The structure of dominance hierarchies in the paridae: consequences for foraging efficiency and body condition

Jacqueline Marie Hay

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The Structure of Dominance Hierarchies in the Paridae: Consequences for Foraging Efficiency and Body Condition.

Jacqueline Marie Hay

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University of Durham

School of Biological and Biomedical Sciences

2003

This thesis is dedicated to the memory of

Prof. Peter R. Evans

(1937-2001)

For my Mam and Dad

"Good parents give their children Roots and Wings....Roots to know where home is, wings to fly away and exercise what's been taught"
--Jonas Salk--

The Structure of Dominance Hierarchies in the Paridae: Consequences for Foraging Efficiency and Body Condition.

Jacqueline Marie Hay **PhD** **2003**

In species that form social foraging groups during all or part of their lifecycle, individuals are subject to costs in terms of a higher frequency of aggressive interactions and having to share resources with group members, which must be outweighed by the benefits of flocking for all individuals concerned if it is to remain an Evolutionary Stable Strategy. In many group living species, dominance hierarchies exist that reduce the need for repeated agonistic interactions between the same individuals, which use valuable energy and may result in injury. Dominance hierarchies allow the most dominant individuals priority of access to contested resources whilst subdominant individuals may suffer as a consequence. In this thesis, I examined how dominance hierarchies were structured in great tits, blue tits and coal tits and how dominance status affected an individual's foraging efficiency and body condition.

The food handling times or vigilance levels of great tits and blue tits were not governed by dominance status but dominant coal tits were less vigilant than subdominant conspecifics thus probably allowing more time for foraging and other social activities *i.e.* mate finding and territory defence. Though subdominant great tits did not suffer costs in terms of food handling times, they were affected more by interference competition when foraging in mixed tit flocks compared to dominant great tits. Using ptilochronology as a measure of nutritional condition, the results from coal tits in this study contradicted those of previous studies in that dominant coal tits had slower rates of feather growth and produced feathers that were shorter and less dense than subdominant conspecifics, possibly a cost of their high dominance. Feather growth rate in great tits and blue tits was not related to dominance status. The immunocompetence of adult great tits or blue tits was not governed by dominance status nor did great tit or blue tit nestlings show any relationship between their place in the brood competitive hierarchy and immuocompetence.

Declaration

I declare that the material contained in this thesis has not been previously submitted for a degree in this or any other university. All the work recorded in this thesis is entirely my own, unless otherwise stated.

Statement of Copyright

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Chapter 1

General introduction

1.1 General introduction

In many group-living species, dominance hierarchies exist that allow some high-ranking individuals priority of access to food resources (Ens & Goss-Custard 1984; Hake 1996; Carrascal *et al.* 1998), lower risk of predation (Hegner 1985; de Laet 1985) and a greater probability of producing more recruits into the breeding population (Arcese & Smith 1985; Komers & Dhindsa 1989). For subordinates, the advantages of group living are not as great as those experienced by dominant conspecifics, nonetheless, they remain within groups and probably have a higher chance of survival than if they were to forage alone (Hogstad 1987a, 2003). However, high dominance status has been shown to incur costs, mainly in terms of an increase in metabolic rate (Røskaft *et al.* 1986; Hogstad 1987b; Bryant & Newton 1994; Swaddle & Witter 1994; Witter & Swaddle 1994), which must clearly be outweighed by the benefits if dominance hierarchies are to remain an ESS (Evolutionary Stable Strategy) within group systems.

The Paridae are convenient for investigating how high dominance status can affect body condition and survival since they have been intensively studied in the past, providing a large amount of background information from which to base studies (Perrins 1965; for reviews see: Ekman 1989; Hogstad 1989; Lahti 1998). The majority of Parids are also relatively simple to capture since they are easily attracted to artificial food sources using direct flight paths at a height where mist nets can be erected in the right habitat. Because most tit species are robust, free-living birds can be captured, manipulated and returned to the wild with little affect on their survival. Many Parids also use nest boxes when they are made available (Perrins 1979), thus allowing studies of their breeding ecology to be carried out easily and less intrusively than in other species.

1.2 Study species

1.2.1 The Paridae

The Paridae is a family of 42-50 small to medium passerines commonly known as titmice which vary in size from the coal tit *Parus ater*, 110mm in body length and weighing 10g, to the tufted titmouse *Parus bicolor*, 155mm in body length and weighing 21.5g (Harrap & Quinn 1996; Snow & Perrins 1998). The Paridae are widely distributed throughout the northern hemisphere and Africa, but are absent from South America, Australia and Madagascar (Perrins 1979). They inhabit a wide variety of habitats including deciduous, coniferous and mixed woodlands as well as areas of human habitation (Snow & Perrins 1998). Most Parids feed predominantly on insects during the breeding season, which are supplemented during the winter, when invertebrate availability is much reduced, with seeds, nuts, fruits and berries. Many Parids are known to hoard food, especially seeds and nuts for use during the winter though they may also store slugs, caterpillars and aphids (which coal tits store as pellets of 20-50 aphids) (Owen 1945; Southern 1946; Gibb 1960; Perrins 1979). Winter flocking occurs to some extent in all Paridae and flocks may be heterospecific or homospecific. Both homo- and heterospecific flocks are usually governed by dominance hierarchies within and between species (heterospecific dominance hierarchies are usually determined by size) (Baker *et al.* 1981; Alatalo & Moreno 1987; Carrascal & Moreno 1992; Suhonen 1993). This study will consider 3 members of the Paridae, namely the great tit *Parus major*, the blue tit *Parus caeruleus* and the coal tit.

1.2.2 Great tit *Parus major*

The great tit is one of the largest and most widely distributed species of the Paridae family. They are abundant throughout many parts of Europe, NW Africa and Northern Asia where they mainly inhabit mixed woodlands but also commonly populate orchards, gardens and hedgerows (Harrap & Quinn 1996; Snow & Perrins 1998). In Britain, the great tit is a common breeder throughout the country, including Northern Scotland, and some of the outer islands (Harrap & Quinn 1996). The winter diet of great tits varies from that of other British tit species in that, because of their powerful bills, they can utilize the seeds of beech *Fagus sylvatica* and hazel *Corylus avellana*, which other *Parus* species have difficulty manipulating.

Great tits are known for timing their breeding to coincide with the peak in caterpillar abundance during the summer, which provides the majority of food items for the growing nestlings (Perrins 1965, 1979). It is not clear which environmental cues great tits may use to assess when to start breeding but it is suspected that it is linked to the environmental cues that cause caterpillars to emerge (Gibb 1950; Perrins 1979). During the breeding season great tits are territorial, defending an area where they forage which usually has the nest near the centre. The mating system of the great tit is monogamous though cases of bigamy have been reported (Gooch 1935) and one bigamy incident was observed during this study in that the most dominant male great tit in the hierarchy was observed feeding nestlings from two different nest boxes positioned 15 meters apart (both had small clutch sizes of 5 and 6 eggs). Great tits are typically hole nesters and usually lay clutches of 5-12 eggs which are incubated by the female for 13-14 days before hatching and being subsequently fed by both parents until the chicks are independent at 2–4 weeks (Perrins 1965; Harrison & Castell 1998). Second broods are not particularly common in deciduous woodland (5% of British pairs) and were not observed in this study but are more usual in coniferous woodlands (Perrins 1979; Harrap & Quinn 1996).

Following the break-up of family parties and juvenile dispersal during late summer and early autumn, great tits form foraging flocks close to their breeding territories which can become very large since no territory defence takes place (Hinde 1952; Krebs, MacRoberts & Cullen 1972; Ekman 1989). Great tit flocks are usually described as being unstable or semi-stable since smaller stable flocks merge to form larger temporary flocks on a daily basis (Järvi & Bakken 1984; Røskaft *et al.* 1986; Ekman 1989; Matthysen 1990). The smaller stable great tit flocks usually consist of an adult pair and up to eight juvenile birds of mixed sex (Matthysen 1990). Great tits usually begin to form pairs in January and if both partners from a pair that bred in the previous season survive, 67% of those pairs reform (Perrins & McCleery 1989). Mate retention allows birds to breed earlier in the following year (Matthysen 1990).

