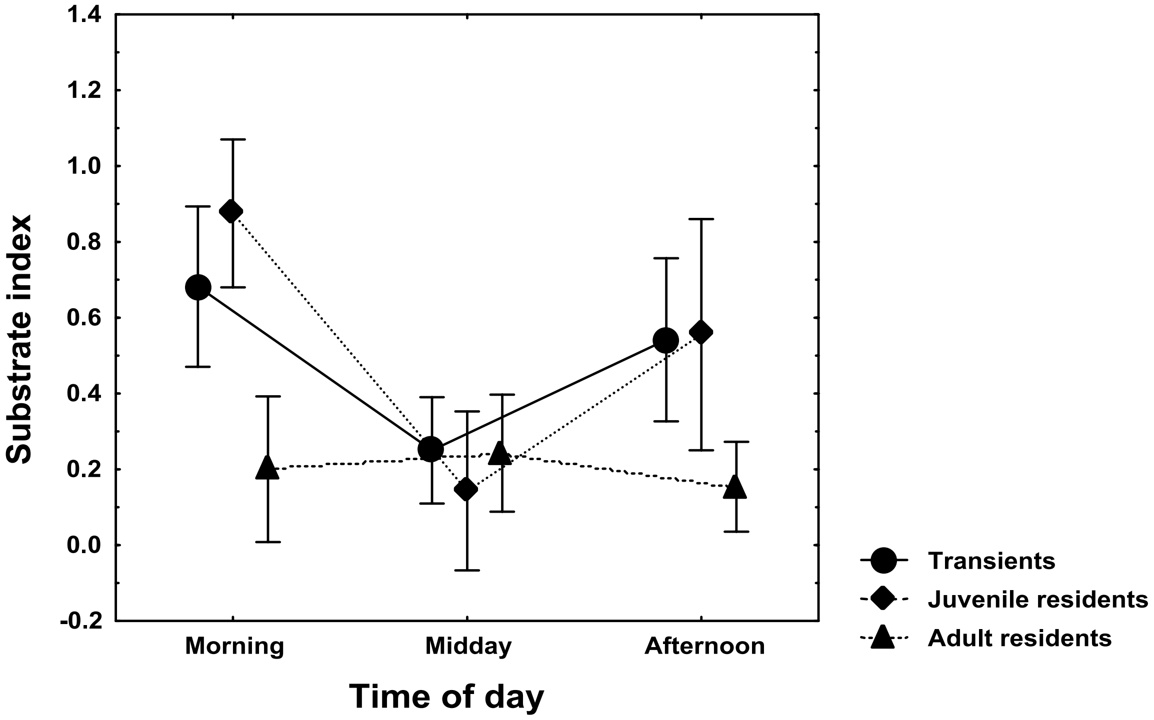


Figure 4. Hoarding microhabitat of Coal tits according to the age and the residence status of individuals (N=215 storing events).

No differences where detected in the storing height of caches among residence groups (group, Change X ^{2}=0.10, Change *df*=1, N.S.). But significant overall differences were detected in respect to when during the day the store was made (time of day, Change X ^{2}=9.13, Change *df*=2, P<0.05). Analysing the different groups separately, a clear pattern emerged, with juvenile residents and transients storing in higher parts of trees in the morning hours, and secondarily in the afternoon (time of day, Change X^2=12.28, Change *df*=2, P<0.01). This pattern was mainly due to the strong hourly dependence that location had in juvenile residents, whereas in transients, storing locations seemed to be only slightly affected in the morning (interaction time of day* group, Change X ^{2}=6.52, Change *df*=2, P<0.05, Fig 5). Again, like in the use of storing substrates, transient birds, but mostly resident juveniles behaved different from resident adults, showing a daily variation in the storing height absent in the latter.

A.



B.

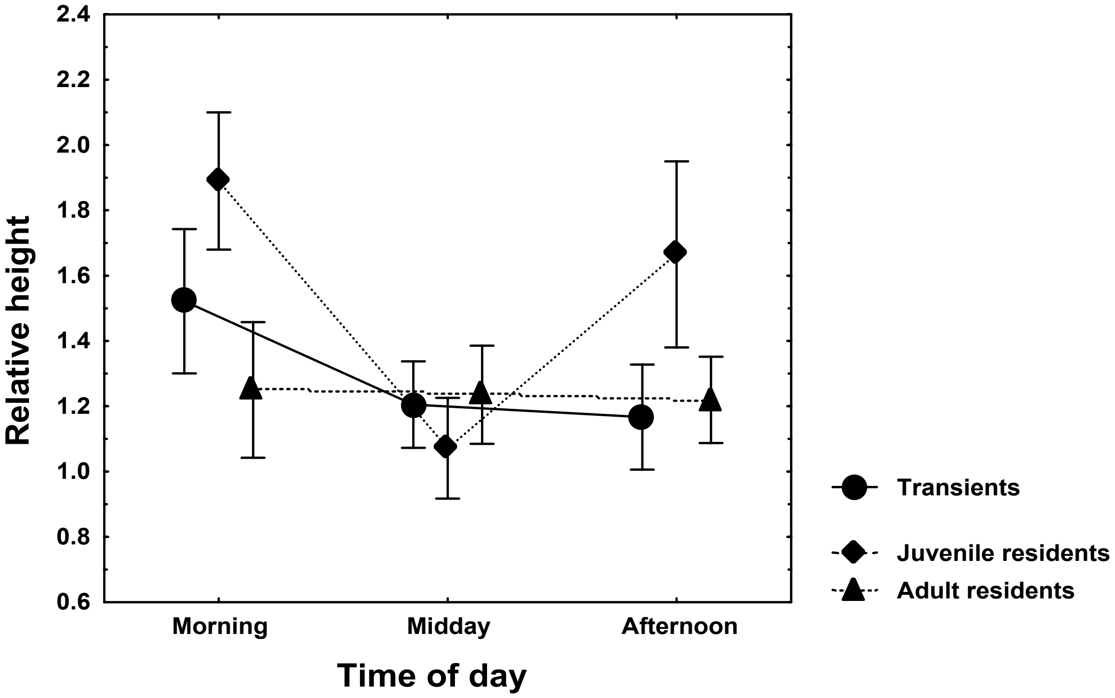


Figure 5. Daily use of storing locations by different residence and age classes. A. Substrate index. B. Relative storing height. Time of day is divided in three periods: Morning, sunrise to 11:00 A.M, midday, from 11:01 A.M. to 14:00 P.M. and afternoon from 14:00 PM to sunset. Bars represent standard deviations and lines are only meant to facilitate the reading of overall tendencies.

DISCUSSION

In spite of their non-territorial social system outside the breeding season, Coal tits in the Pyrenees hoarded food actively during autumn and winter. Hoarding intensities are very similar to those measured for species occupying strict group territories such as the Crested tit (Lens et al. 1994) or the Willow tit (Brodin 1994a). Hoarding rates increased during autumn reaching a peak in November. This seasonal pattern in food hoarding has also been found in the Crested and the Willow tit (Brodin 1994a, Lens et al. 1994), although the Coal tit maintains relatively higher hoarding intensities during late autumn and winter. Observational data during late winter suggests that hoarding takes place regularly also during February and early March. Increasing hoarding intensities during early autumn coincided to a large extent with the ripening of mountain pine cones which are an abundant and constant food source throughout the winter (Génard & Lescourret 1986, Brotons 1997b). Since pine cones are by far the most frequent stored food item, a causal relationship may be established between the increase in hoarding frequencies in mid-autumn and the ripening of pine cones then. Later, the decrease of open pine cone availability may play a role in the observed decrease in hoarding intensities as winter advance. However, this decrease is likely to be more closely related to the increased individual energy requirements as temperature decreases in winter. Previous, more descriptive analyses of the hoarding habit in the Coal tit also clearly seemed to indicate that this species is an active food hoarder during most of the autumn (Haftorn 1956).

Hoarding, Flocking and Spacing Behaviour

Even though they travelled in large groups, Coal tits did not stop hoarding when moving with other birds. However, individuals did not store at random, but rather were seen to select carefully the time and the place when a cache was made. Both, adults and juvenile birds avoided storing in the presence of close conspecifics but the presence of other individuals more than 5 m away did not seem to affect their behaviour. In this way, Coal tits reduce rates of immediate pilfering by birds which might have seen the exact storing place of the item (Stone & Baker 1989, Carrascal & Moreno 1993). Other species of Parids, such as the flock territorial Willow tit *(P. montanus*), seem to have much wider security zones in order to determine whether to hoard a given item or not (Lahti & Rytkönen 1996). Secondly, adults concentrated their stores in the core areas of their home ranges. Adult residents, thereby safeguarding their use for future necessity, heavily use these small areas (Brotons 1997a). Storing in the central areas of home ranges and, thus, avoiding areas of high overlap with neighbouring ranges may partially reduce the pilfering of cached items. Furthermore, cache concentration increases the value of deposits, allowing the caching individual to invest in them by directly defending storing locations from visitors that may constitute a threat. I have repeatedly observed unprovoked attacks on transient birds using the hoarding microhabitat of resident birds in good weather conditions. This behaviour can be interpreted as an aggressive response in which a classical territorial system involving a wide area defended from use by conspecifics becomes a predominantly site-related dominance system where the area is not defended but cached resources within may be (Kaufmann 1983).

Both adult and juvenile Coal tits seemed to hoard with a similar intensity. This disagrees with similar studies in the Willow tit (Lahti & Rytkönen 1996) where yearlings were reported to cache at a higher rate than adults, and with studies on the Crested tit, which reported the reverse trend (Lens et al. 1994). Lahti & Rytkönen (1996) explained such differences by the lower dominance status of juveniles, which might force them to build up a larger larder in order to withstand kleptoparasitism and the consequences of a lower social status (Ekman 1987). Lens et al. (1994) explained their opposite results by stating that the high costs of hoarding due to future competition with adults might limit the hoarding intensity of yearlings. However, in the Pyrenees, the main individual constraints on juvenile Coal tits may differ from those faced by Willow and Crested tits in central and northern Europe. High food availability and relatively low competition with adult birds within Coal tit flocks might lead to the similarity in the hoarding rates of juveniles and adults. On the other hand, the larger home ranges of juveniles in the Pyrenees (Brotons 1997a) suggest a different distribution of hoards from that of adults (Brodin

1992). The clarification of age differences in hoarding patterns requires more detailed studies of the spacing behaviour of juveniles and their hoarding habits.

Some models of the hoarding behaviour of birds predict higher hoarding intensities during morning hours when stores are to be used later on, as an alternative to the accumulation of internal fat reserves (McNamara et al. 1990). This pattern in the daily variation of food hoarding has been described in the Marsh tit (*P. palustris*, Stevens & Krebs 1986) and the White-breasted nuthatch (*Sitta canadiensis*, Waite & Grubb 1988, but see Haftorn 1956). However, if hoards are not only used on a short term basis, a daily routine in hoarding intensity would not necessarily be predicted (Pravosudov & Grubb 1997), as I found for the Coal tit. Rather, hoards would be accumulated with equal probability throughout the day or when conditions are most favourable (i.e. at midday, Lucas & Walter 1991). The difference in the microhabitat of stores made at different times of the day by resident juveniles, indeed, suggests that hoards made at different hours may be of different future use. This may mask possible daily patterns in storing frequency of stores meant as an alternative to internal fat reserves. Furthermore, even if the hoards are used to facilitate the building of overnight reserves, but a number of days after the storing event (Brodin 1994a,b), daily tendencies in storing may be difficult to uncover. The recovery of stores may then follow a daily pattern but storing intensity do not necessarily have to (Pravosudov & Grubb 1997).

Residence and Use of Caches

The differential location of caches according to the age and the residential status of individuals suggests an important variation in the eventual use of stores (Källander & Smith 1990). Consistently during the day, resident adults used protected sites in inner parts of trees (Brotons & Haftorn 1999) more frequently to store caches than did both transients and resident juveniles. These sites are frequently used in adverse weather conditions such as snowfalls (Brotons 1997b). Therefore, caches located there may be of high value to resident birds, allowing them to cope with sudden variations in food supply. In fact, hoarding effort of items stored in inner parts of trees was significantly higher than that in outer parts, suggesting a higher fitness value of hoards there (Moreno & Carrascal 1995), possibly in terms of increased future foraging prospects enhancing sedentarity. On the other hand, juvenile residents and transients hoarded items more frequently in the outer parts of trees, where caches took less effort to be stored. In such sites, caches are more likely to suffer from the effects of wind or to disappear under snow (Petit et al. 1989, Gendron & Reichmann 1995). Therefore, a long-term use of hoards is likely to have higher costs in terms of item loss as the sedentary status an individual decreases. Given the wandering status of transients and the large home ranges of resident juveniles, these groups might benefit to greater extent from the short-term use of hoards. Then, a proportion of caches made by transients and juvenile residents may be conceivably used to delay the build-up of body mass and to maintain higher manoeuvrability during the active period, and thus decrease the risk of predation (Lima 1986, but see Grubb & Pravosudov 1999) without reducing over-night survival. In my study area, transient Coal tits showed higher levels of internal fat reserves than resident individuals (own unpubl. data). This suggests that such individuals indeed have to carry extra costs from the fat load needed to cope with a more unpredictable food supply associated from a transient way of life (Metcalfe & Ure 1995) and will therefore benefit from the short term use of stores.

The daily pattern in the location of stores found in juvenile residents and transients also supports the view that juvenile residents and transient individuals utilise two different types of storing according to the future use of cached items. Stores located in safer, inner and lower tree parts are mainly made around noon, the period when individuals are less likely to be energy constrained. On the other hand, caches made during the morning and afternoon, under a possible higher energy stress, may be located more often in the outer parts of trees where stores were invested less energy and may be given a short term use.

Overall, there was a clear habitat segregation pattern, with adults hoarding more frequently in inner sites such as trunks or thick branches than juvenile birds. Inner parts of trees are often associated with a lower predation risk than outer, more exposed locations and are therefore, assumed to be safer foraging sites (Ekman

1987, Suhonen 1993). Given their dominance over juveniles and priority of resource access, adults might further benefit from storing in these places if later they forage in these more protected sites. Coal tits in the Pyrenees use consistently outer parts of trees for foraging in favourable weather conditions (Brotons 1997b). Because in such conditions, inner substrates are only used as storing substrates and not for foraging, a minor role of direct microhabitat competition for inner substrates is predicted on the choice of the storing location of juvenile residents and transients. However, if age related foraging microhabitat segregation is important in harsher weather conditions, future competition among age groups may then play a role in deciding the storing locations of food items. Unfortunately, data on foraging microhabitat by residence class is lacking at present.

The Evolution of Hoarding

The results of this study show that non-territoriality, understood in its classical sense (Kaufmann 1983), is compatible with hoarding. Individuals, mostly transients and juvenile residents, may use caches on a short term basis as an alternative to internal fat reserves (sensu McNamara et al. 1990). On the other hand, food deposits may be of use in adverse weather conditions, thus, favouring the sedentary nature individuals such as resident adults and juveniles (Brotons & Haftorn 1999). Smulders (1998) suggested the hoarding habit may have originated in a non-territorial species in which memory did not necessarily play a crucial role. In a closed system, winter residence may favour the future acquisition of a territory and thus increase individual fitness (Koivula 1994). Therefore, even in a non-territorial system, individuals seem to benefit from hoards in both, the short term and a longer term when such behaviours favour a non-breeding resident status in a high quality area. Some fine grained behavioural mechanisms also act in order to reduce robbery and ensure the exclusive use of stores. My results showed that hoarding is compatible with a non-territorial, non-breeding social system, offering a frame on which hoarding could have originated in an ancient, non-territorial but sedentary tit species. The higher benefits to be obtained from the exclusive use of hoards in harsher, more variable environments (Brodin & Clark 1997) may have led to the non-breeding, strict territorial system of many temperate and boreal tit species (Ekman 1989, Källander & Smith 1990).

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WINTER TERRITORIALITY AND LIFE HISTORY TRAITS IN THE *PARIDAE*[7]

ABSTRACT : Within *Paridae,* the degree of winter territoriality as a wintering strategy widely varies among species. In some species, attaining a position in dominance structured territorial winter flocks is crucial for juvenile survival, whereas in other species juvenile birds spend winter in large non-coherent groups with a looser structure. We tested the hypothesis that in a closed territorial non-breeding social system where juvenile settlement is time constrained, decreased reproductive output would be an evolutionary adaptive mechanism for time saving in order to cope with such constraints. Using two different comparative methods, we analysed the relation between non-breeding territoriality and two breeding variables in a sample of parids. A significant negative relationship between winter territoriality and both clutch size and proportion of second clutches was found. Evolutionary increases in the degree of winter territoriality were associated with decreases in reproductive output, smaller clutch sizes and lower proportion of second clutches. We concluded that long term indirect factors affecting offspring fitness play an important role in determining breeding strategies in parids, when successful settlement of juveniles in territorial populations is time constrained.

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[7] With Markku Orell, University of Oulu. Submitted.

INTRODUCTION

To maximize lifetime reproductive success, individual birds have to adjust breeding strategies to the prevailing environmental conditions and population characteristics. Many studies have focused on the possible optimisation cues that birds may utilise in order to maximise breeding success through different combinations of clutch size and the number of broods laid per season (Lack 1966, Murphy and Haukioja 1986, Boyce and Perrins 1987, Godfray et al. 1991). Most of such studies have found direct links between the breeding parameters and different ecological factors prevailing during the current breeding attempt. Several factors such as individual and territory quality, food availability, competition and nest predation, have been shown to affect the clutch size and the number of broods laid per season (Perrins and McCleery 1989, Godfray et al. 1991, Martin 1995, Martin and Clobert 1996, Verboven 1997). However, according to the life-history theory, trade-offs between current and future reproductive investments also shape breeding strategies (Stearns 1992). Therefore, life history strategies do not only deal with short term adjustments of breeding parameters to local conditions, but also with the future long term costs and benefits of the decisions made during the current breeding attempt (Haywood and Perrins 1992).

For birds such as tits and chickadees, which live in groups during winter, successful establishment in winter flocks may be an important factor affecting winter survival and future breeding prospects (Nilsson and Smith 1988, Koivula and Orell 1988). Studies on the winter social systems of the genus *Parus* suggest two main different social structures according to the presence of winter territoriality and the coherence and stability of the groups formed (Ekman 1989, Matthysen 1990). In the populations where a territorial coherent system has been found (i.e. flock system, territorial species hereafter), early establishment of juveniles seems to be a key factor because early fledglings have a higher probability of joining a territorial group than later ones (Nilsson 1990). Within a dominance structured and territorial system, joining into a winter flock is crucial to obtain a breeding territory the following summer (Matthysen 1990). As the winter social system becomes looser and less territorial, the costs of late establishment are judged to decrease accordingly (these species will be referred as non-territorial species hereafter). Therefore, individuals of populations where the flock system is common may not maximise production of recruits by maximising the number of offspring produced during the breeding season. Rather, production of high quality offspring early in the breeding season to increase their chances to join a territorial winter flock (Koivula and Orell 1988, Källander and Smith 1990) would be adaptive.

