Locomotion patterns of foraging Coal tits *Parus ater* in a coniferous forest

Lluís Brotons

The use of alternative searching movements may involve different energetic costs. Therefore, birds may gain some advantage by using foraging techniques that permit a reduction in total energy expenditure. In a mountain coniferous forest the movement patterns of Coal Tits were studied by monitoring birds' foraging behaviour with the objective of detecting possible selection patterns in the relative use of different searching movements that differ in their energy costs. In particular, it was expected that different searching movements would not be used at random and would instead correspond to an energy-saving strategy. When foraging in tree canopies, birds moved more often on a horizontal axis than on a vertical one. The relative use of different locomotion modes depended on the direction taken by the bird. Individuals hopped mainly to move upwards, whereas flight – more costly in terms of energy than hopping – was used more frequently in downward than in upward movement. The reduction of energy consumption through selective choice of searching movements may allow birds to reduce their total energy requirements or to allocate more energy to other daily activities, thereby improving their individual fitness.

Key words: Coal Tit, *Parus ater*, energy budget, forest birds, locomotion modes, mountain coniferous forest.

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Received: 08.10.07; Accepted: 02.02.08 / Edited by J. Quesada.

The exploitation of the environment is a widely studied topic in birds and most such studies deal with foraging behaviour and the use of feeding resources (Pyke 1984, Stephens & Krebs 1986). Birds have to balance energy intake and energy consumption in order to survive and so the different factors that influence this process are studied as mechanisms used by birds to optimise foraging activities (Royama 1970, Smith & Sweatman 1974, Krebs *et al.* 1978, Moreno *et al.* 1988, Dall & Witter 1998). Searching techniques employed by birds – especially when costly in terms of energy – play an important part in their energy balance (Norberg 1977). Individuals choose between different foraging techniques and the use of these alternative searching movements may imply different energy costs (Norberg 1977, Matthysen 1990). Thus, birds may gain some advantage by using techniques –or a combination of techniques– that permit a reduction in energy expenditure (Goldstein 1990). Norberg (1981, 1983) showed that birds foraging in trees by vertical climbing or hopping (i.e. treecreepers and woodpeckers) are expected to minimise their energy consumption by means of selective choices of movement patterns. The most economical locomotion pattern seems to be to move upwards in trees by hopping or climbing and then downwards mainly by flying, which is a more costly technique. Norberg argued that for birds that also move vertically upwards within trees by flying the choice of optimal locomotion modes becomes less clear. However, bearing in mind the high energy costs of flying (Tatner & Bryant 1986, Carlson & Moreno 1992) and the poten-

tial benefits of energy saving, birds that also move vertically in trees by flying are not expected to use the different locomotion modes available to them at random. Rather, I predict that individuals use less costly searching techniques more often when going upwards than when moving downwards. In this latter case, the action of gravity would minimise the costs of more expensive movement types that would be used advantageously (Norberg 1977, 1981).

In order to test this prediction, I studied movement patterns of the Coal Tit *Parus ater* in a mountain coniferous forest in the Pyrenees. Birds foraged on pines by hopping and flying, locomotion modes which were checked for random use or selective choice. To my knowledge, this is the first field study that attempts to test Norberg's predictions in a wild bird that often uses flight in a vertical upward direction.

Material and methods

The study area (ca. 150 ha) was located in the Cadí-Moixeró Natural Park, (Pyrenees, NE Iberian Peninsula) at an altitude between 1800-2100 m a.s.l. Mountain pine *Pinus uncinata* dominates the study area, although Scots pine *Pinus sylvestris* becomes dominant on south-facing slopes and at lower altitudes. The understory is sparse and is dominated by *Juniperus communis* and grasses (Vigo 1976). Until recently the forest was exploited in a long-term cycle and as a result tree stands of different ages are found in the area.

The Coal Tit is a small forest passerine (body weight 9.5 g) that forages in tree canopies by inspecting needles and branches in search of small invertebrates and coniferous seeds. The main searching movements used are hopping and flying, but not walking (Cramp 1993, Brotons 1997).

Foraging behaviour was monitored in August and September 1996. On data-collection days I walked through the study area searching for tit flocks. When I located a flock, I recorded searching techniques of birds by continuously following focal individuals (Robinson & Holmes 1982). The sampling of focal individuals started five seconds after the bird was located on the tree. I defined a searching movement as any change in position made by a bird that was searching for prey. The number of hops, short distance flights (<20 cm) and long distance flights (>20 cm) were recorded as searching movements. I noted the direction of any searching movement by observing the final position of the bird in relation to the start of the movement. Upward movement was defined as any movement in which (a) the final position was higher than the original position and (b) the bird followed an angle of less than 35 degrees with respect to the vertical of the tree. Oblique upward movement was defined as any movement in which (a) the final position was higher than the original position and (b) the bird followed an angle between 35 and 70 degrees with respect to the vertical. Horizontal movement was defined as any movement that did not involve an angle change of more than 20 degrees with respect to the horizontal. Downward and oblique downward movements were defined in the same way as upward movements with the difference that they involved a final position that was lower in the tree than the original position (Figure 1). Thus, according to the direction