1.2.3 Blue tit *Parus caeruleus*

The blue tit has a restricted range compared to other *Parus* species, occurring throughout most of Europe and Western Russia (Perrins 1979; Snow & Perrins 1998). Blue tits are common throughout most of Britain, though are absent as breeding birds from Orkney, Shetland and the Outer Hebrides (Perrins 1979; Harrap & Quinn 1996). Blue tits mainly inhabit deciduous or mixed woodland and scrub but are also common in built up areas and gardens where they are regular bird table visitors. However in the northern limits of their range, they are found almost exclusively in broad-leaved deciduous woodland (Perrins 1979).

During the breeding season, pairs of blue tits defend territories beginning in April to mid-May in deciduous woodland where they preferentially nest (Harrap & Quinn 1996; Harrison & Castell 1998). Blue tits are generally monogamous but bigamy often occurs if environmental conditions allow (Snow & Perrins 1998) as was observed in two consecutive years during this study, with one male blue tit feeding two broods of nestlings in nest boxes that were 5 meters apart. Clutch sizes range from 7-13 eggs, are incubated by the female for 12-16 days, and the chicks are then fed on insects by both parents (Nur 1984a;

Harrap & Quinn 1996). Second clutches of blue tits are common in continental Europe but rare in Britain and were not observed during this study.

During the winter months, blue tits join mixed foraging flocks near to their original breeding or natal territory. The semi-stable and loosely organized flocks are thought to be similar to those of the great tit since the flock home ranges overlap to a large extent and no territory defence takes place, giving blue tit flocks the potential to become very large (Hinde 1952; Ekman 1989). However, the blue tit flocking system has not been as intensively studied as has that of other tit species and is not as well understood, so little work has been carried out on dominance hierarchies in blue tit populations (Matthysen 1990). It is known that blue tit winter flocks break up and territories are re-established in late winter with about 75% of pairs from the previous breeding season remaining together if they survive the winter (Matthysen 1990; Harrap & Quinn 1996).

1.2.4 Coal tit *Parus ater*

The coal tit is one of the British tit species that has an extensive range extending over most of the Palaearctic (Harrap & Quinn 1996; Snow & Perrins 1998). In Britain, the coal tit is present across most of the country though is absent as a breeding bird from the outer islands of Britain including Orkney, Shetland and the Outer Hebrides (Perrins 1979). Coal tits generally inhabit coniferous woodland, preferring spruce *Picea* sp. when available but are also common in deciduous woodlands and scrub. It has been suggested that the national population of coal tits is increasing due to the increase in commercial conifer plantations (Harrap & Quinn 1996). Coal tits feed on insects in summer and supplement their diet with seeds and nuts in winter, which they will hoard within their home ranges from June to December mainly in early morning (Harrap & Quinn 1996; Lahti & Rytkonen 1996). Though coal tits form flocks in winter, food hoarding can be adversely affected by the presence of other flock members depending on their distance from a hoarding coal tit (Lahti & Rytkonen 1996; Brotons 2000a).

The breeding season of coal tits in Britain begins from early to mid-April when they produce clutches of 8-11 eggs. The female incubates the eggs but the nestlings are fed on insects by both parents (Harrap & Quinn 1996). Though coal tits use nest boxes for breeding when available, they are often prevented from doing so by great tits and blue tits unless the entrance hole is designed specifically for coal tits (by being smaller). Coal tits are therefore less common than great tits or blue tits in nest box studies (Perrins 1979). During this study, only one pair of coal tits successfully used a nest box for breeding, another female was killed in the nest whilst incubating by a great tit which subsequently used the nest box.

The winter flocking system of coal tits has been described as consisting of adult pairs occupying relatively small home ranges and juveniles having home ranges which overlap with those of adults and other juveniles, resulting in an unstable flocking system (Brotons 2000b). Coal tits form temporary foraging flocks as groups aggregate at foraging sites and may move between sites as foraging groups. The lack of territory defence probably contributes to the instability of the flocking system of coal tits described by Brotons (2000b). At the end of the winter, when territory defence begins to take place, pairing occurs with previous years' pairs remaining together in 82% of cases (Matthysen 1990).

1.3 The formation of foraging flocks

All *Parus* species form social units or flocks during the winter which may contain two or more individuals and can either be temporary aggregations as in the coal tit or more stable and permanent flocks as in the willow tit *Parus montanus* (Hogstad 1989; Matthysen 1990). Other than those species that spend the winter as pairs, the flocks formed by most *Parus* species consist of a former breeding pair and a varied number of juvenile birds or widowed adults with the home range of the flock based around the former breeding territory of the adult pair (Hogstad 1989; Matthysen 1990).

Parid flocks are formed during late summer and early autumn following the break up of family parties and the juvenile dispersal period (Ekman 1989; Hogstad 1989; Matthysen 1990). Family groups usually break up within three weeks of the juveniles fledging due to adult aggression directed towards juveniles and aggression between juvenile siblings (Holleback 1974; Weise & Meyer 1979). Juveniles typically join mated pairs several territories away from their birth place and usually remain with these pairs and any other juvenile flock members throughout the winter until the flocks break up in late winter (Hinde 1952; Holleback 1974; Weise & Meyer 1979). Flocking facilitates mate finding for juvenile and widowed birds (Ekman 1979) as well as providing the advantages of group foraging (discussed in detail later). Some juvenile birds however, remain as floaters without joining a particular group, and drift between different flocks or territories throughout the winter, having larger home ranges than those birds that form flocks (Smith 1984; Hogstad 2003).

1.3.1. Benefits of joining foraging flocks

It has been demonstrated that the survival of Parids during winter is affected by the severity of the weather and the food supply (Perrins 1965; Grubb 1987; Grubb & Cimprich 1990; Verhulst 1992). The effects of harsh weather conditions or a poor and patchy food supply have been shown to be reduced when Parids form foraging flocks during winter in that survival is enhanced when individuals form foraging flocks (Krebs, MacRoberts & Cullen 1972; Lendrem 1984; Carrascal & Moreno 1992; Lahti 1998; for review see: Beauchamp 1998).

Two hypotheses, which are not mutually exclusive, have been proposed to explain why Parids and other animals form flocks. Firstly, detection of predators may be more likely when foraging within a group since there are a greater number of individuals searching for predators (Pulliam 1973; Powell 1974). Secondly, foraging efficiency may be improved within flocks because personal vigilance directed towards predators can be decreased (because there are more birds being vigilant) and individuals can benefit from food found by other group members (Krebs, MacRoberts, & Cullen 1972; Hogstad 1989; Matthysen 1990; Carrascal & Moreno 1992). Grubb (1987) demonstrated that great tits and blue tits formed flocks more readily when food was scarce and there was high predation pressure. However, when food was abundant but predation pressure was still high, birds were less likely to form flocks. Grubb (1987) therefore concluded that flocking behaviour was initiated mainly because of the benefits of increased foraging efficiency. Winter flocking is also known to facilitate finding potential breeding partners and allowing subordinate individuals to remain in optimal habitats (Ekman 1979).

The survival value for birds feeding in flocks has been demonstrated both by observations in the field and by laboratory experiments. Flocking has been shown to benefit flock members in that they may follow other individuals to a food source and therefore learn of its location (Waite & Grubb 1988; Ranta *et al.* 1996; Sasvári & Hegyi 1998; Marchetti & Drent 2000), they can spend more time feeding because they can reduce their vigilance (Lendrem 1984; Grubb 1987; Carrascal & Moreno 1992; Sasvári 1992), they can avoid places already exploited by others (Sasvári & Hegyi 1998) and they can decrease the risks of predation since overall vigilance is higher (Grubb 1987; Hogstad 1987c).