Our working hypothesis is that the breeding strategies of species with a predominant territorial system during winter are affected by the constraints imposed by such a strategy. More specifically, territorial species should lay smaller clutches, and lay a smaller proportion of second clutches than less territorial ones. The constraints leading to earlier laying of the clutch would result: (1) in laying small clutches to ensure high quality offspring, since smaller clutches can be laid earlier and take less time to incubate and raise than larger ones (Nilsson and Smith 1988b), and (2) in a low proportion of second clutches since the lowered quality of the offspring produced later in the season may not be enough to outweigh the possible positive fitness effects derived from additional offspring.

To our knowledge, there are no comparative studies on the relationship between non-breeding social patterns and breeding parameters in birds. We tested the possible association of winter territoriality with different breeding parameters using data available on the well studied group of *Parus* species. Much is known on the breeding and non-breeding behaviour of different species in this group and interesting patterns of co-variation seem to emerge. The few previous efforts to relate interspecific clutch size variation in parids to ecological parameters have failed when comparative studies have been conducted (i.e. the limited breeding opportunities hypothesis, Mönkkönen and Orell 1997).

METHODS

We gathered data on winter territoriality and breeding parameters from different literature sources. In total, we were able to study 13 species of the genus Parus, using the White-breasted nuthatch (*Sitta carolinensis*) as the outgroup in comparative analyses (see appendix).

Winter territoriality was interpreted as the exclusive use and/or active defense of home ranges by the base units of winter social groups (after Matthysen 1990). Since, in addition to inter-species variability, non-breeding social organization is predicted to vary among populations according to local environmental conditions (Smith and Van Buskirk 1988), we took into account the information available for any species included in the study. From two reviews on the non-breeding social organization of parids, Ekman (1989) and Matthysen (1990), we selected population studies conducted on color-ringed populations which were not located in extreme ranges of the species' distribution areas according to Cramp and Perrins (1993) and Harrap and Quinn (1996, see appendix). We also included some studies conducted after 1990 (see appendix). An index of the winter territoriality for each species was calculated as the proportion of studies that found individuals occupying exclusive territories, often in groups of stable membership (defined after Matthysen 1990). Lack of sufficient data for most of the species did not allow controlling for the possible latitudinal variation in territoriality. However, studies of non-breeding social organization have been mainly conducted in optimal habitats for the species (i.e. high density habitat for each species) and estimates of winter territoriality are also thought to be representative of the species.

We used population based studies in order to obtain comparable data of clutch size and proportion of second broods for each species. Data on clutch size were obtained from Mönkkönen and Orell (1997), who based clutch size estimates on populations inhabiting optimal habitats for each species (see appendix). Most of the population studies included in Mönkkonen and Orell (1997) work are the same to those used in the territoriality index. Clutch size values obtained with this method agree to a very high degree with those used by Martin and Clobert (1996) in a sub-sample of 11 species of *Paridae* for which data was obtained also on population based estimates ($r=0.93$, $F_{1,9}= 57.34$, $p<0.001$). In parids, clutch size is not related to body size (Mönkkönen and Orell 1997), therefore, we did not include body size as a covariant in subsequent analyses. The proportion of second broods within species may show considerable variation among different populations (from 0 to 100%, Verboven 1997). We decided to use two approaches to calculate this parameter. First, we used the proportion of second broods using the sample of population studies used in Mönkkönen and Orell (1997, method 1). Second, we included the variation within the species by using the proportion from a sample of studies on each species in which a significant proportion (>5%) of pairs were found to lay second clutches (method 2, see appendix). The two data sets obtained by these two approaches were positively correlated ($r=0.79$, $F_{1,12}= 19.65$, $p<0.01$). Consequently, we were confident that the data on breeding parameters of each species were also representative for the true central tendency for each species.

Statistics

Phylogenetic relationships potentially create a problem of non-independence among species because closely related species may exhibit similar traits simply due to the sharing of a common ancestor (Felsestein 1985). Therefore, to override this problem, we used two comparative methods in order to study the relationship between non-breeding territoriality and breeding parameters in parids. We adopted the information on protein relationships among parids and the phylogeny provided by Gill et al. (1989, fig 1). There are other parid phylogenies available, such as Kvist et al. (1996) based on mitochondrial DNA, and Slikas et al. (1996) based on DNA-DNA hybridization. Recent phylogeny estimates supported main results of previous studies in what refers to the main relationships among Parus main groups (Slikas et al. 1996). Gill et al (1989) was chosen because the other studies on the phylogeny of parids are too limited in scope, and include species with few ecological data available to be useful for the present purpose. For the first analysis, we calculated phylogenetic independent differences (contrasts) between pairs of species in the degree of winter territoriality. These contrasts were then correlated with the contrasts in the breeding parameters of the same species. Because the analyses use independent contrasts between species and not the species as such, problems of non-independence through a common ancestor can be overcome (Felsestein 1985). Least-square linear regressions on transformed variables (degree of winter territoriality and proportion of second clutches were arcsin transformed, whereas clutch size was log-transformed) were calculated through the origin (see Garland et al. 1992). We standardised the independent contrasts by the branch lengths given in Gill et al. (1989) and then we checked for adequate standardisation by correlating the absolute values with their standard deviations (Garland et al. 1992). No such correlations emerged when performing the analyses on the traits used in this study. All the analyses were performed using PDAP 2.0 (Phenotypic Diversity Analyses Program, Martins and Garland 1991).

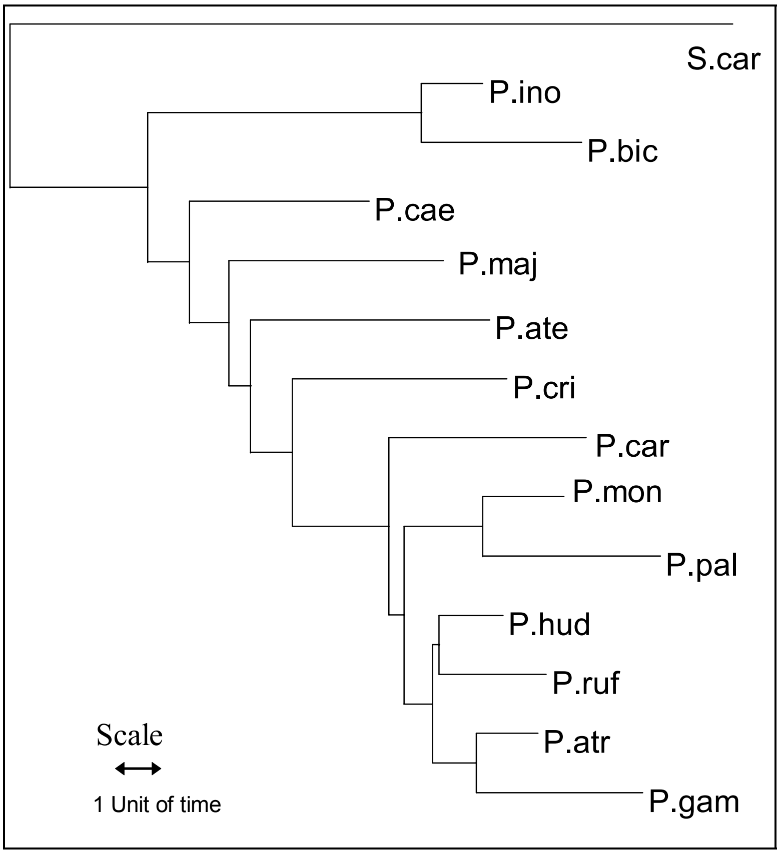

Figure 1. Phylogeny of *Parus* based on protein relationships (Gill et al. 1989). Abbreviations are as follow: Pate, Parus ater; Patr, *Poecile atricapillus*; Pbic, *Baeolophus bicolor*; Pcae, *Parus caeruleus*; Pcar, *Poecile carolinensis*; Pcri, *Parus cristatus*; Pgam, *Poecile gambeli*; Phud, *Poecile hudsonicus*; Pino, *Baeolophus inornatus*; Pmaj, *Parus major*; Pmon, *Parus montanus*; Ppal, *Parus palustris*; Pruf, *Poecile rufescens*; and Scar, *Sitta carolinensis*.

Independent contrast methods that use Felsentein's (1985) assumption of Brownian motion to model evolutionary change across phylogeny have been recently criticised to some degree (Price 1997). Therefore, as an alternative comparative method, we used directional comparisons (sensu Harvey and Pagel 1991). Such comparisons can be used to investigate whether the evolution of two variables is correlated, by comparing the reconstruction of their ancestral states. Ancestral states were first reconstructed using the parsimony method of Huey and Bennet (1987) for a given tree. Then a simple subtraction between the trait values for nodes on the phylogeny yielded the inferred changes in each character. To calculate directional comparisons, we used the procedure Parscont from the program Compare 2.0 developed by E.P. Martins (Martins and Hansen 1996). Several most parsimonious trees (n=9) are possible with the coded protein data from Gill et al. (1989) in addition to the one shown in the original paper. Therefore, we decided to use the strict consensus tree constructed with

Henning86 program version 1.5 (Farris 1988) as alternative phylogenetic information in the directional comparisons (details in Mönkkönen and Orell 1997). Polytomies were present in the consensus tree found in our analyses. They can affect the outcome of comparative analyses and must therefore be considered (Maddison 1990, Losos and Miles 1994). In order to assess the possible influence of partially known phylogenetic information on the relationship between the variables under study, the effect of the consensus tree polytomies on the relationship was assessed by examining the reconstruction of the most and least favourable tree to the hypotheses tested (see Mönkkönen and Orell 1997).

RESULTS

Clutch size

The degree of winter territoriality and clutch size were significantly associated in our data set (r=-0.61, d.f.=12, p<0.001). When phylogenetic relationships were taken into account, we found that the significant negative correlation between the degree of winter territoriality and clutch size in parids remained: the evolutionary increase in winter territoriality was associated with the evolutionary decrease in clutch size (b=-2.22, $F_{1,12}$=15.61, r= -0.71, p<0.001, fig. 2). The evolutionary inverse relationship between winter territoriality and clutch size appeared also to be significant when we used directional methods in our comparative approach. Increases along the branches in the degree of winter territoriality were strongly associated with decreases in clutch size (r=-0.85, d.f=22, p<0.001, using the tree presented by Gill et al. 1989, fig. 3). When we used the strict consensus tree, the relationship remained significant (r=-0.77, d.f.=17, p<0.01), and solving of the polytomies showed that such a relationship is not seriously affected by partially unknown phylogenetic information (r varied between -0.77 and -0.86, d.f.=17, p<0.01, depending on how the polytomies were solved, see methods). Therefore, the results of our data set support the hypothesis of the evolutionary negative relationship between the degree of winter territoriality and clutch size in parids.

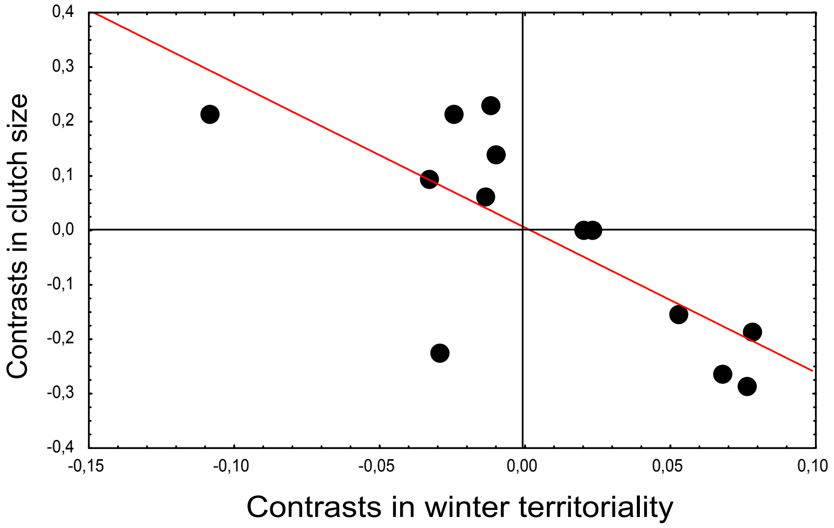

Figure 2. Independent contrasts of clutch size in relation to contrasts in winter territoriality using the phylogenetic information of the tree from Gill et al. (1989).

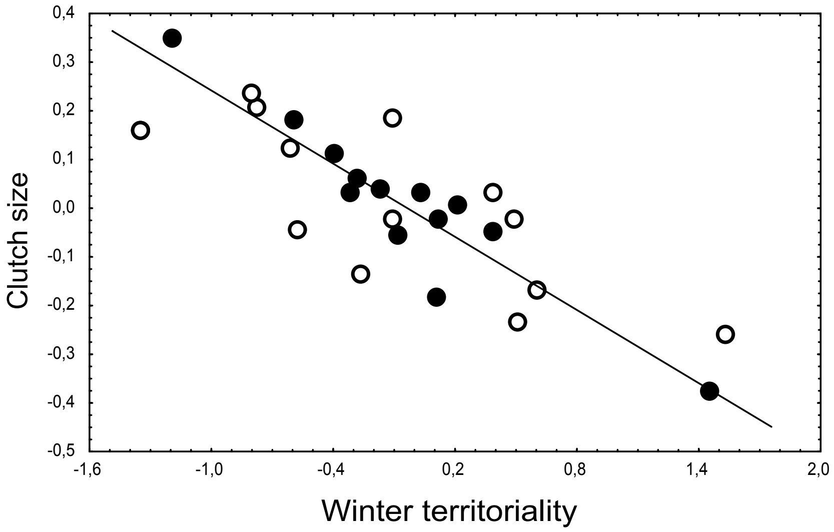

Figure 3. Directional comparisons of changes in clutch size and winter territoriality for the tree of Gill et al. (1989). Open circles represent branches ending with an extant species; solid circles, branches deeper in the tree.

Proportion of second clutches

Our data showed a significant inverse relationship between the degree of winter territoriality and the proportion of second clutches in parids (r=-0.71, d.f.=12, p<0.001). Once phylogenetic effects were removed, the significant inverse relationship between the degree of winter territoriality and proportion of second clutches remained: increases in winter territoriality contrasts were associated with contrast decreases in the proportion of second clutches (method 1, b=-0.39, $F_{1,12}$=19.13, r=0.78, p<0.001, and method 2, b=-1.65, $F_{1,12}$=4.93, r=0.54, p<0.05, fig 4). Directional methods showed the same tendency. Evolutionary increases along branches were associated with a decrease in the percentage of second clutches (table 1). The way that polytomies were solved in the case of the consensus tree did not affect the outcome of the relationship (table 1). Therefore, the hypothesised inverse relationship between the degree of winter territoriality and the proportion of second clutches produced is also supported by our data set.

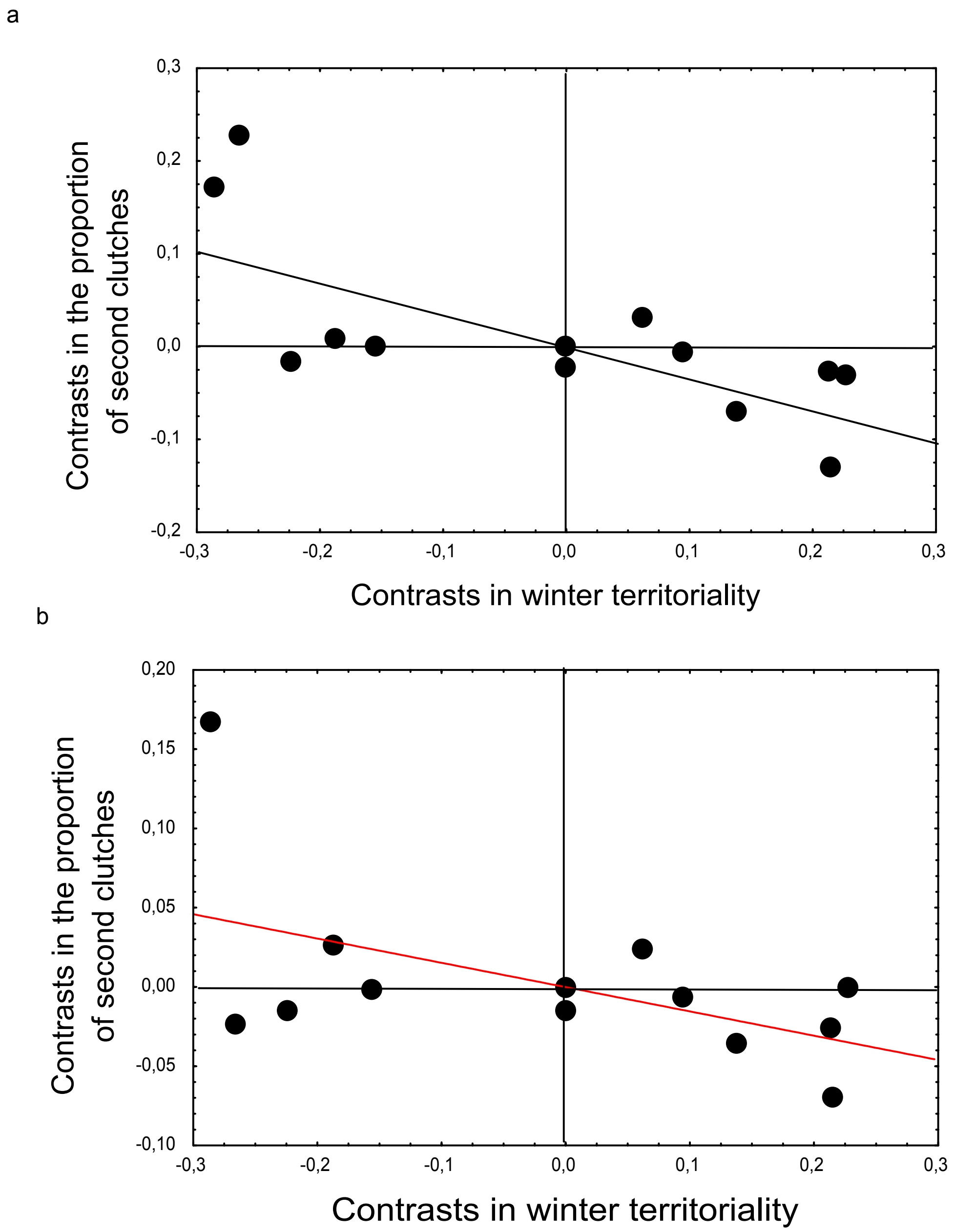

Figure 4. Independent contrasts of the proportion of second clutches in relation to contrasts in winter territoriality using the phylogenetic information of Gill et al. (1989). (a), using method 1 as an estimate of the proportion of second clutches laid per species. (b), using method 2 (see methods).

Tree used in directional comparisons	Proportion of second clutches		Degrees of freedom (d.f)
	Method 1 *	Method 2 **	
Tree of Gill et al. (1989)	-0.88 p<0.001	-0.61 p<0.001	22
Consensus tree	-0.85 p<0.001	-0.71 p<0.001	17
Range of r values according to the way polytomies of the consensus tree were solved			
Maximum	-0.90 p<0.001	-0.74 p<0.001	17
Minimum	-0.84 p<0.001	-0.71 p<0.001	17

Table 1. Results of directional comparisons relating changes in winter territoriality and proportions of second clutches along phylogenetic trees. * Method 1, proportion of second clutches using the sample of population studies used in Mönkkönen and Orell (1997). ** Method 2, estimate based on the proportion of studies on each species in which a significant proportion (>5%) of pairs were found to lay second clutches.