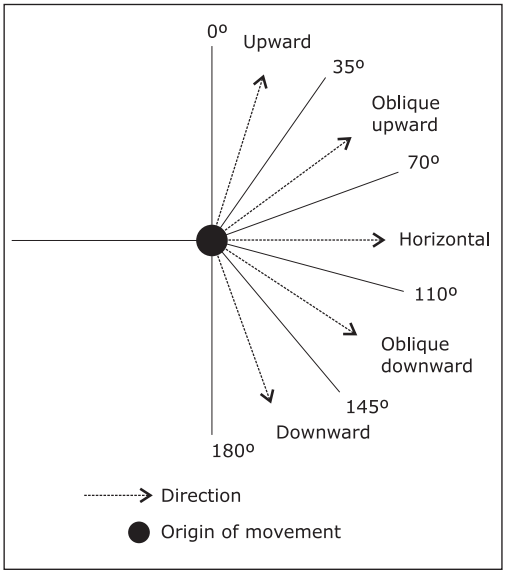

Figure 1. Diagram showing how searching movements of birds foraging in tree canopies were divided into five different categories according to the direction taken from the origin of the movement.
Diagrama que mostra com els moviments de cerca d'aliment dels ocells a les zones de coberta forestal van ser dividits en cinc categories d'acord amb la direcció escollida des de l'origen del moviment.

taken, I divided each of the three main searching movements used by birds into five categories. Such a broad categorisation is necessary because, due to the rapid movement of birds in trees, the direction of displacements can only be recorded approximately. However, these five categories are easily identifiable in the field and because only one previously trained observer collected all the data, errors in direction estimates are likely to be unimportant. Each sequence ended when the bird was lost from sight.

Data was collected from non-ringed birds. In order to avoid pseudoreplication (Leger & Didrichsons 1994), I changed the observation flock after an individual –defined as the primary sampling unit– had been followed. For each individual, I took from one to four sequences of data and used in the analyses the mean values of the variables. These analyses only included foraging sequences longer than 60 seconds ($\bar{X}$=134 s, SE=12.9) that were long enough to minimise the effect of individuals foraging in restricted areas. Sequences were collected between 8:00 and 14:00 hours under similar temperature and wind speed conditions, two environmental factors that may influence the use of space by forest birds (Grubb 1979). In total, 24 individuals were followed with a total of 3,124 seconds of observations. The main substrates and the height of the trees used by birds were also registered for each sequence.

In order to compare the relative use of different searching methods and movement directions, variables (number of searching movements/unit time) were converted to proportions relative to the total number of movements for each movement type and each individual. I used analyses of repeated-measures variance (ANOVA) to compare means after error variances had been homogenised by arcsin transformation (Zar 1984). The hypotheses under study were tested by analysing the interaction