1.3.2 Costs of joining foraging flocks

Despite the considerable benefits of foraging within flocks, costs are imposed through the close proximity of individuals to each other during feeding. The increase in the number of encounters between conspecifics leads to an increase in the number of agonistic interactions, resulting in time being wasted on interacting, the possibility of being injured and an increase in personal vigilance directed towards aggressive conspecifics that may pose a threat (Pulliam & Caraco 1984; Waite 1987a, 1987b; Sasvári 1992; Ranta *et al.* 1996; Brotons 2000a). The costs of flocking may be considerable for subdominant individuals since vigilance directed at conspecifics is rank related with subdominants having to observe a greater number of birds that are dominant to them, to avoid being attacked, compared to dominant conspecifics (Ekman

1987; Waite 1987a, 1987b; Pravosudov & Grubb 1999; Smith, Ruxton & Cresswell 2001). For all individuals within a flock, higher competition levels for food than would be realized when foraging alone is another potential cost of group foraging since any food found by an individual will be utilized by many flock members which may eventually lead to patch depletion (Baker *et al.* 1981; Delestrade 1999).

1.4 Dominance hierarchies within flocks

Within the foraging flocks of most Parids, linear and usually stable dominance hierarchies exist between conspecifics (Baker *et al.* 1981; Arcese & Smith 1985; Hogstad 1987d; Lahti *et al.* 1996). Dominance hierarchies may also develop interspecifically in heterospecific foraging flocks usually depending on the body sizes of the species' involved (Carrascal & Moreno 1992; Suhonen 1993; Krams 1998a). Intraspecific dominance hierarchies are usually established during flock formation in late summer or early autumn and generally remain stable throughout the winter unless flock members disappear, in which case, their position in the hierarchy is filled by the individual immediately below in rank (Hogstad 1989). During flock formation in tufted titmice, juveniles that arrive in the flock earliest, following dispersal, are often more dominant than those that arrive later (Brawn & Samson 1983). Between conspecifics of most Parid flocks, it has been established that males usually dominate females and within the sexes, adults dominate juveniles (Hogstad 1987d, 1992; Lahti *et al.* 1996; Barluenga, Moreno & Barbosa 2001).

1.4.1 Benefits of high dominance status

The costs and benefits of foraging within flocks are not equal and dominant individuals typically gain more of the benefits than do subdominants (Baker *et al.* 1981; Hegner 1985; De Laet 1985; Ekman 1987). Dominant Parids have access to the best quality food resources and forage in the areas with the lowest predation risk. Evidence to support this has been provided mainly from studies on the willow tit which have demonstrated that subdominant individuals are prevented from using the upper half or the inner branches of coniferous trees by dominant adult birds, since these are the preferred feeding areas because of their low predation risk (Ekman & Askenmo 1984; Ekman 1986, 1987; Hogstad 1988). As a consequence of being forced to forage in higher risk areas, subdominants have less time available to them for foraging since they have to increase their vigilance in order to detect predators (Ekman 1987). Presumably as a result of having access to the better foraging areas, dominant flock members also have higher survival rates and therefore higher probability of being recruited into the breeding population than do subdominant flock members (Ekman & Askenmo 1984; Arcese & Smith 1985, Frank 1986). The benefits of having a high dominance status within foraging flocks have been recognized in great tits and willow tits by using ptilochronology. This indicates that dominant individuals can grow induced feathers at a faster rate than can subdominant conspecifics, because of their better nutritional condition (Hogstad 1992; Carrascal *et al.* 1998).

Baker (1978) stated that only dominant great tits increased their intake rate when foraging within a flock and that subdominants only benefited when food patches were large enough to allow them to feed. This raises the question of why subdominants should remain within foraging flocks. However, although subdominant individuals benefit from group foraging to a lesser extent than their dominant conspecifics, they do benefit from the need for lower rates of vigilance than they would experience when foraging alone (Ekman 1987; Hogstad 1988) and since most subdominants are juveniles (Hogstad 1992; Brotons *et al.* 2000), they can also learn about different foraging locations from the more experienced dominant adult flock members. Hogstad (1987a) demonstrated that when dominant individuals were removed from willow tit flocks, the survival rate of the subdominant birds was reduced, thus suggesting that dominant birds were increasing the probability of survival of the subdominant flock members. The benefits of flocking for subdominants were also indicated recently in the willow tit, in that floaters (birds that had no permanent flock membership) grew induced tail feathers at a slower rate than the lowest ranking flock members in the same habitat. This suggests that subdominant birds within flocks have a better nutritional condition than floaters and therefore benefit more from flocking than they would if foraging alone (Hogstad 2003).

The benefits of high dominance status may begin early in life since it has been demonstrated that nestlings with the highest competitive ability have higher growth rates (Nilsson & Svensson 1996a). It has also been reported that the most competitive nestlings can have greater immune function and therefore better body condition than less competitive nestlings (Hõrak *et al.* 2000; Fargallo *et al.* 2002). Since the largest nestlings are the first to fledge (Nilsson & Svensson 1996a; Nilsson & Gårdmark 2001) and juvenile birds that join flocks earliest, attain the highest dominance status (Brawn & Samson 1983), competitive ability in chicks may be important in determining future dominance status. It has been shown that juvenile carrion crows *Corvus corone* that had low competitive ability as nestlings, were those birds that became subdominant in flocks after fledging (Richner, Schneiter & Stirnimann 1989).

1.4.2 Apparent costs of high dominance status

Although dominant individuals within flocks benefit from a decrease in predation risk and higher foraging efficiency compared to subdominants and to what they could achieve when foraging alone, group foraging apparently also entails costs for dominant individuals, brought about by the need to maintain their high dominance status (Røskaft *et al.* 1986; Hogstad 1987b). It has been reported that dominant great tits and willow tits have a higher metabolic rate than the subdominant individuals from their flocks (Røskaft *et al.* 1986; Hogstad 1987b). For instance in willow tits, the metabolic rates of alpha males (the top ranking birds) were up to 25% higher than the lowest ranking birds of the same flock (Hogstad 1987b). It has been confirmed that the increased metabolic rate of alpha male willow tits is the result of being the highest ranking bird since, when alpha males were removed from their flocks, the beta males (the second-ranked birds) which replaced them, consequently increased their metabolic rates to a greater extent than did lower ranking individuals from the same flock (Hogstad

1987b). It is not known whether the increase in metabolic rate experienced by dominant Parids is enough to cause a detrimental effect on health or survival, although a similar study found that the energy balance and survival of dominant dippers *Cinclus cinclus* were not seriously affected by their increased metabolic rates (Bryant & Newton 1994).

A cost of high dominance status has also been demonstrated during feather growth in European starlings *Sturnus vulgaris*. During moult, dominant individuals produced primary feathers with a higher degree of fluctuating asymmetry than subdominant birds (Swaddle & Witter 1994; Witter & Swaddle 1994). Fluctuating asymmetries have been found to be stress-induced and result from the inability of an individual to produce a bilateral trait so that it is the same on either side of the body (Palmer & Strobeck 1986; Parsons 1990; Swaddle & Witter 1994). It was suggested by Witter and Swaddle (1994) that dominant individuals only benefited from their high dominance status when competition was high, since in their study, birds were kept in solitary confinement. This complements evidence from free-living great tits studied by Carrascal *et al.* (1998), which found that dominant great tits grew an induced feather at a faster rate than subdominants in an area with colder temperatures and lower food availability.

1.5 Aims and objectives

The overall aim of this study is to determine exactly how the above described dominance status is achieved in flocks of great tits, blue tits and coal tits, and how individuals benefit from their dominance ranks. Though tits have been the subjects of many studies that have shown dominant individuals to benefit from their high status, there are still gaps, particularly with regards to coal tits and blue tits. Seed handling times and interference competition have not been studied with regards to tits possibly because of the difficulties involved in observing these activities (tits tend to fly to areas with dense cover to handle food) (Walther & Gosler 2001). Ptilochronology has been carried out on great tits in the past but despite the ease of measuring feather growth rate in blue tits and coal tits, these species have not featured in ptilochronological studies. Studies that have investigated immunocompetence in birds have been carried out using great tit adults and nestlings. However, the effects of dominance status on immunocompetence have not been given much attention in nestling or adult great tits or blue tits. During this study, I aim to determine:

- how dominance hierarchies are structured in great tits, blue tits and coal tits with respect to age, sex and body size.
- whether conspecifics interact at random or whether they "choose" their opponents in a non-random manner.
- if a difference exists in the food handling times and therefore foraging efficiency of dominant and subdominant birds and whether this is related to their vigilance.
- whether great tits suffer from interference competition and if this is related to their place in the dominance hierarchy.
- if feather growth rate and apparent quality of tail feathers induced during the winter is related to dominance status in great tits, blue tits or coal tits.
- whether the health status of great tits or blue tits with regards to immunocompetence and health status is related to their dominance status.
- whether the competitive hierarchy within broods of nestlings is related to the health status of nestling great tits or blue tits.