DISCUSSION

Our results show that, in parids, winter territoriality has evolved in a close association with the reproductive effort. Hence, increases in the degree of winter territoriality are related to decreases in both the clutch size and the proportion of second clutches. Because changes in social organization are expected to be more variable and plastic than breeding variables such as the clutch size and the tendency to lay second clutches, we argue that, in parids, it is the changes in the non-breeding social organization which have significantly affected the breeding strategies of the different species of the taxon. There are good reasons to think that this was actually the evolutionary pathway. For example, if a third variable increases the advantage of, e.g. larger clutch sizes, birds would produce more fledglings, thus lengthening the time needed to produce the clutches and leading to the later independence of the young. However, late-produced young would not be at an advantage if the optimal winter system were territorial in the population, because late settlement in territorial parids is associated with a smaller breeding probability (Nilsson and Smith 1988, Koivula and Orell 1988). Instead, selection for a territorial system in winter would strongly favor reduction of reproductive effort in terms of offspring quantity to satisfy the time constraints of beneficial early settlement. An increment in the reproductive effort does not easily lead to an open system when environmental conditions favor an early settlement strategy (Brotons unpubl. data) because individuals with such a strategy would be at an advantage irrespective of the density of other strategies in the population.

As a consequence, less territorial species tended to show higher reproductive outputs than more territorial ones. This finding is consistent with previous studies on co-existing species. Orell and Ojanen (1983b) showed that non-territorial species, such as the Great tit, (*P.major*) seemed to be more r-strategist than the territorial species such as the Willow tit (*P.montanus*) inhabiting the same area. Great tits seemed to maximize their fitness through the number of offspring produced rather than through their quality when compared with more territorial species (Orell and Ojanen 1983b). Because of the loose social system of the Great tit during winter, the fitness benefits of late produced offspring would be higher thus, leading to an increase in their total number. In this case, other factors, such as proximate conditions during the egg-laying period, are likely to be more important in shaping life history traits because long-term constraints are predicted to be smaller than in territorial species (but see Haywood and Perrins 1992).

One risk when examining life-history traits is that any correlation between traits could emerge because both are related to a third trait. Life-history theory suggests a relationship between reproductive effort and adult survival during the non-breeding season (Stearns 1992). Large investment in reproduction may increase winter mortality but winter mortality may also be related to other factors such as social organization. It can be that the pattern we found for parids would be in fact related to adult winter survival and not to winter social organization per se. Although winter survival data for all the species included in this study are scarce, available estimates imply that this variable does not differ to a great extent in species differing in social systems, although the existing wide intraspecific variation (Clobert et al. 1988, Cramp and Perrins 1993). As an example, survival estimates in non-territorial species range between 0.60-0.65 for the Coal tit (*P.ater*, own unpubl. data), and 0.40-0.93 for the Blue tit (*P.caeruleus*, Blondel et al. 1992). Similar estimates in more territorial species range between 0.50-0.71 for the Willow tit (Orell et al. 1994), and 0.69 for the Siberian tit (*P.cinctus*, Orell et al. 1999). Furthermore, in a detailed study, Blondel et al. (1992) tested explicitly the hypotheses of a negative correlation between fecundity and adult survival in the Blue tit. Their results run counter the idea of higher survival rates in low fecundity populations, suggesting that trade-offs between reproduction and adult survival may involve many more life-history traits than just the number of fledglings per pair and adult survival. However, possible survival benefits resulting from decreased reproductive effort are worth to be more deeply investigated and further insights will have to focus on the investigation of covariation patterns between winter survival of species differing in social patterns.

One prediction derived from our working hypothesis is that if fecundity is higher in non-territorial species, they are expected to be closer to the reproductive carrying capacity than the territorial species and thus, suffering more from increases in the reproductive effort (i.e. cost of reproduction). So far, evidence supporting this prediction is rather contradictory. Brood size manipulations in different *Parus* species do not show consistent patterns across species (Lindén and Moller 1989, Bailey 1992). Some studies have found a cost associated with an artificial increment in the reproductive effort (Nur 1984, Lindén and Moller 1989). However, Orell et al. (1996) manipulated clutches within the natural range of the Willow tit, failing to reveal an intragenerational cost of reproduction in this territorial species. The authors concluded that the current reproductive rate of the species may be not maintained by reproductive costs only. The hypothesis analysed in the present study offers a complementary explanation about the possible reasons why experimental increases in the reproductive effort may not be linked to future survival costs, if species are under a relaxed reproductive stress due to future social constraints on the offspring produced.

Ekman and Askenmo (1986) compared the breeding strategies of Crested (*P.cristatus*) and Willow tits in the same area, relating lower clutch sizes in the former species to differences in nest predation coming from their earlier laying dates. But, if Crested tits are more time constrained due to their social organization than Willow tits, then Crested tits would be predicted to lay as early as possible in spite of the possible predation costs involved in early breeding. This would also result in a selection for smaller clutches allowing early reproduction onset. Differential time constraints derived from selection for early settlement would be the mechanism explaining differences in laying date and reproductive effort between the two species. More studies comparing the cost of reproduction in co-existing species differing in their winter sociality are needed to complement the picture and control for the confounding effects of varying environmental conditions.

Our data are not based on the total number of species of the *Paridae.* However, with the set of species used, the results are clear and unambiguous. Further improvements of the hypothesis raised in this study remains waiting for more complete and detailed information on the phylogeny of the *Paridae,* and other genera with parallel characteristics.

To conclude, life history strategies are shaped by a number of factors. Long term indirect factors affecting offspring survival seem to play an important role in some group-living birds such as parids, when successful establishment in territorial winter groups is time constrained. Because attaining a position in a dominance structured winter flock enhances survival, early breeding and production of high quality descendants are crucial in species occupying exclusive territories in winter. We suggest that these indirect factors are more important than suspected before in shaping breeding strategies of birds.

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WINTER TERRITORIALITY AND THE ERUPTIVE BEHAVIOR IN THE *PARIDAE*[8]

ABSTRACT : Eruptions are defined as irregular mass movements performed outside the main breeding areas of species. In this study, I analyzed the possible links between winter territoriality, fecundity and eruptive behavior in parids. Using a comparative method, which allows including the information of a known phylogeny, the degree of winter territoriality was compared in eruptive and non-eruptive species according to data collected from the literature. Differences were found between the two groups in the degree of winter territoriality, but not when annual fecundity was taken into account. Furthermore, in a logistic regression analyses which included the genus of the species, annual fecundity and winter territoriality as a dependent variables, annual fecundity was found the best and only significant predictor of eruptive behavior in parids. Therefore, in this group, the eruptive habit does not appear to be directly associated with winter territoriality, but rather indirectly through the larger fecundity of less territorial species. The larger reproductive effort predicted in the less territorial species suggests that these species may be more easily involved in eruptive movements.

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INTRODUCTION

Eruptions are defined as irregular mass movements performed outside the main breeding areas of species (Svärdson 1957, Bock and Lepthien 1976). These movements commonly involve juveniles or individuals with poor competitive ability (Smith and Nilsson 1987) and are often attributed to large scale variations in the food supplies or great variations in weather conditions leading to populations booms (Bock and Lepthien 1976, Perrins 1979). Eruptions may be produced after years of large crop production followed by a successful breeding season (Ulfstrand 1963, Perrins 1979, Bejer and Rudemo 1987, Hussell 1996). But, anomalous seed crop production may be interpreted only as the proximate cause for the eruptive behavior in parids (Ulfstrand 1962) or fringilids (Jenni 1987). Large seed crops increase resource availability and may lead to high population densities, which in turn may force some individuals to move far from original areas (Ulfstrand et al. 1974, Svensson 1981). However, some related species within parids largely match in foraging behavior and habitat selection patterns (e.g. Great Tit, [*Parus major*] and Marsh Tit, [*P.palustris*], or Coal Tit, [*P.ater*] and Crested Tit, [*P.cristatus*]; Cramp and Perrins 1993) but show very different eruptive patterns. These ecologically similar species have different responses to the variation in crop size, resulting in specific eruptive tendencies.

Comparative studies are necessary to examine variation among species, but they only provide correlations and do not distinguish cause and effect (Harvey and Pagel 1991). Yet, comparative approaches, that take phylogeny relationships into account can allow a careful examination of adaptive hypotheses of the evolution of trait variation and co-variation with results that can be tested and confirmed by intraspecific studies (Harvey and Pagel 1991, Martin 1995). Few studies have been conducted on the ecology and the mechanisms of the eruptive habit in a wide range of bird species (but see Bock and Lepthien 1976). In this study, I used comparative methods, to analyze the possible links between winter territoriality and the eruptive habit in parids. Differences in non-breeding social systems, for example, the degree of winter territoriality, are known to affect spacing mechanisms of individuals (Matthysen 1990). Therefore, an increase in the degree of winter territoriality would likely reduce the benefits of roaming behavior (Ekman 1989) and thus, limit the benefits of the eruptive behavior. Since territoriality favors early establishment of juveniles (Nilsson and Smith 1988), and the increased dispersal distance associated with the eruptive behavior would postpone establishment date of juveniles (Nilsson 1990), winter territoriality would be expected to correlate negatively with the eruptive habit. Species like the Great Tit or the Blue Tit (*Parus caeruleus*), loosely territorial in winter, seem to be regularly involved in eruptions, thus fitting the pattern described above. I also assess the relative importance of annual fecundity in the predicted relationship between winter territoriality and the eruptive behavior, since large fecundity favors offspring production and therefore, it may lead to eruptive episodes.

METHODS

I gathered data on winter territoriality and eruptive tendency from different literature sources (see Appendix). In total, I studied 13 species of parids and used the White-breasted Nuthatch (*Sitta carolinensis*) as an out-group species in comparative analyses (see Appendix). The 14 species included in the study were divided in two groups according to their tendency to eruptive movements. Eruptive species were assigned that status according to the information gathered from Cramp and Perrins (1993) and Harrap and Quinn (1996). Although some degree of intraspecific geographic variation in eruptive behavior seems to exist in parids, my coarse grained classification allows high confidence that the data are representative of the true central tendency for each species. Territoriality concept has been subjected to a considerable debate, and within parids similar behavioral observations are interpreted in different ways (Desrochers and Hannon 1989, Matthysen 1990). In this study, winter territoriality was interpreted as the exclusive use and/or active defense of home ranges by the base units of winter social groups (after Matthysen 1990). Because, in addition to inter-species variability, non breeding social organization is predicted to vary among populations according to local environmental conditions (Smith and Van Buskirk 1988), I took into account the information available for any species included in the study. I chose only studies conducted on color-ringed populations which were not located in extreme ranges of the species' distribution areas according to Cramp and Perrins (1993) and Harrap and Quinn (1996, see Appendix). An index of the winter territoriality for each species was calculated as the proportion of population studies which found individuals occupying exclusive territories, often in groups of stable membership (defined after Matthysen 1990). Lack of sufficient data for most of the species did not allow controlling for the possible latitudinal variation in territoriality. However, studies of non-breeding social organization have been mainly conducted in optimal habitats (i.e. high density habitat for each species) and estimates of winter territoriality are also thought to be representative of the species.

I used population based studies in order to obtain comparable data of clutch size and proportion of second broods for each species. Data on clutch size were obtained from Mönkkönen and Orell (1997), who based clutch size estimates on populations inhabiting optimal habitats for each species (see appendix). Most of the population studies included in Mönkkonen and Orell (1997) work correspond to those used in the territoriality index. Clutch size values obtained with this method agree with those used by Martin and Clobert (1996) in a sub-sample of 11 species of Paridae for which data were obtained also on population based estimates (r=0.93, F = 57.34, *d.f.* = 3 and 9, P<0.001). In parids, clutch size is not related to body size (Mönkkönen and Orell 1997), therefore, I did not include body size as a covariate in subsequent analyses. The proportion of second broods within species may show considerable variation among different populations (from 0 to 100%, Verboven 1997). I decided to use two approaches to calculate this parameter. First, I used the proportion of second broods using the sample of population studies used in Mönkkönen and Orell (1997, method 1). Second, I included the variation within the species by using the proportion from a sample of populations on each species in which a significant proportion (>5%) of pairs were found to lay second clutches (method 2, see Appendix). The two data sets obtained by these two approaches were positively correlated (r=0.79, F = 19.65, *d.f.* = 1 and 12, P<0.01), and therefore, only the first method was used in later analyses. Consequently, I was confident that the data on breeding parameters of each species were also representative for the true central tendency for each species. In order to obtain an estimate of the annual reproductive effort of each species, a new variable was calculated as the product of clutch size and the proportion of second clutches laid plus 1 (annual fecundity hereafter).

Because of the hierarchical nature of phylogenetic descent, species may not represent statistically independent data points, degrees of freedom may be inflated, and significance levels derived from conventional tests cannot be trusted (Garland et al. 1993). Therefore, to avoid this problem a first comparative method was used in order to study the relationship between the eruptive behavior and non-breeding territoriality in parids. I adopted the information on protein relationships among parids and the phylogeny provided by Gill et al. (1989). There are other phylogenies available on parids, such as Kvist et al. (1996) based on mitochondrial DNA, and Slikas et al. (1996) based on DNA-DNA hybridization. More recent phylogenies (Slikas et al. 1996) supported Gill et al. (1989) main results of Paridae branching relationships. Gill et al (1989) was chosen because the other studies on the phylogeny of parids are too limited in scope, and include species with few ecological data available to be useful for the present purpose. In order to test whether eruptive species differ from non-eruptive ones in the degree of winter territoriality, I used the phylogenetic ANCOVA approach described by Garland et al. (1993). I conducted a conventional ANCOVA that disregarded phylogenetic effects by comparing the ordinal F statistic obtained with a null distribution created from computer simulations of characters evolving up the phylogenetic tree, instead of using the conventional tabular value shown in statistical textbooks. These empirical null distributions allow one to set critical values for hypothesis testing that account for non-independence due to a specified phylogeny topology, branch lengths and model of evolutionary change. Computer simulations were repeated 1000 times for each trait analyzed using the software (PDSIMUL) described by Garland et al (1993). Simulations were conducted under Brownian and punctuated evolutionary models, setting upper and lower limits with the replace option that were equivalent to the largest and smallest values, respectively recorded for the species included in the present study. Average trait values and their variances were set on values based on the empirical data analyzed here. Degree of winter territoriality was arcsin transformed, whereas annual fecundity was log-transformed in order to meet the requirements of parametric analyses.

I also used a logistic regression analysis to identify the relative importance of the factors analyzed in this study influencing the probability of a species being eruptive. To override phylogenetic effects in this approach, I include in the analysis the genus information for each species of the Paridae included in this study *(Poecile, Baeolophus* and *Parus*), as a categorical factor (Harvey and Pagel 1991), according to most recent phylogenetic group subdivisions (Gill et al. 1989, Slikas et al. 1996, see Appendix). Then, a backward removal procedure was used to select only the significant factors associated with the eruptive habit in parids (Crawley 1993).

RESULTS

Eruptive species tended to be less territorial than non-eruptive ones (territoriality index, Eruptive species, 0"SE = 0.13 " 0.43, *n*=7 and non-eruptive species, 0"SE = 0.93 " 0.12, *n*=7, *F* = 4.97, *df*= 1 and 12, *P* <0.05 under the three models of evolutionary character change). However, a high reproductive effort might also favor the eruptive habit, and in fact, annual fecundity was significantly larger in eruptive species (fecundity index, Eruptive species, 0"SE = 11.28 " 1.37, *n*=7 and non-eruptive species, 0"SE = 6.59 " 1.40, *n*=7, F = 6.75, *df*= 1 and 12, *P* <0.05 under the three models of evolutionary character change). Therefore, I took this effect into consideration by including it as covariate when analyzing the effect of winter territoriality upon the eruptive habit in the ANCOVA analysis. After the phylogeny was taken into account, the correlation between winter territoriality and annual fecundity was highly significant under either model of evolutionary change (covariate, Table 1), that is, the *F* value obtained from a typical ANCOVA procedure was always significant when compared with the *F* values obtained from the computer simulations which included the phylogenetic information about the evolution of characters studied into account. The analysis including fecundity as covariate, showed that eruptive and non-eruptive species did not differ in the degree of winter territoriality (main effect, Table 1).

							Brownian	motion				
					Conventional tabular		Gradual		Speciational		Punctuated equilibrium	
Source of variation	Sum of Squares	*d.f.*	Mean Squares	*F*	Critical value	*P*	Critical value	*P*	Critical value	*P*	Critical value	*P*
Main effect	0.02	1	0.02	0.02	4.84	N.S.	4.62	N.S.	4.52	N.S.	4.48	N.S.
Covariate	2.28	1	2.28	21.92	4.84	<0.01	5.81	<0.01	6.42	<0.01	6.74	<0.01
Explained	3.45	2	2.40	23.17	3.98	<0.01	4.04	<0.01	4.37	<0.01	5.16	<0.01
Error	1.14	11	0.10									
Total	4.85	13										

Table 1. ANCOVA comparing winter territoriality (main effect) between eruptive and non-eruptive species, with annual fecundity used as covariate. Critical values for *F* statistics and associated significance levels are presented for conventional tabular values, which would be appropriate only if all species radiated instantaneously from a common ancestor, and based on analyses of data simulated along the phylogeny of Gill et al. 1990 under different models of character change. Significant effects occur when the *F* obtained is larger that the critical value resulting from the computer simulations.

I performed a logistic regression model with genus classification, fecundity and territoriality index as independent variables and eruptive tendency as the dependent variable. The genus did not seem to affect the probability of a species being eruptive (X^2 = 3.57, *df* = 2, *ns*). The best final model explaining variation in the eruptive tendencies in parids removed the factor territoriality (X^2 = 0.02, *df* = 1, *ns*), and included as the only significant factor the annual fecundity of species (X^2 = 7.21, *df* = 1, *P* < 0.01). Therefore, the results of this study suggest that the eruptive behavior in parids is not directly related to the winter social organization of the species, but indirectly associated to the higher reproductive output of less territorial ones.

DISCUSSION

The results of the present study do not support the hypotheses that the non-breeding social systems and degree of winter territoriality are directly linked to the tendency of eruptions in parids. Rather, eruptive behavior of less territorial species may be indirectly favored through their larger fecundity (L. Brotons and M. Orell, unpubl. data). Of course, interspecific comparisons cannot determine causation, but the correlations can potentially provide insight into causes and may highlight potential evolutionary influences that may not be uncovered by intraspecific tests.

Large fecundity is likely to lead to a higher variation in population density and, in good years with high fledging survival, to a surplus of juveniles which are the main component of individuals involved in eruptive movements (Ulfstrand 1963, Smith and Nilsson 1987). In this context, large pine or beech seed crops would be the proximate mechanisms leading to high over-winter survival and probably to higher breeding densities in the following season (Bejer and Rudemo 1985). In such situations, if breeding is successful, large production of fledglings would force the autumn and winter movements of juveniles further away than in normal years. However, in different species, large crop production by itself would not lead to eruptions if large production of offspring is not allowed by the reproductive set of that species. As an illustrative example, the Coal Tit and the Crested Tit inhabit coniferous forests in most of Europe (Cramp and Perrins 1993). Both species feed largely on pine seeds, and both hoard food during autumn and winter, the Crested Tit usually being dominant over the Coal Tit (Cramp and Perrins 1993, Brotons and Haftorn 1999). Whereas the Coal Tit is frequently involved in eruptions, the Crested tit has hardly ever been reported to undergo any kind of extensive movements from breeding areas (Scherrer 1972, Cramp and Perrins 1993). Variation in seed crop production is present for both species and should affect both to similar degree. Higher reproductive output of the Coal Tit would favor larger breeding populations after large crop productions through higher survival, leading to eruptive episodes. Differences in the life history strategies of the two species and differential spacing patterns during winter can explain the differences observed in their reproductive output (Ekman and Askenmo 1986, Cramp and Perrins 1993, this study). The Crested tit is often dominant over the Coal tit. This species may, therefore, be involved more easily in eruptive movements since it would perceive a hypothetical food shortage earlier than its close dominant heteroespecifics. However, in the Paridae, competition seems to be only secondarily involved in the tendency to erupt, since other eruptive species such as the Great tit are clearly dominant over the rest of species of the group (Perrins 1979).