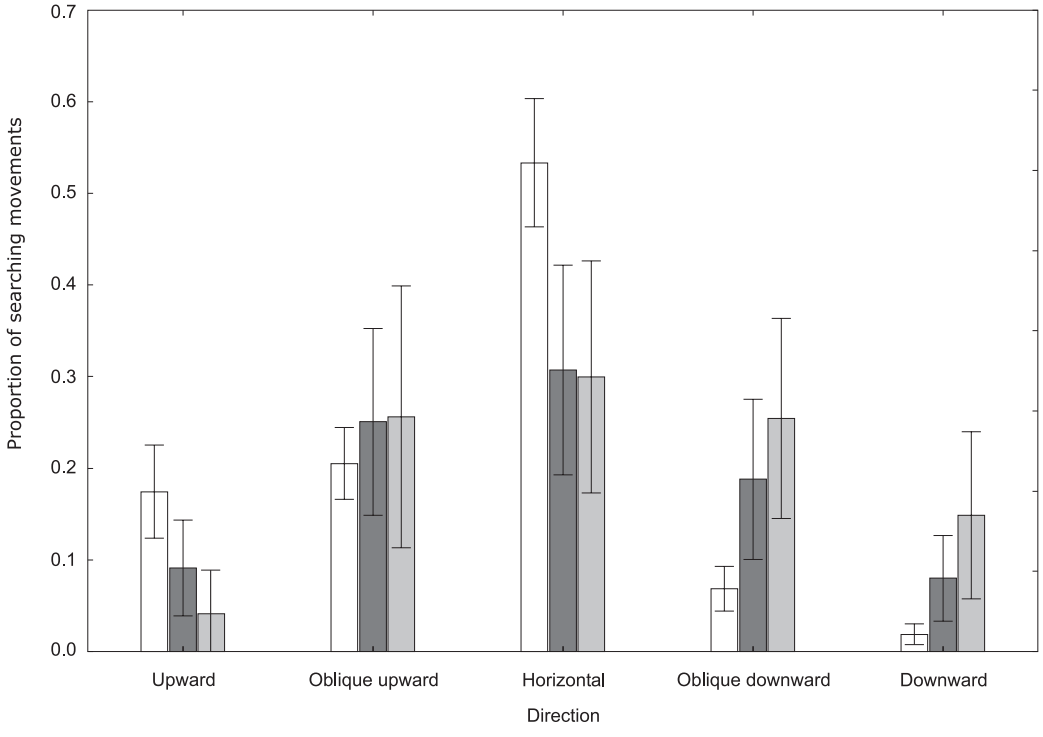

Figure 2. Frequency use of the different locomotion modes according to the direction taken by birds. Bars represent standard errors.
Freqüència de l'ús de les diferents maneres de locomoció d'acord amb la direcció escollida per l'ocell. Les barres representen els errors típics.

term in the ANOVA with searching method and movement direction as the main within-subject factors. A significant interaction term would indicate a selective choice in the searching method according to the direction of movement.

Results

Coal Tits used mountain pines that were around 12 metres high (SE=1.2), foraging mainly on needled twigs (50% of observations) and twigs (30% of observations), as has been previously widely described for this species (Cramp 1993). Analyses of searching patterns showed clearly that birds did not use different locomotion modes at random; rather, birds made consistent choices of locomotion modes according to the direction of movement involved.

Firstly, Coal Tits moved horizontally more often than they moved vertically (Direction, $F_{4,92}=21.81$, $p<0.001$, Fig. 2), but did not use any one movement type more often than any other (Movement type, $F_{2,46}=2.09$, N.S., Figure 2). Secondly, the relative use of each searching method varied according to the movement direction used by individuals (Interaction term, $F_{8,184}=4.49$, $p<0.001$). In particular, Coal Tits appeared to use hopping mainly as an upward and horizontal movement type (Figure 2). In terms of downward direction movements, the relative use of flights was considerably higher than the use of hopping ($F_{2,46}=6.2$, $p<0.05$), and the change in the relative use of different movement types seems to be mainly the result of the little use individuals made of hopping as a downward movement (Figure 2). Furthermore, the total number of long-distance flights in a pure downward direction was significantly higher than the number of flights in a pure upward direction ($F_{4,92}=3.18$, $p<0.05$, Figure 2). Although there was a significant difference in the use of vertical directions taken by birds when using flight for short distance displacements ($F_{4,92}=5.03$, $p<0.05$), this was due to a greater use of horizontal than either downward or upward flights.

Discussion

During late summer and autumn Coal Tits usually forage in tree canopies among needles and twigs as they search for small arthropods. In our study area, individuals did not make random use of locomotion modes. Birds have to forage through canopies by careful horizontal and vertical travelling and Coal Tits make different use of locomotion modes depending on the direction of travel involved. Horizontal movements were more common than vertical ones and involved the three types of locomotion recorded in this study. When moving in a vertical sense, birds employed hopping almost exclusively for going upwards, used short flights indifferently for going up or down within canopies, and travelled longer distances by flight more often in downward than in upward displacements. Why do individuals use this pattern of locomotion that involves making a selective choice of the movements and directions available? According to foraging theory, birds should balance intake rates and foraging costs in order to optimise foraging (Stephens & Krebs 1986, McNamara *et al.* 1994, Bautista *et al.* 2001). Because the energy cost of locomotion for some foraging birds may easily be equivalent to 5-10 times (or even higher) the basal metabolic rate (Moreno *et al.* 1988, Carlson & Moreno 1992), the searching techniques used by birds may have a significant influence on their energy balance (Goldstein 1990). Birds have to choose from among several search and pursuit methods that consist of various locomotion modes associated with different metabolic energy costs and efficiencies (Maccarone & Brzorad 2007). Dall and Witter (1998) have shown that under unpredictable feeding regimes, Zebra finches reduced the relative use of highly costly activities rather than use fat accumulation strategies in order to balance their energy budget, thereby reducing their overall energy consumption. In forest passerines it is widely known that flight is energetically very costly and more expensive than hopping (Tatner & Bryant 1986, Carlson & Moreno 1992). Thus, if somehow birds are energy limited (Polo & Bautista 2002), I expect birds to use searching behaviour that minimises locomotion costs by reducing the number of flights and situations when flying is more expensive (i.e. flying upwards is more costly than flying downards due to the action of gravity). From this point of view, birds may save energy without decreasing their searching efficiency by climbing up trees by hopping (i.e. increasing

their position in trees) and then by losing height by flight (Norberg 1981, 1983). Other things being equal (i.e. efficiency of searching movements) and whenever possible, individuals moving upwards vertically would benefit from the use of hopping because it is energetically cheaper than flight.