Chapter 2

Study site and methodology

2.1 Study site

2.1.1 General description

All aspects of this study were carried out at West Hollingside (National Grid Reference NZ274405), an area of mixed woodland situated at the southern end of Durham City and forming part of Great High Wood. Great High Wood is a low maintenance mixed woodland with several rights of way, which belongs to the University of Durham. West Hollingside is the property of the School of Biological and Biomedical Sciences through which there are no public rights of way. It is unmanaged and its principal use is for undergraduate teaching purposes and ecological research projects.

West Hollingside (Figure 2.1) has a total area of 3.16 hectares and is bound on the north side by the University's Botanical Gardens, which support a wide range of native and non-native plants. Rough grazing, as well as a small sewage works at the south end, borders the south and west of West Hollingside. The latter backs onto a mature conifer plantation used as a vegetation tip by the Botanical Gardens. The east side of West Hollingside flanks Great High Wood. West Hollingside is the small wooded valley of a stream that flows in a southerly direction through the site (Rowarth 2000). The two valley sides separated by the stream will be referred to as the West area and the East area (Figure 2.1). The West area has an easterly aspect and the

East area has a westerly aspect, the latter valley side having a steeper gradient than the former.

2.1.2 West area

The western area of the study site has a total area of 1.52 hectares and has thirty nest boxes (density: 19.7 per hectare) that are suitable for great tits, blue tits and coal tits. This area supports mixed woodland that is approximately 30-40 years old (Rowarth 2000) which now has a closed canopy throughout most of the area but opening out considerably at the south end. Beech trees dominate the north end of the woodland mixing with Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* through the central area. The area's southern end is dominated by the conifers with the addition of oak *Quercus* sp, sycamore *Acer pseudoplantanus* and birch *Betula pendula.* There is a substantial understorey of holly *Ilex aquifolium*, bramble *Rubus fruiticosus* and willow *Salix* sp. throughout the woodland.

2.1.3 East area

The total area of the eastern side of West Hollingside is 1.64 hectares and supports 69 nest boxes (density: 42 per hectare). This area is dominated by broadleaves of mixed age, the main species including oak, ash *Fraxinus excelsior*, sycamore and birch with a few larch *Larix decidua*. The understorey, which is patchy in places, is denser than that of the West area and is comprised mainly of bramble, holly, willow, honeysuckle *Lonicera periclymenum* and rowan *Sorbus aucuparia*. Overall, the East area is of uniform structure and species richness throughout with an open canopy particularly at the north end.

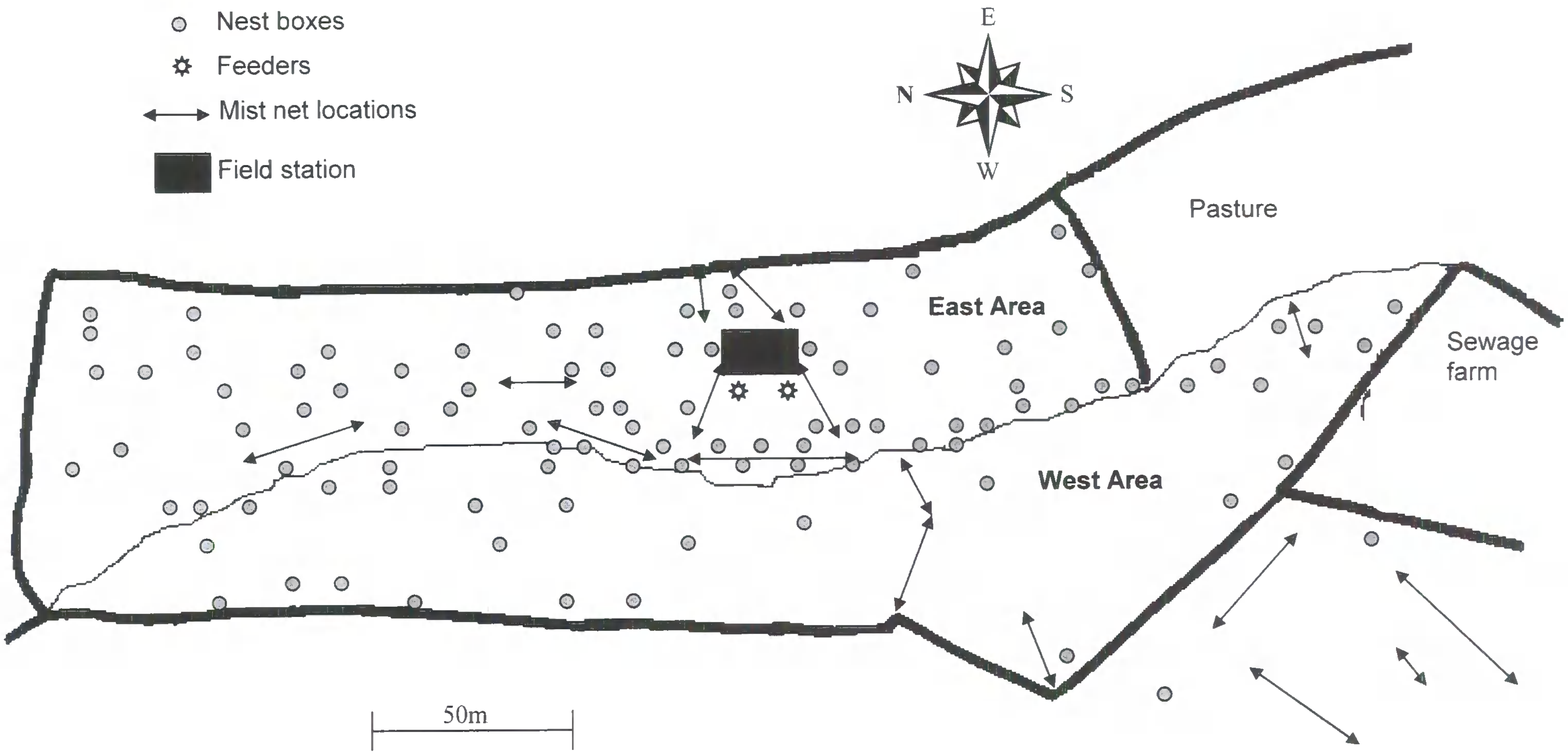

Figure 2.1: The study site, West Hollinside, showing locations of nest boxes, positions of mist nets (though not all positions were used during every catching period), bird feeders and the field station from where observations took place.