One risk when examining life-history traits, is that any correlation between traits could emerge because both are related to a third trait. Life-history theory suggests a relationship between reproductive effort and adult survival during the non-breeding season (Stearns 1992, Martin 1995). Large investment in reproduction may increase winter mortality but winter mortality may also be related to other factors such as social organization. It can be that the pattern I found for parids in eruptive tendencies would be in fact related to adult winter survival and not to annual fecundity. Although winter survival data for most species included in this study are scarce, available estimates imply that this trait does not differ to a great extent in species differing in the social systems, although the existing wide intraspecific variation (Clobert et al. 1988, Cramp and Perrins 1993). As an example, survival estimates in non-territorial species range between 0.60 to 0.65 for the Coal Tit (Own unpubl. data), and 0.40 to 0.93 for the Blue Tit (Blondel et al. 1992). Similar estimates in more territorial species range between 0.50 to 0.71 for the Willow Tit (*P. montanus*, Orell et al. 1994), and 0.69 for the Siberian Tit *(P.cinctus*, Orell et al. 1999). Furthermore, in a detailed study, Blondel et al. (1992) tested explicitly the hypotheses of a negative correlation between fecundity and adult survival in the Blue Tit. Their results run counter the idea of higher survival rates in low fecundity populations, suggesting that trade-off between reproduction and adult survival may involve many more life-history traits than just the number of fledglings per pair and adult survival. However, possible survival benefits resulting from decreased reproductive effort are worth to be more deeply investigated and further insights will have to focus on the investigation of covariation patterns between winter survival of populations differing in social patterns and eruptive tendencies.

This study supports the view that eruptive behavior is a characteristic associated to the fecundity of a given species rather than to its non-breeding social system. Large variation in food abundance would be only the proximate cause of the survival of the high number of individuals needed for an eruption to take place. The association found between life history traits of species and their eruptive tendencies, suggests that some species are indeed predicted to be involved in invasion episodes more likely than others and that the mechanisms between this link may be uncovered. Further insights into the eruptive mechanisms should use closely related species, or populations within species, with similar ecological habits and different eruptive tendencies to identify the exact role of different life history traits as the ultimate causes of this behavior.

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	Degree of winter territoriality (Number of territorial populations /number of populations surveyed)	Clutch size	Proportion of second clutches		Tendency to eruptions **	References ***
			Method 1	Method 2 (Number of populations surveyed)*		
Black-capped Chickadee (*Poecile atricapillus*)	0.75 (6/8)	6.6	0.05	0.05 (1/20)	1	1,2,19
Mountain Chickadee (*Poecile gambeli*)	1.00 (3/3)	7.2	0.10	0.10 (1/10)	1	2,3,4,19
Boreal Chickadee (*Poecile hudsonicus*)	1.00 (2/2)	6.5	0.00	0.00 (-)	1	2,5,19
Chestnut-backed Chickadee (*Poecile rufescens*)	1.00 (1/1)	6.1	0.00	0.00 (-)	0	2,4,19
Carolina Chickadee (*Poecile carolinensis*)	1.00 (3/3)	6.1	0.00	0.00 (-)	0	2,6,7,19
Marsh Tit (*Parus palustris*)	0.80 (4/5)	7.2	0.05	0.08 (1/13)	0	2,8,9,10,19
Willow Tit *(Parus montanus*)	0.80 (4/5)	7.8	0.00	0.00 (-)	1	2,8,9,11,19
Crested Tit (*Parus cristatus*)	1.00 (3/3)	6.3	0.11	0.14 (3/21)	0	2,8,9,12,19
Coal Tit (*Parus ater*)	0.25 (1/4)	8.9	0.67	0.69 (9/13)	1	2,8,9,13,19
Great Tit (*Parus major*)	0.00 (0/6)	9.4	0.20	0.92 (12/13)	1	2,8,9,14,15,19
Blue Tit (*Parus caeruleus*)	0.00 (0/2)	10.5	0.38	0.58 (7/12)	1	2,8,9,16,19
Tufted Titmouse (*Baeolophus bicolor*)	0.75 (3/4)	5.7	0.00	0.10 (1/10)	0	2,8,17,19
Plain Titmouse (*Baeolophus inornatus*)	1.00 (2/2)	5.4	0.00	0.00 (-)	0	2,8,4,19
White-breasted Nuthatch (*Sitta carolinensis*)	1.00 (2/2)	7.3	0.00	0.00 (-)	0	18,19

Appendix. Summary of data on winter territoriality, clutch size, proportion of second clutches and tendency to eruptions of the species included in the present study. *Species with no populations recorded laying a significant proportion of second clutches (>5 %) show a minus sign in the table. ** Species recorded as being regularly involved in eruptions have value 1, species rarely or not at all involved in such movements show value 0. *** (1) Smith 1991 ; (2) Matthysen 1990 ; (3) Dahlsten and Cooper 1979 ; (4) Dahlsten unpublished data ; (5) McLaren 1975 ; (6) Tanner 1952, (7) Brewer 1963 ; (8) Ekman 1989 ; (9) Cramp and Perrins 1993 ; (10) Ludescher 1973 ; (11) Orell and Ojanen 1983a ; (12) Löhrl 1991 ; (13) Brotons, unpublished data ; (14) Verboven 1997, (15) Orell and Ojanen 1983b ; (16) Delmee et al. 1972 ; (17) Grubb and Pradosudov 1994 ; (18) Pravosudov and Grubb 1993 ; (19) Harrap and Quinn (1996).

MAIN RESULTS AND DISCUSSION

VARIATION IN THE NON-BREEDING SOCIAL ORGANISATION OF PARIDS

Hoarding behaviour is associated with a territorial system in the *Paridae* (Ekman 1989a). However, the detailed analyses of a food hoarding Coal tit population, together with the indications from other Coal tit studies (Nakamura 1975) suggest that this association does not always hold.

Therefore, what are the ultimate factors behind the variation recorded in the non-breeding social systems of parids? Enhanced predator protection or food efficiency are factors which make sociality beneficial (Pulliam & Caraco 1984, Lima & Dill 1990), but whether individuals become residents or they coalesce into social units also depends upon the options available and their long term consequences. An approach to identify the main factors involved in social variation must include a detailed analysis of the strategies used by juveniles to enter the breeding population (Matthysen 1990).

In order to study the pay-off of different settlement strategies for juveniles in parids, I have applied a slightly modified version of the modelling approach used by Ekman (1989a). The main question behind Ekman's approach is: How long should dispersing juveniles take until they finally settle in an area? This is a crucial question, since variations in settlement choices are associated with a variable degree of juvenile residence after autumn dispersal, thus leading to distinct social structures. Delayed settlement is likely to result in an open and unstable system, because juveniles hardly establish bonds with an area. In contrast, early settlement is more likely to produce a closed, stable and territorial system.

When a habitat is optimal and there is free space, the best strategy for juveniles is to establish a territory there and breed the following summer. However, this situation is rare. Adults who have bred there in previous seasons often already occupy such habitats. The remaining option is then to wait for an opening to appear (i.e. after the death of an adult). The most beneficial strategy should maximise the probability of obtaining a vacancy in the system, thus, allowing a juvenile to obtain a breeding position in the best habitat available. If the gradient in habitat quality is not very steep, it is still beneficial for a juvenile to settle in a habitat of lower quality and establish a new territory there. However, as the habitat gradient increases, the costs of staying in the lower quality habitat also increase. Therefore, to enter the optimal habitat it is more advantageous for the juveniles to adopt a queuing strategy (Fretwell 1972, Ekman 1989b) by waiting for a vacancy (Fretwell and Lucas 1970, Lens and Wauters 1996).

In an optimal habitat it is not feasible for a juvenile to evict a resident bird or take over its territory because dominance in parids is clearly biased towards adults (Koivula & Orell 1988, Hogstad 1989, Smith 1991). Thus, the remaining strategies open to juveniles are to settle with an adult pair and wait for an opening within that formed group (settler strategy), or to keep searching for a vacancy elsewhere (floater strategy). By definition, being a floater implies having a large home range because roaming areas will include several settled groups in which there might be a chance of settling.

Settling early in the season may incur a considerable cost as the juvenile risks foregoing the opportunity to find a better position in other social groups. Therefore, juveniles should adopt the strategy that maximises long-term fitness. Ekman (1989a) showed that juveniles benefit from floater status when the benefits outweigh those obtained from settling as a permanent group member:

$$\mathrm{P}_f(\mathrm{S}(t))\mathrm{P}(\mathrm{vacancy}(t))\mathrm{P}_i(\mathrm{S}(T\text{-}t)) > \mathrm{P}_{i+1}(\mathrm{S}(t))\mathrm{P}(\mathrm{vacancy}(t))\mathrm{P}_i(\mathrm{S}(T\text{-}t) \qquad (1)$$

Therefore, floaters benefit from not settling immediately, when the probability of survival as floaters $\mathrm{P}_f(\mathrm{S}(t))$ until they find and occupy a vacancy $\mathrm{P}(\mathrm{vacancy}(t))$ and, thereafter, surviving to breeding as established individuals, $\mathrm{P}_i(\mathrm{S}(T\text{-}t))$, overrides that of a settled flock member $\mathrm{P}_{i+1}(\mathrm{S}(t))$ occupying a vacancy within its own group

P(vacancy(t)) and, thereafter survive until the following spring $P_i(S(T-t))$. In a continuous time model this expression becomes:

$$\frac{(1 - \exp(-Nm_i t)) - (yN)}{(1 - \exp(-m_i t))} > \frac{\exp(-m_{i+1} t)}{\exp(-m_f t)} \qquad (2)$$

Where N is the number of groups available per floater (N=1 in the case of established group members), m_I is the mortality of a group member of rank I (f for floaters) and t is the time available for settling (Ekman 1989a). I have modified Ekman's approach to incorporate the variable y, which represents floater efficiency in inspecting groups. This modification was necessary as the probability of occupying a vacancy is not likely to increase linearly with the number of groups inspected, but it will tend to decrease because a vacancy may arise and may not be filled or may be occupied by another bird. Therefore, inspection efficiency depends on two secondary variables. The first is the distance between groups which is related to the density of already established groups (i.e. high density populations would facilitate floater inspection by increasing the number of possible vacancies in an area and thus, y would be low). The second variable is floater abundance, since a high number of floaters will reduce inspection efficiency due to competition. This model assumes that a settled subordinate can advance only within its own group, and that, according to some observational and experimental evidence (Smith 1984, Hogstad 1990a), that floaters can directly enter a vacancy of rank i that appear in any of the groups inspected. It is also assumed that there is a survival cost associated with being a floater (i.e. $m_f > m_i$). Equation 2 shows that, all things being equal, as mortality rates in the lowest available rank position (m_{i+1}) increase towards that of the floaters, or the mortality of floaters decreases towards that of settled juveniles, the inequality can be satisfied. When the cost of being a floater is so small that it is outweighed by the enhanced fitness value obtained from the improved possibilities to find a higher ranking vacancy, then the floater strategy is the most beneficial option for a juvenile (Figures 5c, 5d).

To some degree, the differences between the mortality rates of floaters and settlers can be attributed to hoarding. In hoarding species, floaters are likely to have lower recovery rate of stores or lower storing rates (Källander and Smith 1990). If this leads to an increase in floater mortality, then hoarding is likely to favour settlers (Figure 5a). In such cases, because of subordination costs (Koivula and Orell 1988), early settlement is decisive because late settlers pay higher subordination costs than early settlers (Nilsson and Smith 1988). Very late settlers may also adopt a floater strategy when subordination costs outweigh the long-term benefits of territory acquisition. In this case, floater status becomes the 'best of a bad job' option *sensu* Hogstad (1990). However, other factors, which reduce the costs of floater status, may be involved in the shaping of social structure. If for instance, there is a large and partially heterogeneous food supply in an area, some juveniles may benefit from becoming floaters and will chose to do so instead of waiting for a vacancy to appear by early establishment in a social group. Dominance costs of floater status may also play a role. If the dominance cost of floating is high, it could increase floater mortality and make their strategy not to pay.

In addition to the mortality rates of floaters and settlers, the relative benefits of both strategies depend on the difficulties in finding and occupying an arising vacancy. Such costs are directly related to the distance between inspected groups, and to the number of competitors. When group inspection costs and floater mortality are high, the settlers' strategy is beneficial (Figure 5a). As floater mortality decreases, floating becomes the optimal strategy to follow. However, because of inspection costs, floaters would benefit from a limited number of groups being investigated (Figure 5d), and therefore, from partial residence in the area. Floater ranges overlapping a number of resident groups could originate the "basic flock", non-territorial system described for some parid populations. Most populations of "basic flock" species, have a very high density which may allow the inclusion of several social groups within floater ranges while maximising the probability of occupying any vacancy which may appear within the established groups.

When the costs of inspecting new groups are low, floater status is also beneficial and the optimal range of inspected groups per floater increases as well, possibly resulting in enlarged home range sizes (Figure 5c). In the case of high floater mortality, soon after an initial benefit of floating, the benefits in terms of enhanced survival prospects favour the settler strategy of queing (Figure 5b).

In summary, the simple model described here, suggests that the floater behaviour of juveniles, which may be associated with a looser social system, becomes a beneficial strategy when, (1) travelling and vacancy inspection costs among winter flocks are low, and/or (2) the relative differences in the mortality of floaters and resident juveniles which settle are small. In some environments, hoarding may lead to an increase in mortality differences between floater and settler strategies, favouring the latter strategy.

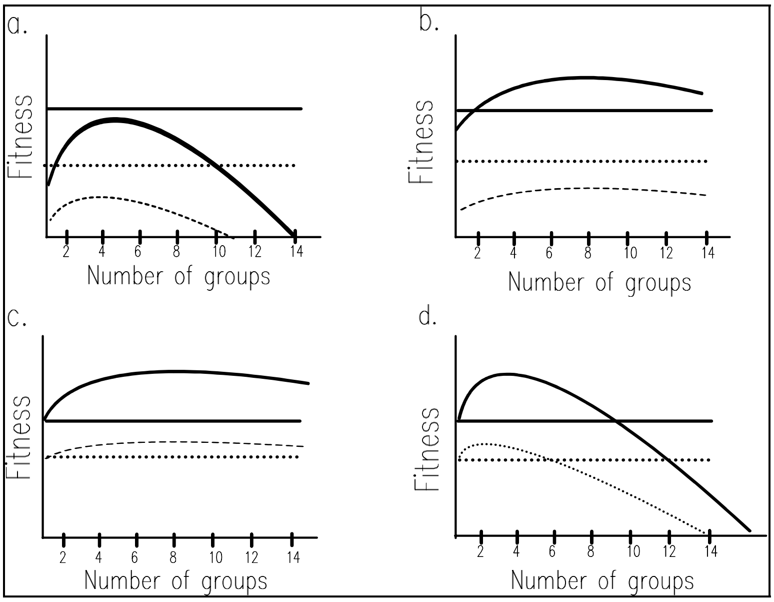

Figure 5. Fitness curves derived from equation 2 and showing the pay-off of the distinct settlement strategies available to juveniles under several conditions. Horizontal lines represent fitness gain for a juvenile settling in a flock (constant for a given *N*) . Curves represent fitness of floater juveniles as a function of the number of groups inspected (*N*). *N* is the number of groups or pairs where vacancies may occur and, thus, are available per inspecting juvenile floater. According to the data available (Cramp & Perrins 1993), mortality of previous breeding pairs (m_i) was set at 0.4, and the mortality of settled juveniles (m_{i+1}) at 0.5. Continuous lines (*t*) represent conditions earlier in the season than dashed lines (*t'*, where *t*<*t'*). a. Floater pay-off when inspection cost between groups and floater mortality are high (a=0.1, m_f=0.9), b. Juvenile floater pay-off when inspection cost is low but floater mortality high (a=0.01, m_f=0.9). c. Pay-off of the two strategies when inspection cost is low and floater mortality approaches that of settlers (a=0.01, m_f=0.5). d. Pay-off when inspection cost is high but floater mortality similar to settlers (a=0.1, m_f=0.5).

Social organisation in the Willow tit

The non-breeding social system of the Willow tit has been studied in several boreal forest populations, and also Finnish area where the study described in Chapter 5 was carried out (Ekman 1979, Hogstad 1987, Koivula and Orell 1988). Early settlement of juveniles in small territorial flocks, which vary in size, has been extensively reported (Ekman 1989a, Matthysen 1990, Nisson 1990). Taking into account the environmental conditions of the areas where most of the studies have been carried out, territoriality is easily predicted in this species. First, in northern areas hoarding is crucial for the survival of individuals. Therefore, if floaters do not integrate into a territorial flock and built up a food store for the coming winter, the costs of a wandering status will turn very high. Furthermore, in many areas studied, population density is very low. Therefore, inspection costs of more than one group are high in relation to the possible benefits obtained from arising vacancies (Hogstad 1990). Therefore, I suggest that the factors that may lead to a territorial coherent system in the Willow tit are:

1- Adults become sedentary which may be associated with improved breeding prospects through territory acquisition in the following season (Smith 1991, Koivula et. al.1996).
2- High survival costs of floater status (i.e. costs associated with non-hoarding and subordination to residents) and high inter-group distance, may favour the early settlement of juveniles with an established resident pair (Hogstad 1990b, Koivula et al. 1996).
3- Low population density and high energetic value of ranges occupied (i.e. food stored) may also favour territorial defence by flock members (Kaufman 1983).

Social organisation in the Coal tit

Using data on home range, range overlap and social coherence, the spacing of the non-breeding system of the Coal tit in the Pyrenees was analysed. The social system was found to be based on adult birds which had previously bred together and which occupied relatively small home ranges. Resident juveniles had larger home ranges than adults, which overlapped extensively with those of adults and neighbouring resident juveniles. However, resident juveniles were re-sighted much closer to their ringing site than was expected at random, which suggests restricted floater ranges. Associations, composed mainly of juveniles, seemed to be rather large and loose, with low coherence values between individuals. No territorial defence by any group of birds was detected during the study. Therefore, the social organisation described for the present Coal tit population is similar to the looser, non-territorial “basic flock system” described for some non-hoarding species (Nakamura 1975, Saitou 1978, Drent 1983). Resident social patterns seemed to be linked to the availability of breeding resources, which probably lead to the high site fidelity, by adults and the floater status of resident juveniles. On the other hand, short-term factors such as a rich food supply, may attract transients and drive short-term flocking strategies. High food availability allowing a high population density seems to be the main proximate factor which influences the spacing patterns described. Coal tit populations inhabiting boreal coniferous forests in northern Europe seem to be mainly territorial (Ekman 1989a). Lower density of individuals in such areas may shift optimal spacing patterns to territoriality by decreasing the number of possible intruders and thus, the cost of defending home ranges.