My results suggest that long-distance flights are the movements chosen by individuals to return downwards in order to restart searching sequences (Norberg 1981, 1983). Coal Tits move among the outer parts of trees where hopping is often not possible and only short flights allow displacements to be carried out. Norberg (1981) argued that in such cases (i.e. birds having to move vertically by flying and not only by hopping) optimal movement patterns would be difficult to predict. Nevertheless, this study suggests that the main features of energy saving by choice of movement patterns can also be applied to these cases because birds may still gain some benefits from a non-random use of locomotion modes when choice is possible. Even when some energy saving may be achieved, other factors such as predation pressure (Matthysen 1989), variation in food location (Moreno & Carrascal 1993, Brotons 1997, Elchuck & Wiebe 2002) and competition with other species (Sorensen 1996) may favour individual behavioural plasticity and thus act against a further minimisation of energy expenditure through optimal movement patterns, as in the case of treecreepers. The reduction of energy consumption may allow birds to reduce their overall energy consumption or to assign to other activities such as vigilance, cleaning or moulting some of the energy that otherwise they would have allocated to searching and foraging (Lima 1990, Suhonen 1991). As a consequence of the possible fitness value gained, I expect that more often than hithertho believed the choice of movement patterns by birds may become an important way by which individuals optimise energy balance.

Acknowledgements

I would like to thank the staff of the Cadí-Moixeró Natural Park for their help in the of the study area. Earlier drafts of the manuscript were improved by Domingo Rodríguez Teijeiro, Ake Norberg and an anonymous reviewer. This study was supported by a grant from the Cadí-Moixeró Natural Park and a grant from the Comissionat per a Universitats i Recerca de la Generalitat de Catalunya.

Resum

Patrons de locomoció de la Mallerenga Petita *Parus ater* en un bosc de coníferes

L'ús de diferents moviments de cerca d'aliment pot implicar diferents costos energètics. Per tant, els ocells poden obtenir avantatges mitjançant l'ús de tècniques de cerca d'aliment que permetin una reducció de la despesa energètica total. En un bosc de coníferes i a través de l'observació del comportament d'alimentació, es van estudiar els patrons de moviment de la Mallerenga Petita amb l'objectiu de detectar possibles patrons de selecció en l'ús relatiu de diferents moviments de cerca d'aliment que es diferenciessin en els seus costos energètics. En particular, s'esperava que els diferents moviments de recerca no fossin utilitzats a l'atzar i s'ajustessin a una estratègia d'estalvi d'energia. Quan els ocells s'alimentaven a les cobertes forestals, aquests es van moure més sovint en l'eix horitzontal que en el vertical. L'ús relatiu dels diferents patrons de locomoció va dependre de la direcció presa per l'ocell. Els individus utilitzen principalment el salt en els moviments ascendents mentre que els vols, més costosos energèticament, són utilitzats més freqüentment en els desplaçaments cap avall que en aquells que es realitzaven cap amunt. La reducció del consum energètic a través de la selecció dels moviments de cerca d'aliment podria permetre als ocells reduir les seves necessitats totals d'energia, o d'assignar més energia a d'altres activitats quotidianes i millorar d'aquesta manera l'eficiència de l'individu.

Resumen

Patrones de locomoción del Carbonero Garrapinos *Parus ater* en un bosque de coníferas

El uso de diferentes movimientos de búsqueda de alimento puede implicar distintos costos energéticos. Por lo tanto, las aves pueden obtener alguna ventaja mediante el uso de técnicas de búsqueda de alimento que permitan una reducción del gasto energético total. En un bosque de coníferas y a través de la observación del comportamiento de forrajeo, se estudiaron los patrones de movimiento del Carbonero Garrapinos con el objetivo de detectar posibles pautas de selección en el uso relativo de diferentes movimientos de búsqueda que se difereciasen en sus costos energéticos. En particular, se esperaba que

diferentes movimientos de búsqueda no debieran ser utilizados al azar y debieran ajustarse a un estrategia de ahorro de energía. Cuando las aves forrajearon en las cubiertas forestales se movieron más a menudo en el eje horizontal que en el vertical. El uso relativo de los diferentes patrones de locomoción dependió de la dirección tomada por el ave. Los individuos utilizaron principalmente el salto en los movimientos ascendentes mientras que los vuelos, más costosos energéticamente que los saltos, fueron utilizados más frecuentemente en los desplazamientos hacia abajo que en los que se realizaron hacia arriba. La reducción del consumo energético a través de la selección de los movimientos de búsqueda de alimento podría permitir a las aves reducir las necesidades totales de energía, o asignar más energía a otras actividades cotidianas, mejorando de esta manera la eficiencia del individuo.

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