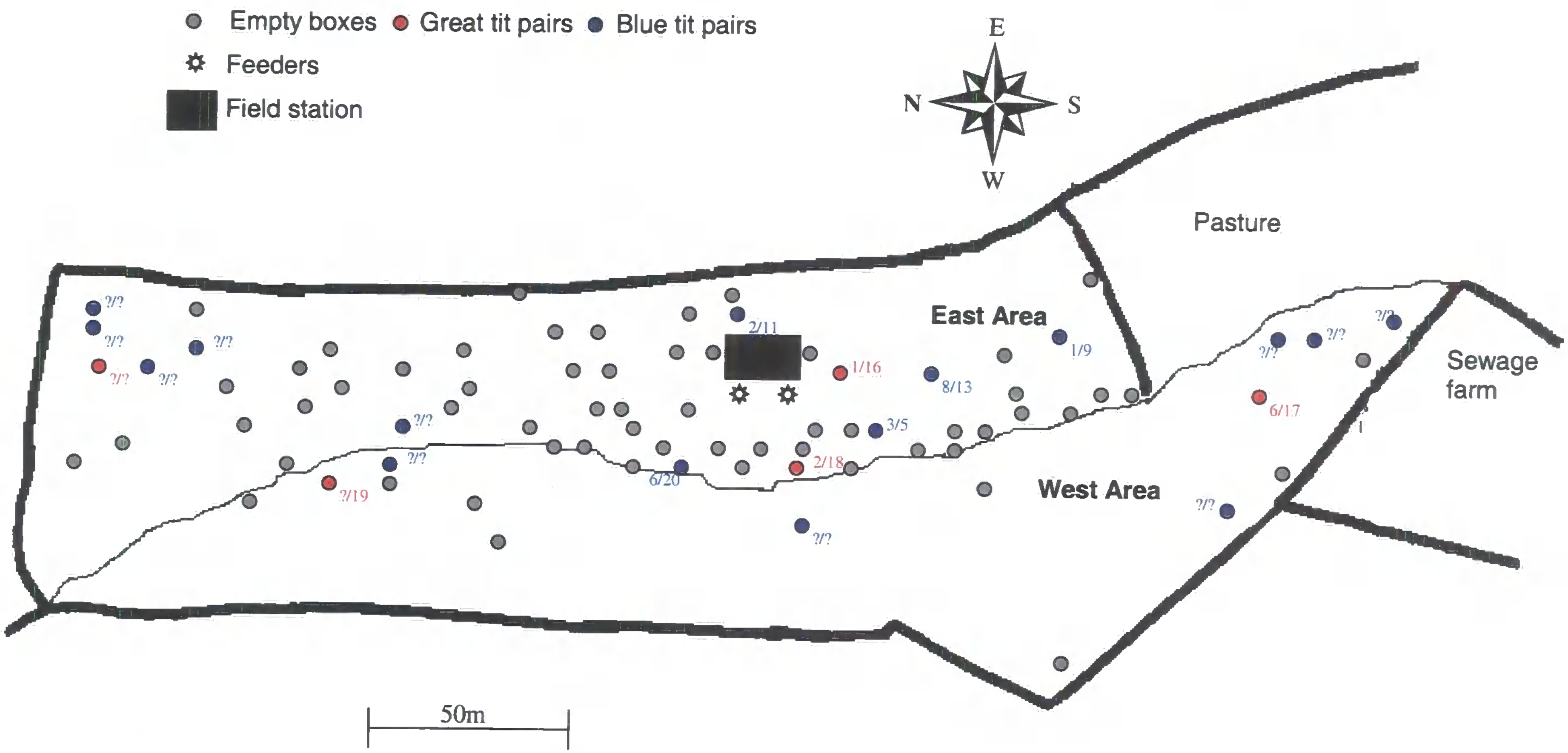

Figure 2.2: The distribution of breeding great tits and blue tits that used nest boxes during the 2001 breeding season. The numbers adjacent to the used boxes show the dominance ranks of the male and female birds (male/female) with 1 being the highest dominance score and 24 and 21 being the lowest dominance scores for great tits and blue tits respectively.

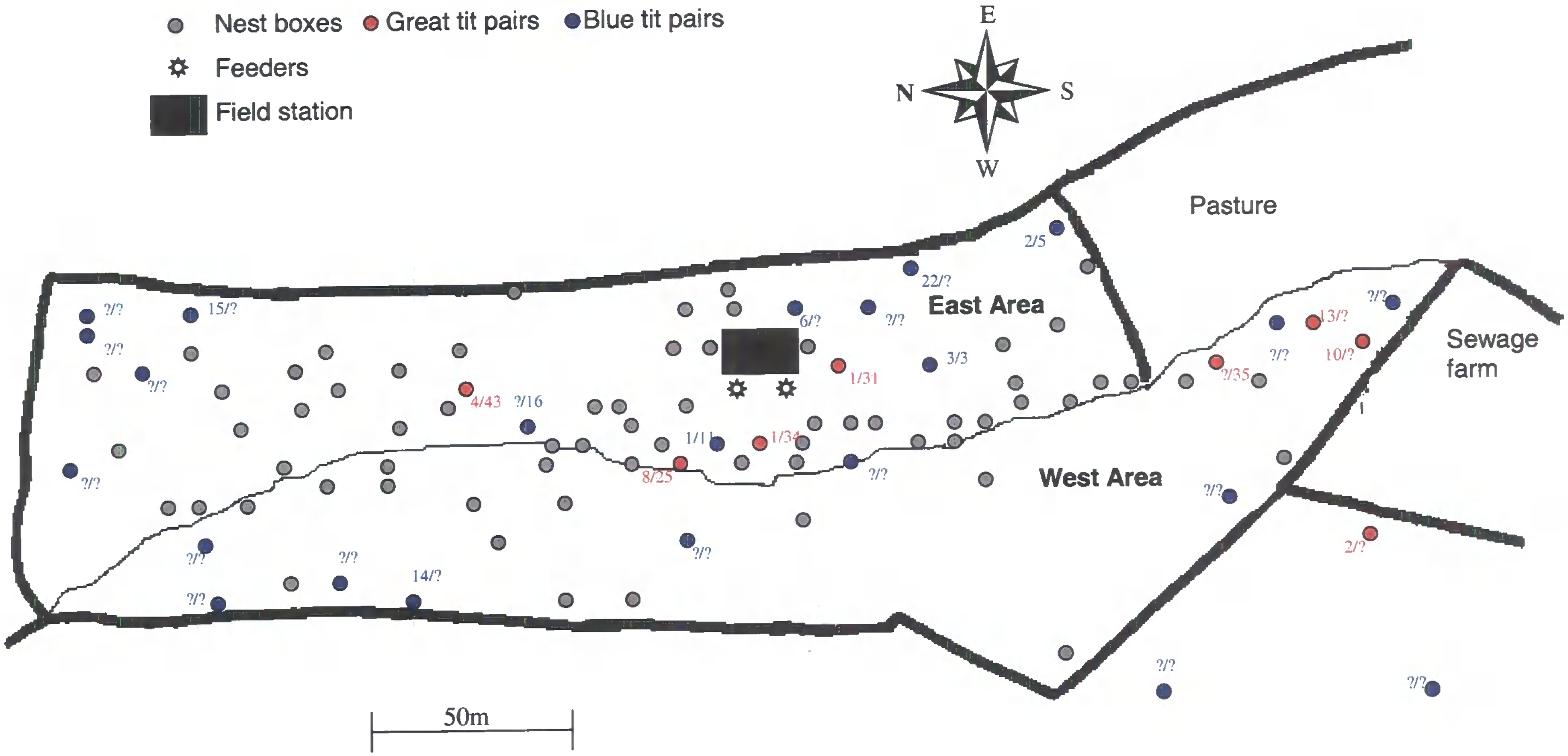

Figure 2.3: The distribution of breeding great tits and blue tits that used nest boxes during the 2002 breeding season. The numbers adjacent to the used boxes show the dominance ranks of the male and female birds (male/female) with 1 being the highest dominance score and 49 and 23 being the lowest dominance scores for great tits and blue tits respectively.

2.1.4 Use of study site

The Biological Sciences Field Station, which was used during this study as an observation point when recording bird behaviour, is positioned in the East area of West Hollingside. Two feeders used to attract the birds, were positioned approximately two meters from the front of the field station's west side. Birds were captured throughout West Hollingside where the vegetation facilitated mist netting across flight lines but with the main catching effort concentrated around the Field Station (Figure 2.1).

2.2 Nest boxes

One hundred nest boxes were constructed using 150mm x 25mm rough fencing timber. Entrance holes with a 28mm diameter were used thus allowing access to great tits, blue tits and coal tits. The nest boxes were placed around West Hollingside in suitable areas attached to trees between approximately two and four meters above ground (Figure 2.1). Suitable areas were characterized as trees with a diameter greater than 25cm and understorey within four meters of the tree. There was no selection with regards to tree species. During the 2001 breeding season, seven great tit pairs and seventeen blue tit pairs occupied nest boxes (Figure 2.2), and during the 2002 breeding season nest boxes were occupied by eight great tit pairs, one coal tit pair and 23 blue tit pairs (Figure 2.3).