Following the same tentative pathway than for the Willow tit, the main points that are suggested to lead to the social system described for the Coal tit in the Pyrenees are as follows:

1- Breeding adults become highly sedentary as site fidelity enhances future breeding prospects.
2- Survival cost of floating status may be low due to high food availability (i.e. pine seeds). Therefore, the cost of becoming a floater with a large home range may not be high.
3- High density of individuals may impose high costs on territorial behaviour because active defence of an area is energetically very costly, and results in overlapping ranges of both adults and juveniles inhabiting the area. Benefits of group formation would drive short-term flocking, resulting in highly changeable flocking patterns.

Further studies are needed to confirm some points of these tentative and at present, rather speculative reasoning. In particular, survival estimates of juveniles with differing settlement strategies and spacing patterns are required to complete the present picture. Estimates of the settlement success of juveniles according to different residence status are also needed to validate the assumption that floating is indeed the best choice available to juvenile Coal tits in the Pyrenees. It is also necessary to test whether floaters with restricted ranges of differing size and transients differ in their recruitment probabilities and if so, to what extent.

Status signalling in the Coal tit

Within non-breeding flocks of group living species, individuals compete for the priority of access to resources such as food or shelter (Gauthreaux 1978, Baker et al. 1981). Competition through agonistic interactions is energetically costly (Hogstad 1987). I predicted that given the loose social system of the Coal tit during the non-breeding season, indirect signalling mechanisms of resource holding potential of individuals would be critical in determining dominance outcomes. I experimentally tested the prediction that status signalling is decisive in settling dominance outcomes among individuals that lacked knowledge of opponents but not among already known individuals (Senar 1999). Results supported the hypothesis that status signalling is an important mechanism by which individuals lacking experience with rivals estimate their potential. Because flocks of Coal tits in the Pyrenees are of very loose composition, status signalling may be of great importance in settling dominance interactions between juveniles that move between unstable flocks.

NICHE SHIFTS IN ADVERSE WINTER WEATHER CONDITIONS

Winter is an adverse time for birds. The adversity is commonly attributed to the food shortage determined by winter climate rather than by the winter conditions per se (Jansson et al 1981, Spencer 1982, Lahti et al. 1998). Temporary or long-term food shortage imposes several foraging constraints on tits that inhabit subalpine and boreal environments. Therefore, the study of the behavioural responses of birds to harsh weather may enable us to understand better the responses of birds to a changing environment and the role of a determinate social system. In the case of hoarding species, the study of individual behaviour in adverse weather conditions becomes very important in understanding the role of hoarding in the ecology of winter groups of tits.

The Willow tit (*Parus montanus*)

I studied Willow tit flocks during warm (>0ºC) and cold (<-4ºC) conditions in order to analyse the possible factors involved in habitat segregation between flock members. What are the influences of harsh, stressful conditions on the flocking behaviour and the structure of the groups? In cold conditions juveniles and adult birds travelled together, often using the same foraging tree, more frequently than in mild, warmer conditions. Foraging site selection in cold and mild conditions was similar in both adults and juvenile birds, and therefore, main microhabitat segregation patterns among ages were similar in different weather conditions. During cold conditions, the use of foraging microhabitat is predicted by the hoarding distribution in autumn. The adults' selection of the inner safer and perhaps richer parts of trees for hoarding, may determine foraging segregation patterns during winter (Suhonen 1993). Furthermore, this segregation may also indirectly affect microhabitat use in warmer conditions, mostly in autumn. Because juveniles are forced to occupy outer parts of trees in stressful conditions, they built up food reserves through hoarding in these parts. In mild weather when juveniles have free access to foraging sites, juveniles trade the use of potentially dangerous microhabitat against the benefits of storing energetically cheap and large food reserves. I suggest that if predation costs are low, this balance should progressively shift from the use of safer microhabitats (i.e. inner parts of trees preferred by dominant adults) towards the energy saving benefits of food caching and more efficient foraging patterns coming from a differential microhabitat use (i.e. use of outer parts of trees also in mild conditions) as found in this study (Lens and Dhondt 1994, Chapter 5).

The Coal tit (*Parus ater*)

The behaviour of the Coal tit in subalpine coniferous forests greatly differs from the Willow tit. In sub-alpine Mediterranean areas, the winter is not as extreme as in boreal forests, nor is the day as short. Furthermore, food is abundant for species able to take advantage of pine seeds because seed crop production in the Mountain pine is high and constant form year to year (Genard & Lescourret 1986). However, in winter subalpine systems can occasionally be very harsh. During wind blizzards, or snow storms (Carrascal 1988) and especially after heavy snowfalls outer needle and cone substrates may remain hidden for some time and thus inaccessible for birds.

This transient decrease in food availability may reduce survival rates or force emigration. I compared tree site use and the foraging techniques used by birds in snowy and snow-free conditions in the Pyrenees. Under snowy conditions, Coal tits foraged in the lower and inner parts of trees, using trunks and thick branches as their main foraging substrate. In snow-free conditions, birds used upper and outer parts of trees and fed mainly on pine cones and needles. Movement patterns differed also from one condition to the other. During snow free conditions, birds used more costly energy methods, mainly flight and hanging positions, while in snowy conditions they used lower energy consuming methods, mainly hopping. These observations support Norberg's hypothesis (1977) that when the prospects of obtaining prey increase, foraging methods requiring higher energy consumption are used. Therefore, birds may save energy in adverse conditions through adapting their habitat use to environmental changes. The higher the prospect of energy acquisition, the more costly the methods used to acquire food. Hoarding also plays a crucial role in smoothing transient adverse conditions, allowing individuals to hedge variability in the food supply.

FOOD HOARDING

The Willow tit

Food hoarding in the Willow tit has been extensively studied in northern boreal populations (Haftorn 1956b, Pravosudov 1985, Brodin 1994b, Lahti et al. 1998). As I have already discussed, individuals foraged in cold weather conditions in the same microhabitats where they had hoarded during autumn (Lahti et al. 1998). This has also been shown by Brodin (1994a). However, these two studies differed in the kind of microhabitat segregation found between adults and juveniles. In Brodin’s study, segregation between subordinate (juveniles) and more dominant Willow tits (adults) was in the vertical component. Several predation risk regimes may explain the differences detected.

In boreal areas, hoarded food is extremely important. Brodin (1994b) estimated that in such forests hoarded food may compose up to 25% of the food consumed during winter. During colder winters, which incur higher energetic stress, stored supplies may be even more decisive, perhaps accounting for 50% of the total food consumed (Haftorn 1956b, Brodin 1994b) by tits in winter. Since food supply is low and available foraging time during winter short, increasing food availability through hoarding enhances sedentariness and increase the survival of individuals (Lahti et al. 1998). In addition to group territoriality, individuals use a number of behavioural strategies to assure exclusive use of caches; i.e. memory (Sherry and Duff 1996, Dhondt and Smulders 1997), and avoidance of conspecifics (Stone and Baker 1989, Lahti and Rytkönen 1997).

The Coal tit

This species hoards food during autumn and winter. I analysed the choice of microhabitat for hoarding in two populations inhabiting coniferous forests in Norway and the Pyrenees. The two populations differed in the degree of sedentariness and the number and density of possible tit species competitors present in the habitat. Hoarding differed greatly between the two populations. The more northern population used exclusively needles and outer parts of trees (Haftorn 1956a), whereas the southern population used inner substrates such as trunks and thick branches. In Norway, birds may be subjected to higher levels of competition. Commonly dominant species such as the Crested tit and the Willow tit use inner parts of trees to store food, therefore interfering with the possible hoarding pattern of the Coal tit. In Norway, the Coal tit is much less sedentary than the other tit species and during most of the winter had a very reduced population in the study area. Lack of safer hoarding sites in preferred areas due to competition may prevent individuals from becoming sedentary. On the other hand, in Norway, hoarding may still be mainly used as a short-term measure or as an alternative to body fat accumulation (McNamara et al. 1990, Witter and Cuthill 1993, but see Pravosudov and Grubb 1998). The higher proportion of insects, which have a higher perishability (Brodin 1994a), hoarded in Norway supports this hypothesis. In the Pyrenees, Coal tits are subjected to lower competitive interspecific pressure and they use similar hoarding sites to those foraging sites used in adverse weather conditions (i.e. after the snowfalls), but very different from normal foraging microhabitat in good weather conditions.

I analysed in more detail the hoarding behaviour of Coal tits in a colour-ringed population in the Pyrenees. Age and residence status of individuals were known, and therefore, these variables were analysed in relation to the hoarding microhabitat of birds within the same population. Individuals hoarded intensively from early autumn till the end of the study in winter, reaching a marked peak in November, which coincided with the maximum opening of mountain pine cones. When travelling in flocks, birds hoarded items avoiding only the close proximity of neighbours. Adults concentrated stores around the centres of their home ranges. Juveniles hoarded at similar rates to adults, and also show the same avoidance of closer neighbours. Birds hoarded more actively around midday. Caches located in outer parts of trees required more effort to store than those in inner parts of trees, suggesting a lower survival value and possibly a distinct future use by individuals. Furthermore, resident adults stored in inner, presumably safer caching locations more often than juvenile residents and transient birds. There was a significant effect of time of day on the storing location patterns of juvenile residents and transients birds further supporting the view of a bimodal utilisation of stores located in different parts of trees.

In summary, the Coal tit in the Pyrenees did not use territoriality to reduce cache robbery, but individuals used a number of alternatives to increase chances of selfish benefits of using the items stored. Firstly, individual Coal tits did not store randomly, rather the storing probability was dependent on the presence of conspecifics and the distant from the storing individual, therefore decreasing the probability of immediate robbery. Sedentary adults concentrated their stores in the core of their home ranges. In this way, adults reduce the overlap in hoarding distributions with neighbouring sedentary adults and furthermore, concentration may facilitate active, punctual defence against the visits of other individuals (pers. obs.). Segregation of hoarding sites between individuals was very clear. Hoarding sites only coincided with foraging sites in stressful conditions, but not in normal conditions when food availability was high. Furthermore, I found age and residency related hoarding microhabitat segregation matching that found in interregional comparisons (Chapter 6). Individuals reduced probabilities of future robbery, and increased probabilities of future use of stored items by storing in different niches away from foraging sites of possible competitors (Brodin 1994a).

THE EVOLUTION OF FOOD HOARDING AND WINTER SOCIAL ORGANISATION

Smulders (1998) presented a model in which he demonstrated that a specialised memory system is not necessary for food hoarding behaviour to appear in a population as long as winters are severe. He suggested a plausible scenario for the origin of food hoarding in *Paridae*, which included the idea that the ancestral social organisation of parids was probably closer to a looser non-territorial type of winter social organisation. The results obtained in my study do not support the idea of a unequivocal relation between hoarding and winter territoriality. Hoarding favours sedentariness but territoriality seems to be located one step further as a mechanism that enhances the benefits obtained from hoarding. The findings of this study on the Coal tit hoarding and winter social patterns supports Smulders (1998) hypotheses. They offer a working frame in which hoarding is compatible with the non-exclusive use of home ranges, and favours sedentarity of resident individuals by partially ensuring a food source in moments of a sudden decrease in food availability. This may have been a common situation in ancient parids that inhabited temperate areas. Birds may have benefited from finding not previously consumed food ‘by accident’ (Vander Wall 1990). In this situation no specific memory was necessarily involved. A bird which forages in the same locations where the food has been 'left', can still benefit from it (without any role of memory, Brodin and Clark 1997), if it has a higher probability of returning to that place than other birds (Sherry and Duff 1996). If sedentarity is beneficial for birds and allows, for instance, early breeding or a high position in the local dominance hierarchy, the recovery of early harvested food would promote sedentarity. Often tits harvest their items in inner parts of trees which are more used in adverse conditions (Chapter 3). This provides a mechanism by which some birds could found food items not totally consumed in early foraging events (Vander Wall 1990).

For more northern populations of parids such as the Willow tit or the Crested tit, hoarded food is an essential energy source during winter, and therefore, strongly influences the survival of individuals. Once food hoarding is established in a population, the presence of pilferers will be avoided by keeping flock size as small as possible. This can be done by defending the home range against other individuals (Smulders 1998). Furthermore, a lower population density associated with harsher environmental conditions makes territorial defence feasible. In such conditions, and once hoarding has originated, the mechanisms involved in cache defense would progressively shift the original looser non-breeding social system into a more territorial one found in most temperate hoarding parids.

THE INDIRECT IMPLICATIONS OF NON-BREEDING SOCIAL SYSTEMS ON LIFE HISTORY STRATEGIES

Winter territoriality and fecundity

Within parids, the presence of territoriality as a wintering social strategy varies widely between species. In some species, attaining a position in dominance structured territorial winter flocks is crucial for juvenile survival, whereas in other species juvenile birds spend the winter in large non-coherent groups with a looser structure (Nilsson and Smith 1988, Koivula et al. 1994, see also the first part of this Chapter). I tested the hypothesis that in a closed territorial non-breeding social system where juvenile settlement is time constrained (Nilsson 1990), decreased reproductive output is an evolutionary adaptive mechanism for time saving in order to cope with such constraints. Using two comparative methods, I analysed the relation between non-breeding territoriality and two breeding variables in a sample of Parid species. These methods accounted for the effects of phylogeny on the hypothesised relationships. A significant negative association between winter territoriality and both clutch size and proportion of second clutches was found. Evolutionary increases in the degree of winter territoriality were associated with decreases in reproductive output, smaller clutch sizes and lower proportion of second clutches. The results support the hypothesis that indirect long term factors affecting offspring fitness may play an key role in determining breeding strategies in parids. In species with a closed, territorial spacing system during winter, juvenile settlement in autumn is seriously time constrained (Nilsson 1990). Therefore, individuals in such species would benefit from the time saving mechanisms associated with lower fecundity. Number of offspring produced seems to be lower, but of higher quality in terms of enhanced possibilities of recruitment into the future breeding population. In more lax social systems, recruitment might be shaped by other factors rather than establishment time, making these species more fecund.

Winter territoriality and the eruptive behaviour

Eruptions are defined as irregular mass movements outside the main breeding areas of a species. I analysed the possible links between winter territoriality and eruptive behaviour in a group of parids. Using a comparative method that allows including the information of a known phylogeny, the degree of winter territoriality was compared between 7 eruptive and 7 non-eruptive species according to data collected from the literature. Differences were found between the two groups in the degree of winter territoriality, but not when annual fecundity was taken into account. Therefore, in parids the eruptive habit does not appear to be directly associated with winter territoriality, but indirectly associated through the larger fecundity of less territorial species. The larger reproductive effort predicted in the less territorial species suggests that these species may be more easily involved in eruptive movements. The results support the view that eruptive behaviour is a characteristic associated with the fecundity of a given species. Large variation in food abundance would be only the proximate cause of the survival of the high number of individuals needed for an eruption to take place.

MAIN CONCLUSIONS

1- The non-breeding social system of the Coal tit does not always involved exclusive use of home ranges. In spite of being a hoarding species, the high density, sub-alpine population located in an optimal habitat presented a loose social system where territoriality was absent.

2- The non-breeding social structure of the Coal tit in the sub-alpine forest studied was centred around resident adult pairs that had settled in the area during previous seasons. Some juveniles were residents to some extent, and overlapped ranges with several resident adults. However, most of the juveniles in the study area appeared to be transients attracted to the area by its rich food supply. Flocking led to large aggregations of loose membership. Aggregations were composed mainly of juveniles.

3- Status signalling mechanisms based on the black badge of Coal tits are used in determinate conditions to settle conflict outcomes among flock members. Primarily, individuals use status signalling mechanisms when they lack previous knowledge of opponents. Therefore, the status signalling may be an important determinant of dominance in large associations of Coal tits in loose social systems.

4- Hoarding is a key factor determining non-breeding social systems. The settlement strategies of juveniles will have different values due to the importance of stores in some areas. Sedentary birds increase survival prospects through hoarding, thus favouring their sedentarity and more territorial social systems. However, hoarding is a critical proximate factor, but not **THE** only factor, behind non-breeding social strategies in parids.

5- Behavioural plasticity appears very important when facing transient periods of stress due to adverse conditions during winter. Plasticity in the use of substrates and prey allow individuals to adjust energy requirements to energy acquisition.

6- Stressful periods during winter also play an important role in shaping age segregation patterns in Willow tit flocks. Furthermore, foraging segregation during such periods fits the hoarding distribution of food items that the same population shows during autumn.

7- At least in moderate competitive conditions, and seemingly low predation pressure, the individual juvenile morphology also plays a role in the choice of a foraging microhabitat within trees. In such conditions, heavier birds tend to occupy inner parts of trees, whereas lighter individuals forage outer and higher up in the tree canopy.

8- Because juveniles are forced to occupy outer parts of trees in stressed conditions, they built up food reserves through hoarding in such outer areas. In mild weather, when juveniles are free to choose foraging sites, individuals balance the costs of using a potentially dangerous microhabitat with the benefits of building energetically cheap and large food reserves through hoarding.

9- Hoarding behaviour differs between populations of the same species according to environmental and competitive conditions. Coal tits in a Norwegian population hoarded in outer and higher parts of trees than a population inhabiting a subalpine forest in the Pyrenees. High competitive pressure and a low degree of residence in the Norwegian population may induce individuals to use outer storing locations for short-term use. In contrast, Coal tits in the Pyrenees used inner locations among tree canopies, those used by birds during adverse weather conditions. Therefore, in the Pyrenees individuals seem to use stores in a longer-term perspective in order to reduce fluctuations in the food availability due to bad weather.

10- Within the Pyrenean population studied, I observed similar storing segregation patterns to those observed interregionally. Resident individuals hoarded in inner parts of trees more than transient birds, which mainly seem to use the stores in a short-term perspective. Within resident birds, adults also stored in inner parts of trees than juveniles did. Since storing in inner parts of trees takes longer than items located further out, it is suggested that such caches are of higher survival value for individuals.

11- Analyses of individual hoarding decisitons showed that individuals stored even when travelling in large associations. However, Coal tits did not randomly selected the time of storing. They avoided the presence of closer neighbours, but stored homogenously throught the day. Adult residents used central parts of home ranges much often than expected. In this way Coal tits may reduce immediate threats to stores and the probability of future cache pilfering.

12- Life-history traits in parids may be partially affected by the indirect constraints imposed by winter sociality. Closed, territorial systems and the constraints associated in terms of juvenile settlement, are associated with a decrease in fecundity in parids. The hypothesis, supported by the analysis conducted, is that a reduction in the fecundity of species (i.e. proportion of second broods and clutch size) might be beneficial because they are time saving mechanisms that favour early establishment of juveniles in a closed system. As predicted also, less territorial species, lacking to some degree the constraints derived from an early settlement of juveniles, showed higher fecundity than more territorial species.

13- The eruptive behaviour in some species of parids do not seem to be directly associated with the non-breeding territoriality (i.e. social organisation). The analyses conducted indicated that the larger fecundity associated with territorial social systems may influence more strongly the eruptive behaviour in this group of passerines. Therefore, species with a high fecundity may be more easily involved in eruptive episodes if some proximate variable (i.e. availability of food supply) produces a strong increase in population size.

RESULTATS PRINCIPALS I DISCUSSIÓ

VARIACIÓ EN L'ORGANITZACIÓ SOCIAL DELS PÀRIDS DURANT L'ÈPOCA NO REPRODUCTORA

En els pàrids, el comportament d'emmagatzemament està sovint associat a un sistema social territorial (Ekman 1989a). D'altra banda, l'anàlisi detallat d'una població emmagatzemadora juntament amb les indicacions d'altres estudis sobre la Mallerenga petita (Nakamura 1975) suggereixen que aquesta associació no és inequívoca (Capítol 1).

Així doncs, quins són els factors que hi ha darrera de la variació detectada als sistemes socials dels pàrids? L'increment en l'eficàcia antipredatòria o en l'eficiència alimentària són factors que fan que la vida en grup sigui beneficiosa (Pulliam & Caraco 1984, Lima & Dill 1990), però el fet que els individus esdevinguin residents o formin grups de composició estable depèn de les opcions disponibles i de les seves conseqüències a llarg termini. Per tal d'aclarir quins són els factors involucrats en la variació dels sistemes socials i quin paper hi juguen, s'han d'analitzar detalladament les estratègies de reclutament dels joves en la futura població reproductora (Matthysen 1990).

Amb l'objectiu d'estudiar els possibles beneficis de diferents estratègies d'establiment dels joves, es va aplicar l'aproximació modelitzadora empreada per Ekman (1989a) en una forma lleugerament modificada. La pregunta principal darrera de l'aproximació d'Ekman és: quan de temps han d'esperar els joves en dispersió abans de decidir finalment a establir-se en una àrea determinada? Aquesta pregunta és d'una importància capital ja que variacions en les decisions d'establiment van associades amb graus variables de residència dels joves després de la dispersió de tardor, i això donaria lloc a estructures socials molt diferents. Així doncs, un establiment endarrerit resultaria, molt probablement en un sistema obert, ja que els joves no establirien lligams forts de residència fins molt avançat l'hivern o fins la primavera. D'altra banda, un establiment ràpid podria generar fàcilment un sistema més tancat i estable amb una alta probabilitat d'esdevenir territorial.

Quan un hàbitat és òptim i els joves hi troben una zona buida, la millor decisió a prendre és la d'establir-se allà i esperar fins a la següent estació reproductora per criar. Però aquesta situació s'esdevé poques vegades. En general, els hàbitats de qualitat estan ocupats pels ocells adults que ja han criat a la zona en estacions anteriors. Llavors, l'opció és esperar fins que apareixi una vacant (e.x. després de la mort d'un individu adult). La decisió correcta d'establiment serà doncs, aquella que maximitzi la probabilitat d'aconseguir una posició de cria al millor dels hàbitats possibles. Si el gradient en qualitat d'hàbitat no fos molt elevat, encara seria avantatjós per un jove establir-se en un hàbitat de qualitat més baixa. Però quan el gradient en la qualitat de l'hàbitat augmenta, els costos d'establir-se a un de pitjor qualitat augmenten i per tant, també augmenten els avantatges d'esperar en un de millor (Fretwell 1972, Ekman 1989b) fins que apareixi una vacant (Fretwell & Lucas 1970, Lens and Wauters 1996).

A un hàbitat òptim, prendre la posició a un ocell resident i quedar-se amb el seu territori tampoc no sembla una opció factible pels joves, perquè als pàrids, la dominància està clarament esbiaixada a favor dels adults (Koivula & Orell 1988, Hogstad 1989, Smith 1991). Així doncs, les estratègies que queden obertes pels joves són, d'una banda, l'establir-se amb una parella adulta i esperar una vacant en el grup (estratègia d'establiment), i de l'altre, el seguir buscant vacants a altres grups (estratègia flotant). Per definició, esdevenir flotant comporta tenir àrees de deambulació considerables, ja que han d'incloure els grups on les vacants poden aparèixer.

Si un jove s'estableix a principis de l'estació, pot caure en el considerable cost que suposa perdre l'oportunitat de trobar una posició millor. Depenent de les dificultats per trobar una vacant a la població i dels costos de supervivència de cada una de les estratègies, els joves haurien d'escollir l'estratègia que maximitzés la seva eficàcia biològica a llarg termini. Com Ekman (1989a) mostra, els juvenils es beneficiaran de la vida flotant quan els beneficis de ser-ho superin els obtinguts en establir-se com a membre permanent en un grup adoptant una estratègia d'espera:

$$P_f(S(t))P(vacant(t))P_i(S(T\text{-}t)) > P_{i+1}(S(t))P(vacant(t))P_i(S(T\text{-}t) \qquad (1)$$

Així és, els individus flotants es beneficiaran de no establir-se ràpidament si : la probabilitat que sobrevisquin sent individus flotants $P_f(S(t))$ abans de trobar una vacant $P(vacant(t))$ i, després sobrevisquin com a membres establerts fins a la següent estació reproductora $P_i(S(T\text{-}t))$, supera la d'un individu establert $P_{i+1}(S(t))$ que ocupa una vacant dins del seu propi grup $P(vacant(t))$ i que després sobreviu fins la següent primavera $P_i(S(T\text{-}t))$. En un model de temps continu, l'expressió esdevindria :

$$\frac{(1 - \exp(-Nm_i t)) - (yN)}{(1 - \exp(-m_i t))} > \frac{\exp(-m_{i+1} t)}{\exp(-m_f t)} \qquad (2)$$

On N és el número de grups disponibles per individu (N=1 en el cas dels membres ja establerts en un grup determinat), m_i és la mortalitat d'un membre de rang i en la dominància local (m_f pels individus flotants), i t és el temps disponible per l'establiment dels individus en una unitat social (Ekman 1989a). He modificat l'aproximació d'Ekman per incorporar-ne l'expressió que inclou la variable y, que seria l'eficiència en la inspecció dels grups. Aquesta modificació és necessària perquè la probabilitat d'ocupació d'una possible vacant no sembla augmentar linealment amb el número de grups inspeccionats. Més aviat tendirà a disminuir quan el número de grups inspeccionats sigui massa gran. En aquest cas, podria aparèixer una vacant que l'ocell en qüestió podria no trobar abans que fos ocupada per altres ocells. Així doncs, l'eficiència d'inspecció depèn de dos variables secundàries no analitzades en detall en aquest estudi. La primera seria la distància que cal salvar entre grups, que està relacionada amb la densitat dels grups existents (ex. densitats altes facilitarien la inspecció per part dels individus flotants mitjançant l'increment en el número de possibles vacants per àrea). La segona, la densitat d'individus flotants, que disminuiria l'eficiència d'inspecció de grups per efecte de la possible competència entre diversos individus per la possibles vacants. S'assumeix que, en un grup ja establert, un ocell subordinat només pot adquirir una posició millor dins del seu mateix grup, i que, d'acord amb alguns estudis experimentals i observacionals (Smith 1984, Hogstad 1990a), els individus flotants poden establir-se directament en vacants de rang i aparegudes a qualsevol dels grups inspeccionats. Donada la subordinació a ocells residents, s'assumeix també que existeix un cost en termes de supervivència intrínsec al fet de ser flotant (ex. $m_f > m_i$). De l'equació 2, se'n deriva que, a igualtat de condicions la desigualtat es pot satisfer a mesura que, a) les taxes de mortalitat en les posicions més subordinades dels grups establerts (m_{i+1}) s'incrementen, aproximant-se cap a les dels individus flotants, o b) la mortalitat d'aquest s últims es redueix. Això doncs, quan la penalització de ser individu flotant és tan petita que pot ser superada pels beneficis d'explorar més grups on trobar possible vacants, l'estratègia flotant esdevé la millor opció pels joves en dispersió (Figures 5 c, d).

Un factor important a l'hora de determinar les taxes de mortalitat dels individus és l'emmagatzemament. En les espècies emmagatzemadores, els individus sedentaris podran gaudir amb més facilitat dels beneficis derivats de l'emmagatzamement (Källander & Smith 1990). Si aquest fet es tradueix en una reducció de la mortalitat dels residents, es pot veure fàcilment que l'emmagatzemament pot produir una asimetria en la supervivència dels individus relacionada amb la residència, i per tant, tendirà a afavorir un establiment ràpid dels ocells en grup sedentaris (Figura 5 a). En aquests casos, a causa dels costos de subordinació (Koivula & Orell 1988), un establiment ràpid esdevé decisiu, ja que els joves s'estableixin més tard hauran d'ocupar forçosament posicions baixes en la jerarquia de dominància (Nilsson & Smith 1988). En aquestes condicions, els ocells que triguin molt en establir-se, es veuran forçats a adoptar també una estratègia flotant quan els costos de la subordinació superen els beneficis a llarg termini provinents de l'esperança d'aconseguir un territori. En aquest cas, la vida flotant es converteix en la millor de les pitjors opcions en el sentit de Hogstad (1990). D'altra banda, qualsevol altre factor relacionat amb una disminució dels costos de ser flotant serà, amb una alta probabilitat, un condicionant important a l'hora de determinar l'estructura social de la població en qüestió. Si, per exemple, hi ha una font d'aliment abundant, i heterogèniament distribuïda, els joves podrien sortir beneficiats, en termes de supervivència, de portar una vida transeünt. Els costos de dominància relacionats amb la vida flotant també juguen un paper important: si els costos de dominància que paguen els individus flotants són molt alts, llavors s'incrementa la seva mortalitat i la seva estratègia esdevé també una mala opció.

A banda de la mortalitat relativa d'individus flotants i dels que s'estableixen més ràpidament, els beneficis relatius d'aquestes dues estratègies, depenen de l'efectivitat en trobar i ocupar una vacant quan aquesta apareix en la població. Aquests costos estan relacionats directament amb la distància entre els grups inspeccionats i el número de competidors per cada vacant apareguda. Quan els costos en la inspecció de grups són alts, els ocells establerts amb rapidesa tenen avantatge si el risc de mortalitat dels individus flotants és elevat (Figura 5 a). En canvi, quan la mortalitat dels flotants disminueix, aquesta estratègia esdevé de nou la més òptima. En aquest darrer cas, i degut a l'elevat cost d'inspecció dels grups, els individus flotants resten parcialment residents, solapant les àrees de deambulació entre un número limitat de grups residents (Figura 5d). Aquests individus flotants podrien originar el sistema no territorial de floc bàsic descrit per algunes espècies de pàrids. En moltes d'aquests poblacions, la densitat és molt elevada. Una densitat elevada afavoreix la inclusió de varis grups dins les àrees de deambulació dels invididus flotants el que maximitzaria la probabilitat d'ocupació d'una hipotètica vacant.

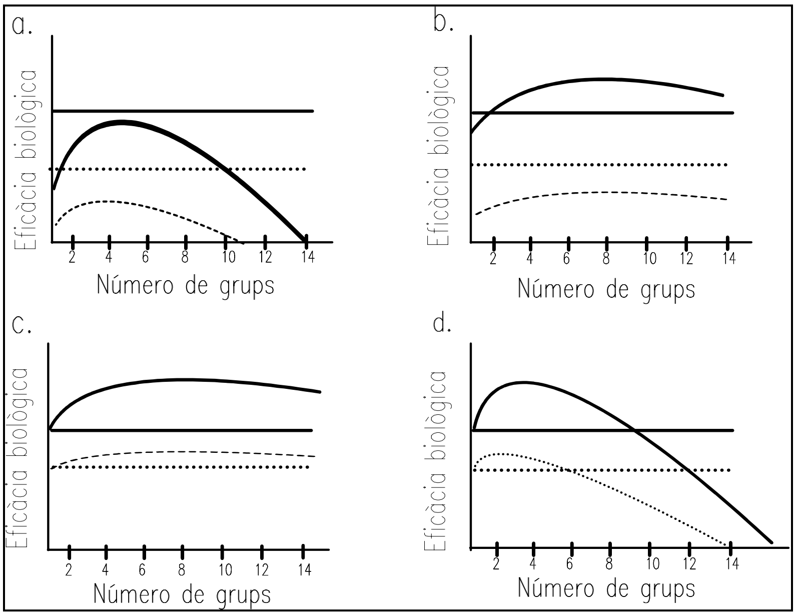

Figura 5. Corbes d'eficàcia biològica (equació 2) dels costos i beneficis de l'estratègia dels individus flotants en front dels que s'estableixen ràpidement en un grup resident. Les línies horitzontals representen l'eficàcia guanyada pel joves establerts en un grup concret (que és constant per una *N* donada). Les corbes representen l'eficàcia dels joves flotants en funció del número de grups inspeccionat (*N*). *N* és el número de grups o parelles on les vacants poden aparèixer, i per tant estar disponibles per un individu flotant. D'acord amb les dades disponibles (Cramp & Perrins 1993), la mortalitat de les parelles establertes en estacions anteriors (m_i) es va fixar a 0.4, i la mortalitat dels juvenils establerts (m_{i+1}) a 0.5. Les línies contínues (t) representen condicions temporalment més primerenques que les discontínues (t', on $t<t'$). a). Corba d'eficàcia prevista per l'estratègia flotant quan els costos d'inspecció entre grups i la mortalitat dels individus flotants són elevats (a=0.1, m_f=0.9), b). Corba d'eficàcia de l'estratègia flotant quan els costos d'inspecció són baixos, però la mortalitat dels flotants elevada (a=0.01, m_f=0.9). c). Corba amb els costos d'inspecció de grups baixos i mortalitat dels indivudus flotants que s'aproxima a la dels joves establerts (a=0.01, m_f=0.5). d). Corba amb els costos d'inspecció elevats i la mortalitat dels flotants baixa (a=0.1, m_f=0.5).

Quan el cost d'inspecció de grups és baix, la vida flotant també tendeix a ser beneficiosa (Figura 5c), però llavors l'àrea òptima d'ocupació dels individus sembla incrementar-se (ex. les àrees de deambulació inclouen més grups per inspeccionar). No obstant, amb valors elevats de mortalitat, l'estratègia flotant esdevé progressivament menys beneficiosa a mesura que el temps passa (Figura 5 b).

En resum, el senzill model aquí descrit suggereix que l'hàbit flotant dels juvenils, que podria estar relacionat amb l'origen d'un sistema social laxe i poc estructurat, esdevindria favorable quan (1) els costos d'inspecció i desplaçament entre grups hivernals fossin baixos, i/o (2) les diferències entre la mortalitat de flotants i la dels joves residents fossin petites. En alguns ambients, l'emmagatzemament podria comportar un increment de les diferències en la mortalitat de les dues estratègies, de manera que les estratègies relacionades amb un establiment ràpid serien més comunes a les espècies emmagatzemadores (Ekman 1989a).

Organització social en la Mallerenga capnegra

El sistema social de la Mallerenga capnegra ha estat estudiat en diverses poblacions d'hàbitats boreals, incloent, a Finlàndia, l'àrea on aquesta espècie va ser estudiada pel present treball (Ekman 1979, Hogstad 1987, Koivula & Orell 1988). L'establiment ràpid en petits flocs territorials de mida variable ha estat la regla en aquests estudis. Tenint en compte les condicions ambientals de la majoria de les àrees estudiades, la territorialitat i un establiment ràpid dels joves són característiques fàcilment predibles. En primer lloc, en àrees nòrdiques, l'emmagatzemament d'aliment és crucial per a la supervivència dels individus (Källander & Smith 1990). Així doncs, els individus flotants pagaran un cost elevat si no s'estableixen en un floc territorial i emmagatzemen prou aliment per passar l'hivern. A més, la densitat de població a aquestes àrees acostuma a ser molt baixa. En aquests casos, els costos d'inspecció de més d'un grup podrien ser molt elevats en comparació als possibles beneficis obtinguts de la possibilitat de trobar altres vacants (Hogstad 1990). Així doncs, els punts que podrien haver conduït a un sistema territorial i estable com el de la Mallerenga capnegra en boscos boreals són :

1- Els adults es converteixen en sedentaris perquè aquesta estratègia s'associa amb una probabilitat de cria més elevada gràcies a la facilitat per adquirir un territori la següent estació de cria (Smith 1991, Koivula et. al.1996).
2- Els elevats costos de supervivència que suposa la vida flotant (ex. associats amb la dominància i l'absència d'emmagatzematges) i la gran distància entre grups, afavoreixen l'establiment primerenc dels joves juntament amb els adults residents, formant grup dins dels quals s'esperar que apareguin les possibles vacants (Hogstad 1990b, Koivula et al. 1996).
3- La baixa densitat de població i l'elevat valor de les àrees ocupades (ex. aliment emmagatzemat) també afavoreixen la defensa territorial de les àrees de deambulació dels membres d'un floc (Kaufman 1983).

Organització social de la Mallerenga petita (*Parus ater*)

Utilitzant dades de la superficie de les àrees de deambulació dels individus, de solapament, i d'estabilitat social, s'analitzà la distribució en l'espai i l'organització social de la Mallerenga petita als Pirineus. El sistema social es va centrar en les parelles adultes que havien criat a la zona l'estiu anterior i ocupat àrees relativament petites. Els joves residents tenien àrees de deambulació molt més grans que els adults, solapant-se amb les d'aquests i amb les d'altres joves veïns. Els joves residents es varen observar a prop de la zona de captura respectiva amb molta més probabilitat de la que s'esperaria a l'atzar, suggerint que, en efecte, alguns dels joves residien a àrees de deambulació extenses però limitades. Les associacions d'individus, formades en gran part per juvenils transeünts (observats a l'àrea un sol cop), eren de mida gran, baixa cohesió i amb una composició temporal variable. No es va detectar defensa territorial per cap tipus social dels analitzats. Així doncs, l'organització social de la Mallerenga petita descrita a aquesta població és similar al sistema no territorial i més laxe de "floc bàsic" descrit per algunes espècies no emmagatzemadores territorials de parids (Nakamura 1975, Saitou 1978, Drent 1983). Els patrons socials dels individus residents semblen estar relacionats amb la disponibilitat de recursos de cria. Una gran competència per aquest tipus de recursos, conduiria a una gran sedentaritat i fidelitat pel lloc de cria per part dels adults i a una vida flotant en els joves residents. D'altra banda, factors que actuarien a més curt termini podrien determinar les estratègies d'agrupació dels ocells transeünts (ex. atracció a una font abundant d'aliment com els pinyons). En general, una elevada disponibilitat hivernal de recursos alimentaris, el que permetria una elevada densitat de població, seria el principal determinant dels patrons socials descrits per aquesta població de Mallerenga petita. Les poblacions de Mallerenga petita habitants de boscos boreals del nord d'Europa semblen ser bàsicament territorials (Ekman 1989a). Una menor densitat de població en aquestes àrees i una menor abundància d'aliment serien l'origen d'aquesta variació respecte els patrons espacials i socials descrits als Pirineus. En el cas dels ambients borels, la territorialitat seria possible perquè el número de possibles invasors en aquestes àrees seria molt menor disminuïnt així els costos energètics de la defensa.