2.3 Feeding regime

Two bird tables were constructed with 10mm plywood and a wire bird feeder was attached to the top surface of each table to deter grey squirrels (*Sciurus carolinensis*) from removing food from the tables. The total feeding area of the bird feeders was 400cm^2. The feeders were placed approximately two meters from the field station and were filled daily with either black sunflower seeds or bird cake (a mixture of lard and sunflower seeds). During observation days, the feeders were kept filled such that there was no noticeable decline in the food resource.

2.4 Bird capture

Fully grown great tits, blue tits and coal tits were captured in mist nets, potter traps or from nest boxes whilst they were roosting at night (Bub 1995) and fitted with a uniquely numbered metal BTO ring (under license from British Trust for Ornithology, Thetford) and a unique combination of three colour rings (manufactured by A.C. Hughes, Middlesex). All birds were ringed and processed (see sections 2.6-2.8) in the University Field Station and then released within twenty minutes of extraction from the mist net or trap.

During the 2000-2001 field season a total of 90 great tits, 110 blue tits and 31 coal tits were colour-ringed and during 2001-2002 88 great tits, 88 blue tits and 37 coal tits were colour-ringed. Table 2.1 gives an indication of the population structure from the numbers of each sex and age colour-ringed during each winter field season. Table 2.2 shows the numbers of nestlings of each species metal ringed during the 2001 and 2002 breeding seasons. Of the nestlings that were metal ringed in 2001, two great tits and one blue tit were recaptured in the subsequent winter field season suggesting either high mortality rates or high dispersal rates.

Species	Number of Birds Captured							
	2000-2001				2001-2002			
	adult male	adult female	juv male	juv female	adult male	adult female	juv male	juv female
Great tit	18	15	23	34	25	24	20	19
Blue tit	13	18	24	55	18	19	25	26
Coal tit	5	6	10	10	15	12	8	2

Table 2.1: The numbers of each species captured during both winter field seasons and the structure of the colour-ringed population (the age and sex of a small number of birds remained unknown throughout the study and comprised of two great tits during the 2000-2001 field season and in the 2001-2002 field season, one great tit, seven blue tits and one coal tit).

Species	Number of Nestlings Ringed		Number of Broods Ringed	
	2001	2002	2001	2002
Great tit	18	50	4	8
Blue tit	109	187	15	22
Coal tit	0	7	0	1

Table 2.2: The number of nestlings of each species that were metal-ringed during each breeding season and the number of broods that were involved.

2.4.1 Capture of feeding birds

Mist netting was carried out regularly (approximately twice a week) from November 2000 - April 2002 at West Hollingside and the adjacent conifer plantation, used as a dumping site by the Botanical Gardens. Mist nets were set across natural flight lines concentrated around the Field Station and in other suitable areas around the study site (Figure 2.1). Usually three to six, four shelf mist nets (two were nine meters and all additional nets were eighteen meters long) were operated at any one time with two nets at either side of the bird feeders being operated during all mist netting sessions. Mist netting always began at dawn and finished at around 13.00pm during the breeding season or dusk during the winter.

Seven potter traps were set around the base of the bird feeders and baited with peanuts or sunflower seeds during the winter of 2001-2002. On the occasions when potter traps were being used, usually because it was too windy for mist netting, most of the bait was put into and around the traps with the feeders only containing a small amount of food that was out of reach for the birds (but that would attract birds to the area). Birds were removed from the potter traps immediately upon capture and then processed in the field station.

2.4.2 Capture of roosting birds

Roosting birds were captured during the winter of 2001-2002 only. This method involved lining the base of all nest boxes with paper towel and then checking the towels for fresh droppings the following day to find which boxes were being used by roosting birds. Boxes that were being used by roosting birds during one evening were always occupied during the following evening and the birds could be removed from the boxes after dark, processed and then retained overnight in the Field Station. The birds were always released at dawn of the next day.

2.4.3 Capture of breeding adults at nest boxes

Incubating females were captured during the weekly checks of nest boxes throughout the breeding season. Females that had not been ringed previously were ringed with BTO metal rings, aged and sexed, then returned to their nests. Colour rings were not fitted and biometrics were not taken from these birds so that they could be returned to their nests to incubate as soon as possible with minimal handling. Nest box entrance holes were covered for one minute after returning females to their nests in order to let the birds settle.

Attempts were made to catch male birds when they were feeding nestlings during the second week of nestling rearing. Large paper clips (60mm in length) were attached to the inside of the nest box entrance holes with rubber hinges so that they acted as trapdoors to the adult birds returning with food (adults could enter the nest box to feed the chicks but could not leave). Nest boxes were checked for adult birds after ten minutes and the trap doors were left in place for a maximum time of fifteen minutes. This method worked well for females but only a few males were captured using this method because they were much more cautious than females when attending a nest box with a trap door attached.

2.4.4 Nestling ringing

All nest boxes were checked on a weekly basis from mid-March until mid-July to monitor nest building and egg laying. Since most British tits lay one egg per day, usually in early morning, the laying date could be accurately estimated from weekly observations of clutch size so long as the clutch was not started and completed between observation periods. Once clutch size had been determined, the nest boxes were checked again 12 days after the start of incubation, which usually begins when the last egg is laid (Perrins 1965). The nest boxes were then checked in early morning on a daily basis until the first egg hatched, usually 12–14 days in all three species, and the date of the first chick hatching could be determined.

Nestlings were ringed with BTO metal rings and weighed when 12 days old. Nestlings were not colour ringed since tit fledglings have a high mortality rate (Bulmer & Perrins 1973) and the number of colour ring combinations allocated to this project was limited. The chicks were removed from the nest, ringed and weighed within ten minutes, which was done in the vicinity of the nest box to prevent the parent birds from entering the nest when it was empty.

2.5 Ageing the study species

Great tits, blue tits and coal tits can be aged, after breeding has finished and before moult has begun (moult takes place in late summer and early autumn), as one of three categories: fledglings, juveniles (birds born in the previous breeding season *i.e.* one year old) and adults (birds that are more than one year old). After moult has been completed (full moult in adults and juveniles and partial post-juvenile moult in fledglings), the fledglings can be aged as juveniles but birds that are one year old and adults cannot be separated and are therefore all categorized as adults.

All three species can be aged according to the colour of their plumage and the variation in colour between different feather tracts brought about by moult. During moult in adults, all the feathers are replaced since they are all one year old and very worn. Moult in fledglings is not as complete since their feathers are only several weeks old so these birds only replace their body feathers and some wing coverts but not their main flight feathers. The post-juvenile moult in fledglings highlights differences in colour between the juvenile feathers grown in the nest and the new feathers moulted in late summer, which are coloured like those of adult birds. This contrast is especially obvious in the wing where all or some greater coverts contrast in colour with the primary coverts, which are not replaced. These differences are apparent throughout the year allowing ageing of these species to take place at any time.

2.5.1 Ageing great tits, blue tits and coal tits

Juvenile great tits have grey-green edged primary coverts that contrast with any blue edged greater coverts that have been replaced and the median coverts and lesser coverts, which are always replaced during partial post-juvenile moult (Svensson 1992). Since many great tits do not replace all of their greater coverts, there may also be a moult limit in the greater coverts resulting in a contrast between the old and new greater coverts (Svensson 1992; Jenni &

Winkler 1994; Ginn & Melville 1983). The shorter and duller tail feathers of juveniles can be used as a supporting characteristic when ageing great tits but since up to 90% of juvenile great tits replace their tail feathers during partial post-juvenile moult, this method is rarely of use (Jenni & Winkler 1994).

Blue tits and coal tits can be accurately aged in a similar way to great tits, according to the difference in colour between their juvenile primary coverts, some of their greater coverts and their lesser and median coverts. Juvenile coal tits rarely replace any tail feathers resulting in the entire tail being narrow and pointed, which can be used as a supporting characteristic with wing moult to age the birds. Blue tits do not usually moult their tail feathers until the full adult moult the following year so birds with narrow, pointed and worn tail feathers can be aged as juveniles in support of the wing characteristics. However, 70% of juvenile blue tits also replace their central tail feathers so may demonstrate a contrast in the colour of the tail feathers (Jenni & Winkler 1994).