Seguint el mateix esquema tentatiu plantejat per l'estudi de la Mallerenga capnegra, els passos que condueixen a un sistema social com el descrit per a la Mallerenga petita als Pirineus són els següents:

1- Els adults es converteixen en sedentaris per tal d'assegurar els territoris de cria any rera any.
2- Els costos de la vida flotant poden ser relativament baixos i per tant, degut a la gran disponibilitat d'aliment (ex. pinyons de pi), aquesta estratègia esdevé òptima. L'elevada densitat de població facilita la inclusió de varies parelles residents a les àrees de deambulació dels joves flotants.
3- L'elevada densitat de població limita la defensa territorial de les àrees de deambulació dels individus, ja que que els costos, en termes energètics, són desmesurats en comparació amb els beneficis obtinguts. Així doncs, les àrees vitals dels individus es solapen les unes amb les altres. Els beneficis de la vida en grup dirigeixen els patrons d'agrupament a curt termini, resultant en flocs de composició molt inestable.

Per tal de confirmar alguns dels aspectes d'aquest esquema tentatiu, encara preliminar i especulatiu, són necessaris futurs estudis. En particular, caldrien estimacions de supervivència de joves que hagin seguit diferentes estratègies i patrons d'espaciació, per tal poder discutir, amb més exactitud, els costos de cada un d'elles. Per tal de completar el quadre, també seria necessari disposar d'estimacions exactes de l'èxit d'establiment dels joves d'acord amb el seu estatus de residència per així poder confirmar la optimalitat de l'estratègia flotant en determinades condicions. Així mateix, s'hauria de testar si els individus flotants residents i els individus transeünts difereixen en les taxes de reclutament i posterior èxit reproductor i en quina mesura.

Senyalització d'estatus en la Mallerenga petita

En grups hivernals d'ocells socials, els individus competeixen per la prioritat d'accés a recursos com aliment o protecció (Gauthreaux 1978, Baker et al. 1981). La competència mitjançant interaccions agonístiques és energèticament costosa (Hogstad 1987). Per tant, és predible que, degut a l'inestabilitat del sistema social de la Mallerenga petita durant l'època no reproductora, existeixin mecanismes indirectes de senyalització d'estatus indicatius del potencial de cada individu a l'hora de resoldre un conflicte social. Es va testar experimentalment la predicció que la senyalització d'estatus és important a l'hora de decidir el resultats de les interaccions entre individus amb manca de coneixement mutu, però no entre individus coneguts entre si (Senar 1999). Els resultats van estar d'acord amb les prediccions de la hipòtesi, segon les quals, la senyalització d'estatus és un mecanisme important utilitzat pels individus per estimar el potencial dels rivals amb els que no han tingut cap contacte prèvi. Com que els grups de Mallerengues petites als Pirineus són de composició poc estable la senyalització d'estatus sembla ser un factor important en l'establiment de relacions de dominància entre els joves de diferents grups.

CANVIS EN L'ÚS DE L'ESPAI EN CONDICIONS METEOROLÒGIQUES ADVERSES

L'hivern suposa un període difícil pels ocells. Sovint, aquesta adversitat s'atribueix més a la manca d'aliment associada amb l'hivern que al clima hivernal per si mateix (Jansson et al 1981, Spencer 1982, Lahti et al. 1998). Les limitacions en la disponibilitat d'aliment, tan si són de curta durada com si no, imposen diferents limitacions a l'alimentació de les Mallerengues d'hàbitats subalpins i boreals. Així doncs, l'estudi de les respostes comportamentals dels ocells en aquestes condicions pot ajudar a comprendre millor la seva ecologia hivernal i els aventatges de sistemes socials concrets. En el cas de les espècies emmagatzemadores, l'estudi del comportament individual en condicions de temps advers esdevé essencial per entendre el paper de l'emmagatzemament en l'ecologia hivernal de les Mallerengues (Brodin 1994b).

La Mallerenga capnegra (*Parus montanus*)

Es van estudiar flocs de Mallerenga capnegra sotmesos a condicions ambientals benignes (temperatura >0ºC), i en condicions fredes (<-4ºC), per tal d'analitzar els possibles factors involucrats en la segregació de l'hàbitat entre els diferents membres dels flocs. Quina és la influència que tenen dels períodes adversos i estresants sobre el comportament d'agrupació i l'estructura dels grups ? En condicions fredes, els membres del grup van moure's junts més sovint que en condicions més benignes de temperatura. De tota manera, els adults i els juvenils mantingueren ocupacions relatives de l'espai molt similars en ambdues condicions ambientals estudiades.

En condicions fredes, la utilització de l'espai durant l'hivern és predible a partir de les distribucions d'aliment emmagatzemat durant la tardor anterior. L'elecció activa que realitzen els adults de les parts interiors dels arbres, més segures i possiblement mes riques, sembla ser el factor últim al darrera de la segregació en l'espai durant l'hivern (Suhonen 1993). A més, la segregació descrita en condicions fredes, afecta indirectament l'ús del microhabitat en condicions més benignes, sobretot durant la tardor. Com en condicions d'estrés, el joves es veuen obligats a ocupar les parts exteriors dels arbres, aquests col.loquen les reserves d'aliment en aquestes mateixes àrees. En condicions favorables de temperatura, els joves decideixen l'ús del microhàbitat com un balanç entre els costos associats amb la utilització d'un lloc potencialment perillós i els beneficis associats amb l'estalvi energètic derivat d'emmagatzemar gran quantitat d'aliment en els microhàbitats on s'alimentaran amb posterioritat. Es suggereix que si els costos de predació no són gaire alts, aquesta decisió tendirà a inclinar-se des de l'ús de microhàbitats més segurs (les zones interiors preferides pels adults dominants) cap a l'ús de les zones més externes on els emmagatzemaments són situats. Aquesta utilització de l'espai per part dels joves, unida a l'existència de patrons d'alimentació associats amb la morfologia dels ocells, comporten un estalvi energètic important (Lens & Dhondt 1994, Capítol 5).

La Mallerenga petita (*Parus ater*)

El cas de la Mallerenga petita en els boscos de coníferes subalpins és molt diferent del de la Mallerenga capnegra. En àrees Mediterrànies subalpines, l'hivern no és climàticament tan extrem com en els boscos boreals, ni el dia tan curt. A més, per les espècies capaces d'aprofitar els pinyons de Pi negre, l'aliment és relativament abundant. La producció de pinyons de Pi negre és considerable i força constant d'un any per l'altre (Génard & Lescourret 1986). De tota manera, durant l'hivern, els climes subalpins poden ser ocasionalment molt adversos. Durant tempestes de neu o cops de vent (Carrascal 1988) i especialment després de fortes nevades, les parts exteriors de les capçades dels arbres on es localitzen els principals substrats alimentaris de les Mallerengues (fulles i pinyes) poden quedar inaccessibles durant força temps. Aquesta disminució temporal de la disponibilitat d'aliment pot ser fatal pels individus en termes de supervivència o emigració forçada. Es va comparar la utilització de l'espai i les tècniques d'alimentació dels ocells en condicions de neu present en les parts exteriors dels pins i en absència de neu. En condicions de presència de neu, els ocells es van alimentar a les parts baixes i més interiors dels arbres, utilitzant els troncs i les branques més gruixudes com a substrats d'alimentació principal. En condicions benignes, els ocells van utilitzar les parts superiors i exteriors de les capçades, alimentant-se sobretot en fulles i pinyes. El patró de moviment dels individus també va diferir entre condicions. En condicions benignes, els ocells van utilitzar mètodes energèticament més costosos, com el vol i la posició penjant, mentre que en condicions de neu es van utilitzar mètodes com el salt, menys cars energèticament. Els resultats recolzen la hipòtesi de Norberg (1977) que quan la previsió d'obtenir aliment s'incrementa, es poden utilitzar tècniques d'alimentació més energèticament costoses. Així doncs, els ocells poden estalviar energia en condicions adverses, mitjançant l'ús d'un microhabitat diferent amb les tècniques de búsqueda que té associades. L'emmagatzemament sembla jugar també un important paper a l'hora d'amortiguar l'efecte dels períodes adversos de temps permetent als individus disminuir la variació en l'abundància d'aliment que se'n deriva.

L'EMMAGATZEMAMENT D'ALIMENT

La Mallerenga capnegra

L'emmagatzamament d'aliment en la Mallerenga capnegra ha estat estudiat en detall en poblacions boreals nòrdiques (Haftorn 1956b, Pravosudov 1985, Brodin 1994b, Lahti et al. 1998). Com ja s'ha discutit anteriorment, en condicions fredes, les Mallerengues capnegres emmagatzemaren en microhàbitats similars als que utilitzen durant la tardor (Lahti et al. 1998). Aquesta coincidència de microhabitat també va ser trobada per Brodin (1994a). Els resultats de Lahti et al. (1998) i Brodin (1994a) differeixen en el grau de segregació trobat en els microhabitats d'alimentació i emmagatzemament d'adults i joves. En l'estudi de Brodin (1994a), la segregació entre les localitzacions d'emmagatzemament de subordinats i dominants va ser en la component vertical solament. Diferents règims de predació semblen ser els responsables de les diferències observades.

En àrees boreals, l'aliment emmagatzemant és extraordinàriament important per la supervivència dels ocells. Brodin (1994b) va estimar que en aquestes àrees durant els mesos de l'hivern, l'aliment emmagatzemat pot arribar a composar el 25 % de la dieta dels ocells. En hiverns especialment freds, amb un estrés energètic elevat, és possible que aquest percentatge s'elevi fins a prop d'un 50 % del total de l'aliment consumit (Haftorn 1956b, Brodin 1994b). Com la disponibilitat d'aliment és baixa i el període de temps disponible per a l'alimentació també, l'aliment extra que suposa l'emmagatzemament incrementa les possibilitats de supervivència dels individus i possibilita la seva sedentarietat (Lahti et al. 1998). A més de la territorialitat, els individus utilitzen un bon número d'estratègies comportamentals per tal d'assegurar l'ús dels emmagatzemaments. Alguns exemples són la memòria (Sherry & Duff 1996, Dhondt & Smulders 1997) o l'esquivar la companyia de conespecífics (Stone & Baker 1989, Lahti & Rytkönen 1997).

La Mallerenga petita

Aquesta espècie emmagatzema aliment activament durant la tardor i l'hivern. Es va analitzar l'elecció del microhabitat d'emmagatzemament de dos poblacions habitants de boscos de coníferes a Noruega i als Pirineus. Les dues poblacions eren differents en el grau de sedentaritat dels individus, en la seva densitat i en el número d'altres espècies de Mallerengues presents. La localització dels emmagatzemaments va ser molt diferent en les dues zones. La població més nòrdica va utilitzar les fulles i les parts més exteriors de les capçades dels pins (Haftorn 1956a), mentre la població Pirinenca va utilitzar substrats més interiors com troncs o branques gruixudes. A Noruega, els ocells semblen estar sotmesos a una competència interespecífica major. En general, les espècies dominants com la Mallerenga emplomallada (*P. cristatus*) o la Mallerenga capnegra utilitzen les parts interiors dels arbres per emmagatzemar, per tant interfereixen amb els possibles patrons d'emmagatzemament de la Mallerenga petita. A Noruega, la Mallerenga petita és molt menys sedentària que altres espècies de Mallerengues, amb una població molt reduïda en l'àrea d'estudi durant la major part de l'hivern. La manca de llocs d'emmagatzemament més segurs a causa de la competència podria no permetre a les Mallerengues petites emmagatzemar en els millors llocs, el que dificultaria la sedentaritat dels individus. D'altra banda, a Noruega, l'emmagatzemament podria ser utilitzat bàsicament a curt termini com una alternativa a l'acumulació interna de greix (McNamara et al. 1990, Witter & Cuthill 1993, però veure Pravosudov & Grubb 1998). L'alta proporció d'aliment d'origen animal (amb un baixa durabilitat, Brodin 1994a) emmagatzemat a

Noruega sembla recolzar la hipòtesi que els emmagatzemaments són utilitzats a curt termini. En els Pirineus, les Mallerengues petites pateixen una pressió competitiva menor i utilitzen microhàbitats similars als que es fan servir en condicions d'adversitat ambiental (ex. després de nevades fortes, capítol 4), però molt diferents dels utilitzats en condicions normals amb bon temps.

Als Pirineus, es va analitzar en detall un població emmagatzemadora de Mallerengues petites on els individus havien estat prèviament marcats amb anelles de color. Es varen poder identificar diferents classes d'ocells segons la seva edat i estatus de residència en la zona. Per tant, es varen poder analitzar en la mateixa població els microhàbitats d'emmagatzemament en relació a l'estatus de residència dels individus. Els individus emmagatzemaren intensament des de principis de tardor fins al final de l'estudi a l'hivern, amb un màxim durant el mes de Novembre coincidint amb el màxim d'obertura de les pinyes de Pi negre. Dins dels grups, els ocells van evitar d'emmagatzemar en presència d'individus propers, però no de veïns situats a més de 20 m. Els adults van concentrar els emmagatzemaments al voltant del centre de les seves àrees de deambulació. Els joves van emmagatzemar a taxes similars a les dels adults, mostrant una evitació similar a emmagatzemar en presència de veïns molt propers. Els ocells no van mostrar cap mena de preferència per emmagatzemar durant una part concreta del dia. L'aliment emmagatzemat en les parts més externes dels arbres estava localitzat a més distància del lloc d'origen i era emmagatzemat amb més cura que l'emmagatzemat en les parts exteriors, el que suggereix un valor i un ús diferent dels emmagatzemaments en relació a la seva localització dins dels arbres. A més els adults, majoritàriament residents, van emmagatzemar en les parts interiors del arbres, presumiblement més segures, més sovint que els joves transeünts o residents.

En resum, la Mallerenga petita en els Pirineus no va utilitzar la territorialitat com un mecanisme per reduir el robatori de l'aliment emmagatzemat, encara que els individus utilitzaren un número d'estratègies alternatives per tal d'incrementar la probabilitat de la seva recuperació. Primer, les Mallerengues petites no varen emmagatzemar a l'atzar. La probabilitat d'emmagatzemament va dependre de la presència de conespecífics propers, fet probablement relacionat amb la reducció de la probabilitat de robatori immediat. Segon, els adults sedentaris varen concentrar els seus emmagatzemaments en zones molt restringides. D'aquesta manera, els adults redueixen el solapament dels emmagatzemaments amb els adults veïns. A més la concentració dels emmagatzemaments, podria facilitar la seva defensa directa en front de visites puntuals d'altres individus com els transeunts (obs. pers.). Tercer, la segregació espacial dels emmagatzemaments entre diferents classes d'individus va ser molt clara. Els llocs d'emmagatzemament varen coincidir majoritàriament amb els llocs utilitzats en condicions meteorològiques adverses. A més, la segregació dels emmagatzemaments estava clarament relacionada amb l'estatus de residència i l'edat dels individus. Els individus redueixen la probabilitat de robatori futur i incrementen la probabilitat de retrobar els emmagatzemament si aquests es localitzen en un microhabitat lleugerament diferent de l'utilitzat per altres individus (Brodin 1994a).

L'EVOLUCIÓ DE L'EMMAGATZEMAMENT DE L'ALIMENT I L'ORGANITZACIÓ SOCIAL DURANT L'ÈPOCA NO REPRODUCTORA

Smulders (1998) va presentar un model en el que argumentava que, sempre que els hiverns siguin prou durs, un sistema especialitzat de memòria no seria necessari per tal de que l'emmagatzemament apareixes en una població d'ocells com les mallerengues. Va suggerir també que un escenari adequat per l'origen de l'emmagatzemament en els parids podria incloure la idea d'una organització social ancestral molt propera al sistema de "floc bàsic" amb grups inestables i no territorials. Els resultats obtinguts en el present treball van en contra d'una inequívoca relació entre l'emmagatzemament i la territorialitat. L'emmagatzemament afavoriria la sedentaritat dels individus, però la territorialitat està situada un pas més enllà en l'evolució social. Les troballes d'aquest estudi en relació amb l'organització social i l'emmagatzemament en la Mallerenga petita recolzen la idea principal de la hipòtesi de Smulders (1998). S'ofereix un marc funcional en el que l'emmagatzemament és compatible amb l'ús no exclusiu de les àrees de deambulació dels individus, a l'hora que afavoreix la seva sedentaritat mitjançant una disponibilitat incrementada d'aliment en moments d'adversitat ambiental.

Aquesta situació sembla haver estat comú en les espècies de pàrids ancestrals habitants d'àrees temperades. Els ocells podrien haver començat a beneficiar-se de la troballa d'aliment no acabat de consumir en el passat. Aquesta troballa accidental no requereix necessàriament un sistema de memòria desenvolupat (Vander Wall 1990). Un ocell que pot alimentar-se en les mateixes zones on va menjar anteriorment, i treure profit d'un aliment no acabat de consumir, pot obtenir-hi un benefici (Brodin & Clark 1997), si té una probabilitat més alta que d'altres ocells veïns de retornar al lloc en qüestió (Sherry & Duff 1996). Si la sedentaritat és beneficiosa pels ocells, permetent per exemple, una cria més primerenca o una posició més alta en la jerarquia de dominància local, la recuperació de l'aliment manipulat amb anterioritat és converteix en un avantatge en termes de facilitació d'aquesta sedentaritat. Sovint les Mallerengues manipulen el seu aliment en les parts interiors dels arbres que són les parts més utilitzades pels ocells en condicions adverses (Capítol 4). Així doncs els ocells poden retrobar part d'aliment no consumit en moments de plenitud alimentària, quan en condicions adverses busquen menjar en les zones internes més protegides de l'adversitat ambiental. Aquest comportament ofereix un mecanisme mitjançant el qual alguns ocells podrien retrobar el menjar no totalment consumit en ocasions anteriors (Vander Wall 1990).

Com es pot deduir dels estudis realitzats en poblacions més nòrdiques de pàrids com la Mallerenga capnegra o l'emplomallada, l'aliment emmagatzemat esdevé essencial per la supervivència hivernal dels individus (Haftorn 1956b, Pravosudov 1985, Brodin 1994b, Lahti et al. 1998). Una vegada l'emmagatzemament s'ha establert en una població, la presència de lladres i el possible perill que representen per l'aliment emmagatzemat, es poden evitar parcialment mantenint les mides de grup el més petites possible. Una manera d'aconseguir una reducció en la mida del grup és defensant una àrea de deambulació davant d'altres individus (Smulders 1998). A més, la baixa densitat de població associada a condicions ambientals molt adverses, converteix el sistema territorialitat en un sistema energèticament suportable. Així doncs, es suggereix que un cop l'emmagatzemament es va originar, possiblement en un sistema social laxe i no territorial, els processos de protecció d'un aliment emmagatzemat progressivament més important, transformaren aquest sistema social en un de més territorial i estable com el conegut actualment en la majoria de pàrids emmagatzemadors (Ekman 1989a, Matthysen 1990).

IMPLICACIONS INDIRECTES DE L'ORGANITZACIÓ SOCIAL DURANT L'HIVERN EN LES ESTRATÈGIES REPRODUCTORES DELS PÀRIDS

Territorialitat hivernal i fecunditat

Dins dels pàrids, la presència de la territorialitat com a estratègia social durant l'hivern varia considerablement entre espècies. En algunes, aconseguir una posició en els grups territorials, estructurats en sistemes de dominància, sembla crucial per la supervivència hivernal dels joves. En altres espècies però, els joves passen l'hivern en grans grups de composició molt variable i inestable (Nilsson & Smith 1988, Koivula et al. 1994, veure també la primera part d'aquest capítol). Es va testar la hipòtesi que en un sistema territorial on l'establiment dels joves està limitat pel temps (Nilsson 1990), una disminució en la capacitat reproductora dels ocells seria una estratègia adaptativa per tal d'aconseguir l'estalvi de temps necessari en un sistema d'establiment limitat pel temps. Utilitzant dos mètodes comparatius diferents, es va analitzar la relació entre la territorialitat hivernal dels sistemes socials dels pàrids i dos variables relacionades amb la capacitat reproductora de les espècies. Aquests mètodes permeten el control dels efectes filogenètics sobre les relacions establertes en les hipòtesis. Es va trobar un associació significativa entre la territorialitat hivernal de les espècies i les dues variables reproductores analitzades. Els increments evolutius en el grau de territorialitat hivernal de les espècies estaven relacionats amb disminucions de la capacitat reproductora de les mateixes, menors mides de posta i menor percentatge de segones postes. En la mostra de pàrids analitzada, els resultats suporten les prediccions que efectes indirectes a llarg termini amb possibles influències sobre l'eficàcia biològica de la descendència afecten les estratègies reproductores. Els joves de les espècies amb un sistema territorial tancat durant l'hivern, estan seriament limitats en les seves possibilitats futures per la data d'establiment en els grups. Així doncs, els individus d'aquestes espècies es beneficien dels mecanismes d'estalvi de temps associats amb una taxa reproductora menor. El número de descendents produïts pot ser més petit, però serien de més qualitat en termes de l'augment de la probabilitat d'èxit en l'establiment dels descendents en la futura població reproductora. En sistemes socials més inestables, les taxes de reclutament semblen estar condicionades per altres factors diferents de la data d'establiment. Així doncs, la fecunditat d'aquestes espècies és més alta que en les espècies anteriors, prioritzant la quantitat de descendents produïts en front d'altres característiques.

Territorialitat hivernal i irrupcions

Les irrupcions es defineixen com moviments irregulars en massa produïts fora de les àrees de cria principals d'una espècie. Es van analitzar els possibles lligams entre la territorialitat hivernal i el comportament irruptiu d'algunes espècies de pàrids. A partir de dades principalment bibliogràfiques i utilitzant un mètode comparatiu per tal d'incloure la informació filogenètica en els anàlisis, es va comparar el grau de territorialitat hivernal entre 7 espècies irruptives i 7 espècies no irruptives. Es van trobar diferències entre els dos grups pel que fa a territorialitat hivernal, però quan la fecunditat anual de les espècies es va incloure en els anàlisis, la relació va desaparèixer. Així doncs, la tendència irruptiva d'algunes espècies de pàrids no sembla directament relacionada amb la territorialitat hivernal si no estar indirectament associada amb la major fecunditat de les espècies no territorials. El major esforç reproductor de les espècies no territorials suggereix que aquestes es veuries més fàcilment involucrades en irrupcions després de temporades de cria molt exitoses. Els resultats de l'estudi suporten la idea que la tendència a realitzar irrupcions és una característica associada a la capacitat reproductora de les espècies i per tant a les seves històries evolutives. La variació en la disponibilitat d'aliment seria només una causa pròxima que permet una alta supervivència dels joves que es veuen involucrats en la irrupció.

CONCLUSIONS PRINCIPALS

1- El sistema social hivernal de la Mallerenga petita no sempre inclou l'ús exclussiu dels dominis vitals per part de les unitats socials o grups. Malgrat ser emmagatzemadora, la població d'elevada densitat estudiada als boscos subalpins dels Pirineus va mostrar un sistema social molt laxe mancat de qualsevol tipus d'estructura territorial típica.

2- L'organització social de la Mallerenga petita als boscos subalpins estudiats es centra al voltant de les parelles adultes que han criat amb anterioritat a l'àrea. Alguns juvenils eren parcialment residents amb àrees de deambulació que es solaparen extensament amb les d'altres joves i amb els de varies parelles adultes. De tota manera, la major part de juvenils detectats en l'àrea d'estudi aparegueren com a transeünts atrets segurament per la gran quantitat d'aliment disponible a la zona. L'agrupació, bàsicament d'individus joves, va donar lloc a grans flocs, molt inestables i de composició variable.

3- La senyalització d'estatus basada en la taca negra del pit de la Mallerenga petita és utilitzada en algunes condicions per determinar el resultat de les interaccions agonístiques entre individus. Els individus utilitzen els mecanismes de senyalització d'estatus en casos de manca de coneixement i experiència prèvia amb els rivals. Així doncs, la importància d'aquest mecanisme és predible que sigui elevada en el cas de les grans associacions individus en la Mallerenga petita, molt inestables i de poca cohesió.

4- L'emmagatzemament és un factor clau en la determinació dels sistemes socials durant l'època no reproductora. En cas de forta adversitat ambiental, l'emmagatzemament afavoreix, en termes de supervivència, les estratègies sedentàries i territorials de manera que aquest comportament afecta indirectament els beneficis de les diferents opcions d'establiment disponibles pels joves després de la seva independència. De tota manera, l'emmagatzemament és un factor important, no L'ÚNIC factor, darrera de la variació observada en l'estructura dels sistemes socials en Pàrids.

5- Durant l'hivern, la plasticitat en el comportament és important a l'hora d'enfrontar-se a períodes adversitat ambiental i estrés energètic. La plasticitat en l'ús de diferents substrats d'alimentació permet als individus ajustar els requeriments energètics a l'obtenció d'energia necessària.

6- Els períodes d'estrés durant l'hivern juguen també un paper important en l'establiment de patrons de segregació espacial dels individus en el flocs de mallerengues. A més en aquests períodes, la segregació en el microhabitat d'alimentació entre individus de Mallerenga capnegra s'ajusta als patrons d'emmagatzemament descrits per a la mateixa població durant la tardor.

7- En condicions de baixa competència intraespecífica, i possiblement baix risc de predació, la morfologia dels individus joves juga un paper important en l'elecció d'un microhabitat d'alimentació en els arbres. En aquestes condicions, els ocells més pesats tendeixen a ocupar les parts més interiors dels arbres, mentre els individus més lleugers s'alimenten en les parts externes i altes de les capçades.

8- Com els joves de Mallerenga capnegra es veuen obligats a ocupar les parts més externes dels arbres en condicions d'estrés ambiental, situen les reserves alimentàries en forma d'emmagatzemaments en aquestes zones. En temps benigne, quan els joves són lliures d'escollir els llocs d'alimentació, els individus opten entre l'ús d'un microhabitat potencialment perillós i els beneficis d'utilitzar aquestes zones per realitzar una reserva d'emmagatzemaments considerable i energèticament el més barata possible.

9- L'emmagatzemament de menjar difereix entre poblacions de la mateixa espècie subjectes a diferents condicions competitives i ambientals. En una població a Noruega, les Mallerengues petites emmagatzemaren en les parts altes i més exteriors dels arbres, mentre que als Pirineus les Mallerengues petites ho van fer en les parts interiors i baixes dels pins. Una pressió competitivada major i un baix grau de residència en la població Noruega sembla forçar als individus a utilitzar els llocs més exposats per emmagatzemar, possiblement com una alternativa a l'acúmul intern de greix. Per altra banda, per emmagatzemar, les Mallerengues petites en els Pirineus van utilitzar les parts interiors de les capçades, que van ser les zones utilitzades més intensament en períodes de temps advers. Així doncs, en els Pirineus, els individus podrien utilitzar els emmagatzemaments en una perspectiva temporal més llarga per tal de disminuir la variació en la disponibilitat d'aliment relacionada amb el temps advers.

10- Dins d'una mateixa població Pirinenca de Mallerengues petites es trobaren patrons d'emmagatzemament, a grans trets, similar als regionals. Els individus adults residents emmagatzemaren més sovint en les parts interiors dels arbres que els ocells joves tant si eren residents com transeünts. Com els emmagatzemaments realitzats en les parts interiors dels arbres van trigar més a ser realitzats i es van localitzar més lluny de l'origen que els realitzats en les parts exteriors, es suggereix que els emmagatzemaments difereixen en el seu ús futur i en el seu valor de supervivència per als individus.

11- L'anàlisi del comportament d'emmagatzemament a nivell individual va mostrar que les Mallerengues petites emmagatzemen aliment malgrat traslladar-se sovint en grups de mida considerable. De tota manera, els individus van escollir el moment i la localització de l'emmagatzemament amb cura. Van evitar la presència d'individus molt propers, però van emmagatzemar uniformement al llarg del dia. Els adults residents concentraren els emmagatzemaments al voltant del centre de les seves àrees de deambulació. D'aquesta manera, les Mallerengues petites reduirien les amenaces immediates als emmagatzemaments i farien minvar la probabilitat de robatori dels emmagatzemaments.

12- Les històries de vida dels pàrids són parcialment afectades per les limitacions indirectes imposades per la socialitat hivernal. Els sistemes territorials tancats i les limitacions associades, en termes d'establiment juvenil, s'associen amb una reducció de la fecunditat de les espècies. La hipòtesi, recolzada pels resultats, senyala que la reducció en la fecunditat de les espècies (ex. mida de la posta i percentatge de segones postes) és beneficiosa ja que s'associaria amb un estalvi de temps que afavoreix el ràpid establiment dels joves en un sistema social tancat. Com es va predir, les espècies menys territorials, amb absència parcial de les limitacions derivades d'un ràpid establiment en grups territorials, presentaven fecunditats més elevades que les espècies més territorials.

13- La tendència irruptiva d'algunes espècies de pàrids no està directament relacionada amb la territorialitat dels sistemes socials durant l'època no reproductora. Els anàlisis realitzats mostraren que la major fecunditat associada amb l'absència de territorialitat sembla el factor que més influencia el comportament irruptiu en aquest grup de passeriformes. Així doncs, les espècies amb una fecunditat major es veurien més fàcilment involucrades en episodis irruptius quan alguna variable externa (ex. disponibilitat d'aliment) facilita la supervivència dels individus i/o la producció de descendents involucrats posteriorment en una explosió demogràfica.

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WRITING OF A THESIS : A PRACTICAL APPROACH[9]

INTRODUCTION

Reaching this part of the thesis is, believe me, a great achievement. It makes you become melancholic by remembering all the strange things that have happened while you were trying to add a tiny new piece of knowledge to our understanding of nature (sometimes I still wonder if I have succeed at all in that). Anyway, I have written a thesis. This is not going to change any world structure, and very likely it is not going to change people's way of life either. However, I HAVE written a thesis and my view about this event can theoretically (I am not sure in practice) be of interest to someone. At worst, some people could identify familiar experiences at several of the stages that my thesis crossed irremediably.

So, the next words, are not as serious as the rest of this book (as if the rest was indeed serious) but not less real or exact. They are the basic steps that a common thesis needs and has (almost inevitably) to follow...

BEFORE ANYTHING

When something happens in our present, there was a time before when it was nothing else that a point in somebody's potential future. The origin of everything is located in a strange and far country located nearby or maybe beyond, the North Pole. Finland. There, as innocent exchange Erasmus student, I got in contact with science (which is a bit sad after 4 years thinking I was already in contact with such a thing, I am not sure whom to blame that for, but I have my suspicions). I met the Evolutionary Biology Group of the University of Oulu and I learnt simple things such as beginning to think by myself (I mean in terms of scientific reasoning, in other fields I still wonder if I am able to...), going into the library because I felt it necessary or being interested in what was going on in science lately.

Markku Orell showed me the way to carefully plan my research and also tele-supervised this thesis from the far side. Thanks for being so kind to a common Catalonian hullivili like me. Well, Kari, Seppo, Kimmo, Petu, Mikko, Jukka, Pasi, Claudia and so many others saw my first steps as a researcher (another topic is if I ever will be able to go much further from that). And I met tits (as study objects) for the first time. And that is worth notice.

After my stay in Finland, things did not promise to be quite easy. But Jacint Nadal was there. His kindness and huge scientific background add what it was needed at that stage and later ones. He was always there when anybody need him to be (he was there and also his famous notebook, with millions of friend names). Just present a problem to him, hear "just a moment..." wait just a moment and the problem is gone somewhere else. The thesis (well, a raw project of it) had been born.

THE FIRST STEPS

Once something has started you have to let it go forward profiting the initial inertia. And, so I did. First, you need some ideas, one (at least) study area and if possible somebody to work with. In my particular case, the ideas were so vague that better you read now in the present shape, in earlier chapters of this magnificent book. The main study area was located in a Natural Park, wonder why? And at the beginning, I even had a kind of working group. And I greet Raimon Mariné and Jose Luis Copete for that, and for teaching me some of the first but not last lessons on how difficult is to live in a social human environment without problems emerging. But the group was reborn again with Juli Broggi and lately with Sergi Herrando. Working days with Juli taught me how hard is to reach conclusions from nice ideas and how enriching is to discuss them with somebody. Laura...Laia....Karina, even Xavier sometimes... they helped me with some of the lab work and I thank them for being also work mates.

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[9] I mean acknowledgements...

THE STUDY SPECIES

What can I say about one's study object. They are essential in any paper anybody has ever published...and they are so often neglected. I will remember mines with love and melancholy. Tits...First sorry for all those things that in name of science (and mine) fucked up precious moments of your busy life. Sorry for collateral casualties, they were few, but felt deeply. To they I owe all the data obtained, the mushrooms I found following tit groups, all those hours of innocent sleep waiting for you to do something. Thanks for making forests in winter so lively. Well, the study objects, a classic...take a reference book and describe yours.

THE DEPARTMENT

During these thesis years, which seem to me many more than really are, there are a couple of special sites that will be forever linked to. One is the "Department". Hundreds (or it seems to me) of people working on particular, sometimes close to secret, topics from small to rather big living beings. Seminars might increase scientific interactions among the "Department" members, although to be successful I suggest them to be moved to the Bar, where the costs of social interactions may be reduced, thus making communication easier.

I think some persons at the department have some kind of specific soul for scientific reasoning I will always run after. Juancho and his monologues, Dani and his invasive study objects, Roger and his parasitic study interests or Sergi and his unreachable warblers. But the Dept. was always boiling of people around you. Eulalia, my, proportionally, most common room mate, Miquel, Alex, Noelia, Diana, Rosa, Joan, Santis, Gustavo, Xaviers, Domingo (... aiii, the sandal stick...), Eli, Miquel, Pep, Toni, Jacob, Dani, Mari, Enric, Giovana, Miguel Angel, Victor, Jordi, Joan Carles, Jorge, Marc, Lena, my bike...and so many others I also greet for all those never ending months of working together at the dungeons of the "DEPARTMENT".

THE STUDY AREA...S

What about knowing by heart every single curve of the road that goes to the subalpine coniferous forests where tits happily inhabit. Or knowing personally almost every single tree where birds forage and every now and them hoard on, almost every piece of grass... In the Pyrenees winter days passed quickly due to the kindness of the people of Ecos the Barna, Carles, Guadalupe, and Estela. At Coll de Pal, they offered me a warm place to stay and sometimes they even fed me instead of the crows. Fortunately, I could also sleep at the five star bedroom of the office of the Cadí-Moixeró Natural Park. TV, attached toilet, photocopy machine...the staff of the Park, Jordi, Ramon, Santi, Fina, Angels, Carme and Montse made the stay in the wild mountains far easier than otherwise would have been. Thanks to them all, Coll de Pal will remain forever as apart of me, sniff, sniff...

Field work in Finland was not easy either and I thank all those who borrowed me warm clothes anytime to withstand those thousands of negative degrees of wild boreal forests. The days with company were far funnier than those without, so the people who were brave enough to come with me, during winter, merit an special mention here...they were very few, that is also true (do you remember Oriol, Arnau, Audrey...). Luckily at least, Finish Universities are nice and equipped with a warm shower...

THE CONFERENCES AND COURSES

I did not think about this when I started this project but I admit that I know the planet we inhabit much better now than four years ago...and most of this is due to the courses and above all conferences, organised as far from each other as possible, meant to discuss really serious matters. These were related most of the times to very interesting subjects such as the mating choice of University girls according to the odour of University boys...well it was nice to take some fresh air every now and then. And in the courses I learned also a lot...thanks to Pilar, Jose and Lali for the Ventorrillo course where I met so many nice people...

THE SOCIAL ENVIRONMENT

By yourself you are nobody, scientifically even less so. But socially one is still very little. So what I tried to do is having people around. Some of them, quite often might be assign to the “friend” category.

I am not going to go further in this point because this is not the place to list all my friends, nor those who I think they are, nor those who think they might be. But I just want to refer to some of them for being special at some times. My several trips to Finland have something in common in addition to snow: David and Raquel. Just keep going and try not to be out of the road. And I thank also Bettina for believe in me and what I was doing when I was looking for what it was left from me after a kind of emotional crash. The list of people who made Finland unforgettable is unbelievable never-ending.

In Catalonia, the list is, how to say, even longer but referring to the CEC and the U.C.B. (Unió de canalles de Bellvitge) environments makes things a lot easier. I thank specially Cel.li for believing in me also when I think, I did not.

I do not know if this is the right place to include anything about a dog. But Tukka was with me in so many moments relieving me from the loneliness of the last months of the thesis story that it merits worth to be noticed. You are indeed a very obedient dog, even if you are always told that.

Family is essential, first because I owe my parents something very special: being. I also share with them a good deal of my genotype. In addition to that I have received everything from them. And that is a lot. So thanks for everything you have done, and for being so patient to me. Above all thanks mama i papa.

And the last piece of a typical social environment... in my case Laia has been so important for me that sometimes I have hardly realised about the importance of what was around this thesis. I still wonder if it has any. But I am completely sure about her importance in my life. Thanks for making me feeling so alive...and for making the impossible to improve my incredible Catalan translation of the discussion of this thesis... and also for being my successful assistant in artistic and design matters...and...

CLOSE TO THE END

Time flies. Then one day you realise that your scholarship is approaching the end, in few months. Your life is then close to the edge for some time (this may be worse if you do not even have a scholarship...). And then you have to write a nice introduction and even a nicer discussion to make the rest of you story a bit more coherent and something believable...Then the members of the tribunal are selected among the best researchers in your field (thanks to them all), choose one day and....what else can I say...?

The last step is already what you have right now in your hands. Cute, isn’t it ? You might think that is not too much. But beyond your opinion, there is a story behind this book, a piece of somebody’s life, in this case it happens to be mine.

Ah, I forgot to mention all those that helped me with the manuscripts either with the English (funny language, thanks Robin...) or with science. Here I thank Svein Haftorn for his incredible help in one of the papers ...and in this last point I included also all those referees, many of them anonymous (like the Spanish romance), who improved, I recognise it, significantly the quality of what I was about to say. I double thank those who were positive in their critics and lead to the acceptance of the manuscript in a ‘serious’ journal.

I am completely sure I have forgotten someone. It could even be that it is someone important for me or for the thesis. So from the deepest of my heart I greet the unknown helpers whose help has been so sadly neglected by me. Thanks and sorry...

WHAT THE FUTURE WILL BRING

Ah, the future, an obscure word whose meaning was probably invented by hoarding tits and later made more perfect by human beings. Mine is indeed dark at the moment, but let's see, light appears, if look for it hard enough, or you have luck and happen to find a lamp...well, I thank André Desrochers, Louis Imbeau and company for their help and suggestions in my stay ...au Québec.

OFFICIAL GREETINGS

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