2.6 Sexing the study species

Both adult and juvenile great tits were sexed from the width and extent of the black breast stripe running from the chest down to the bottom of the breast (males have wider stripes that extend to touch both legs: Svensson 1992). This method of sexing great tits was tested using DNA sex-typing and found to be completely accurate. Blue tits and coal tit are more difficult to sex in the hand and were sexed on plumage colour supported by wing length and discriminant function analysis of their biometrics respectively (these methods of sexing blue tits and coal tits were tested using DNA sex-typing).

2.6.1 Sexing blue tits and coal tits on plumage and biometrics

Blue tits were sexed on the brightness of the blue colouration on their lesser and median wing coverts. After practice, males were easily identified as having brighter plumage than females (Perrins 1979; Svensson 1992) though this may not be the case in all blue tit populations (Scott 1993). Since adults have brighter plumage than juveniles (Perrins 1979; pers. obs), sexing blue tits from the brightness of their plumage was even more accurate when the birds had been aged first. There was also a difference in wing length (maximum chord) between male and female blue tits with males having longer wings than females, which could be used as a supporting characteristic to plumage colour (Figure 2.4). When this method of sexing blue tits was assessed for accuracy by sexing the same birds using DNA from their feather tips (Section 2.6.2), 96% of the blue tits had been correctly sexed.

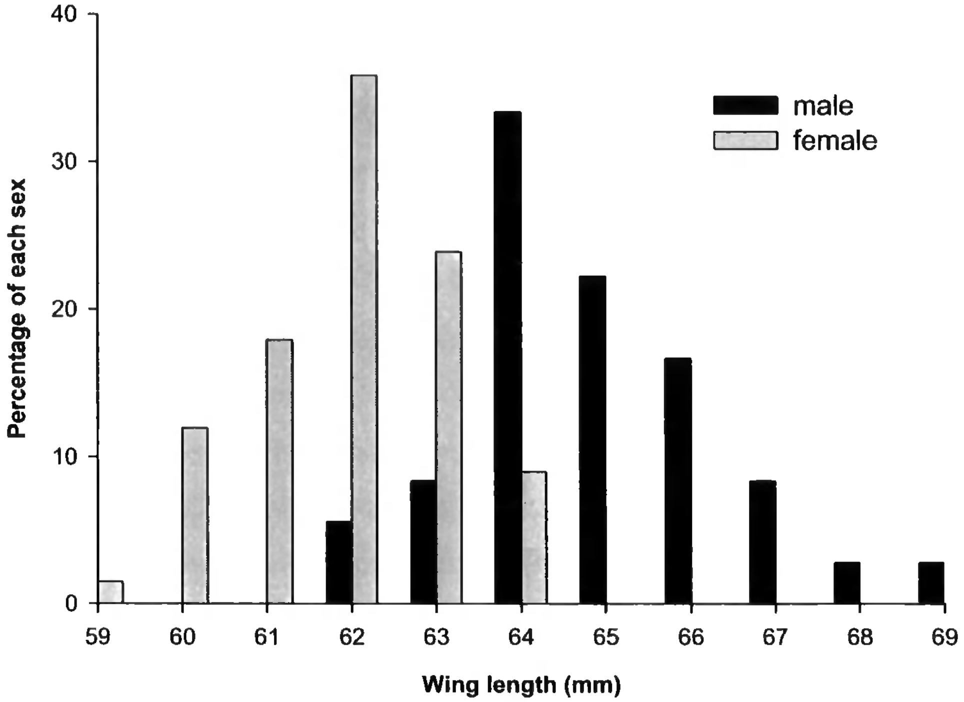

Figure 2.4: Wing lengths of male (*n* = 36) and female (*n* = 67) blue tits during 2000-2002.

Coal tits can be difficult to sex in the hand though several methods have been proposed (Gosler & King 1989; Svensson 1992; King & Griffiths 1994). The method proposed by Gosler and King, which is based on bib type and wing length is able to sex 75% of coal tits accurately within a population. Due to differences in size between populations of coal tits, and the many intermediate birds within this study with regards to bib shape and wing length, the previously described methods were not suitable for sexing coal tits at West Hollingside. The coal tits in this study were sexed using discriminant function analysis using the biometrics that were measured during each year. For the field season spanning the winter of 2000-2001, wing length, body mass, head plus bill length and tarsus length were used in the analysis, which correctly sexed 89% of the birds when checked with DNA sex-typing methods. During the winter of 2001-2002, discriminant function analysis was used with wing length, body mass, head plus bill length, tarsus length and tail length, which correctly sexed 96% of the coal tits from this field season.

2.6.2 Sexing birds using DNA extracted from feathers

Two or four tail feathers were removed from great tits, blue tits and coal tits during both winters and DNA was extracted and isolated from the proximal ends of the feathers using the phenol/chloroform extraction method (usually four feathers were required to provide enough DNA to sex the birds) (Bello, Francino & Sanchez 2001). The birds were sex-typed using the P2 (5'-TCTGCATCGCTAAATCCTTT-3') and P8 (5'-CTCCCAAGGATGAGRAAYTG-3') primers in a PCR amplification reaction, then the product was visualised on a 2% agarose gel stained with ethidium bromide (Griffiths *et al.* 1998). The production of two bands demonstrated the presence of both the CHD-Z gene (carried by both male and female birds) and the CHD-W gene (carried by female birds only). The production of only one band indicated that there were two CHD-Z genes but no CHD-W genes and determined that those birds were male (Figure 2.5).

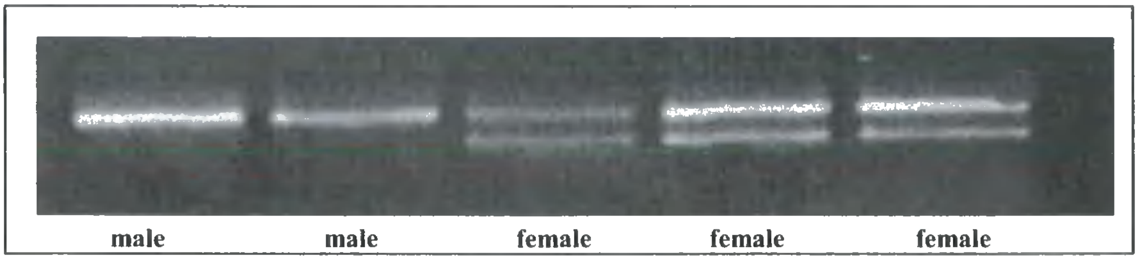

Figure 2.5: The double and single band products of the DNA extraction and PCR amplification methods showing the CHD-Z and CHD-W genes determining the sex of the study species.

2.6.3 Sexing great tit and blue tit nestlings

In order to sex great tit and blue tit nestlings during the 2002 breeding season, approximately 10µl of blood was removed (under Home Office license no: PPL60/2066) from the brachial vein of nestlings by making an incision with a sterile needle and removing the drop of blood that appeared on the skin surface with a capillary tube (this was carried out when nestlings were 15 days old). Half of the blood was used to make blood smears (for method see: Chapter 7) and the remainder was preserved in 150µl of 100% ethanol for six weeks until DNA extraction took place. DNA was extracted from the blood using the ammonium acetate extraction method following Griffiths *et al.* (1998). The methods used for PCR amplification and visualization of the product were as above.

2.7 Measuring Biometrics

During both field seasons biometrics were taken on each bird every time it was captured unless blood samples were being taken or the bird had already been captured that day. Wing length, body mass, tarsus length and head plus bill length were measured during both field seasons. During October 2001 – April 2002, bill length and tail length were also measured. Principal Components Analysis (PCA) was carried out on all of the biometric data from both field seasons to produce a value of PC1 for each individual that would describe body size. During 2000-2001, PC1 explained 44% of the variation in body size in great tits, 42% in blue tits and 45% in coal tits. During 2001-2002, 40% of the variation in the body size of great tits, 42% of blue tits and 38% of coal tits was explained by PC1. The following equations were used to calculate the PC1 values:

2000-2001

Great tit $PC1 = -0.50a - 0.31b - 0.63c - 0.51d$

Blue tit $PC1 = -0.64a - 0.47b - 0.40c - 0.47d$

Coal tit $PC1 = -0.45a - 0.44b - 0.55c - 0.55d$

2001-2002

Great tit $PC1 = 0.53a + 0.28b + 0.33c + 0.47d + 0.46e + 0.30f$

Blue tit $PC1 = -0.51a - 0.37b - 0.51c - 0.40d - 0.42e - 0.11f$

Coal tit $PC1 = 0.48a + 0.14b + 0.52c + 0.46d + 0.43e + 0.29f$

where:

a = wing length
b = tarsus length
c = mass (corrected for date and time)
d = head plus bill length (corrected for date)
e = tail length
f = bill length

Wing length was measured using the maximum chord method (Svensson 1992) to the nearest 1mm using a 300mm stoppered wing rule. Tarsus length, bill length and head plus bill length were measured using Vernier calipers to the nearest 0.1mm and body mass was taken to the nearest 0.1g using a Pesola spring balance. Tail length was measured with an accuracy of 0.5mm using a steel rule (Svensson 1992). The bill depth of blue tits was measured at West Hollingside in March 2003 to the nearest 0.1mm with Vernier calipers. This was done to assist with the interpretation of data in Chapter 4, as a means of testing whether males and females differed in bill shape (Appendix 5).

During both winters, body mass in all three species was affected by time of day (except in great tits during the 2001-2002 field season) and date (except in blue tits during the 2000-2001 field season) (Appendix 1). Head plus bill length was affected by date in all three species during both years (except in blue tits during

2001-2002) (Appendix 2a) and bill length was affected by date in all three species (Appendix 2b) (See also: Gosler 1987). Given the above, these data were corrected for temporal variation by carrying out REML analysis (See: section 2.9) and using the residuals as the data points for the rest of the study.

2.8 Defining the dominance hierarchy

2.8.1 Behavioural observations

Behavioural observations were carried out between December 2000 - March 2001 and October 2001 – February 2002. Colour ringed great tits, blue tits and coal tits were observed and recorded visiting the feeders at the University Field Station in West Hollingside (Figure 2.1) and agonistic interactions were recorded. During the first few months of the 2000-2001 field season, the activities at one of the bird feeders were video recorded so that interactions would not be missed whilst recording activities at the other feeding table. However, during the course of the field season, I became better at recording the colour ring combinations during interactions and subsequent observations were done without the use of a video camera in order to save time that would be spent analysing video footage.

Each time that a bird visited the feeding tables, time of day was recorded (and used in all analysis as a proportion of daylight hours for that day) as well as the species and colour ring combination of the individual bird. Interactions were documented as being either active or passive depending on their severity. Active interactions involved posture displays (particularly in great tits), physical fighting or chasing (very common in coal tits) (Hinde 1952). Passive interactions occurred when one bird arrived at the feeder causing another bird to change feeders or retreat to a nearby perch and wait for another chance to feed. Passive interactions did not involve aggression but were more likely to be the result of avoidance by the losing bird. The colour ring combinations of the interacting birds were recorded and the winner and loser of each interaction were recorded even though one of the birds may not have been ringed.

Because observations were carried out at only one site (the Biological Sciences field station) during this study, site related dominance, which occurs in great tits (Gosler 1993) and may also occur in blue tits and coal tits to some extent might have been an issue under natural conditions. However, because food was supplemented and available most of the time, it was expected that the dominance hierarchy that occurred around the field station would have a significant effect on the body condition and behaviour of the birds since they would spend a greater amount of time foraging in this area and individuals' positions in the hierarchy would determine how much food they acquired. The most dominant male great tit did breed closest to the feeders during both breeding seasons (Figure 2.2, 2.3) suggesting that site related dominance might occur when nesting sites are considered. The most dominant blue tit also nested close to the feeders in 2002 but the high numbers of birds with unknown dominance ranks makes it difficult to interpret whether site related dominance influences nesting sites in a hierarchical order in either great tits or blue tits (Figure 2.3-2.3).

2.8.2 Matman program

Matman (Noldus Information Technology, Wageningen) is a program designed for the analysis of behavioural data, particularly dominance data, and can be used to produce a dominance hierarchy from a matrix of the outcome of interactions between different individuals (de Vries, Netto & Hanegraaf 1993; de Vries 1995a). Matman can accommodate a matrix involving up to 50 individuals and can deal with matrices where there are unknown or tied relationships between individuals (de Vries 1995b). Matman is more accurate than conventional methods of producing dominance hierarchies, which involve defining a hierarchy based on proportion of interactions won and lost, because it takes account of which individuals are interacting and can therefore control for asymmetries caused by the non-random choice of opponents. However, because Matman is based on interactions between individuals, there needs to be a reasonably large sample size of interactions between birds that are both colour-ringed for it to work accurately.

Matman was used in this study to produce a dominance hierarchy for great tits and blue tits during both field seasons but due to a high proportion of unringed coal tits interacting with colour-ringed coal tits during the first field season, Matman was only used to produce a coal tit hierarchy for the second field season. Because there may be asymmetries in the outcome of agonistic interactions due to the circumstances of the interaction, the impact of these was minimized during the production of the matman hierarchies by only entering those birds that had interacted more than five times into the matrix. This increased the likelihood that each dominance score would be representative of an individual's status.

2.8.3 Dominance calculated from PCA

During the first field season (winter 2000-2001), though many coal tits were visiting the feeders and interacting, only a small percentage of the interactions were between two colour-ringed individuals. Though there were many interactions recorded between coal tits, they were usually between a colour ringed bird and a bird that was not ringed. To maximize the use of the data, principal components analysis (PCA) was used to produce a dominance hierarchy for coal tits during the first field season (See: Gosler & Carruthers 1999). The first principal component from a PCA of the number of active and passive interactions won and lost was used to calculate a dominance index for each colour-ringed coal tit that had interacted more than five times. PC1 explained 47% of the variation in the dominance behaviour of the coal tits and was calculated from the equation:

$$PC1 = 0.71a - 0.18b + 0.69c - 0.01d$$

where:

a = actively aggressive interactions won
b = actively aggressive interactions lost
c = passive interactions won
d = passive interactions lost

This method of calculating dominance hierarchies is successful provided that the hierarchy is stable (Gosler & Carruthers 1999). The data proving the stability of the dominance hierarchies for the species featuring in this study are presented in Chapter 3.

For both the Matman and the PCA dominance hierarchies, the birds with the highest dominance status had an index of 1 and those birds with the lowest dominance status had indices with values greater than 1.

2.9 Statistical analysis

All statistical analyses were carried out in MINITAB release 13 for windows except for Residual Maximum Likelihood Models (REMLs) which were carried out in Genstat release 4.2 for windows. REMLs were used in this study because they deal with unbalanced designs, incomplete data sets and repeated-measures data that are not independent (Payne 2000).

All GLM and REML analysis included interaction terms between the two main factors but, because these were often not significant and could amount to a large number of results, the results of the interaction terms between factors are only presented if the results were significant. The interaction terms are represented by a star between the two factors *e.g.* factor1*factor2.

Chapter 3

Structure of the dominance hierarchies

3.1 Abstract

In groups of animals that live together for all or part of their lives, aggression between group members can take up considerable amounts of time that could otherwise be used for foraging and it also carries the risk of being injured. Dominance hierarchies, that form in many social groups of animals, can reduce the need for high numbers of aggressive interactions, since each individual has a place in the hierarchy that is usually stable and determined by its fighting ability or resource holding potential. Sex was the major determinant of dominance status in all three species in this study, though this may have resulted from differences in body size between males and females in great tits. This study did not produce evidence for the determinants of dominance status within the sexes.

Great tits and coal tits did not interact with conspecifics in a random manner but tended to initiate aggressive interactions with individuals that had a similar dominance status. Contrary to previous work (Järvi & Bakken 1984), dominant individuals were not involved in a greater number of aggressive interactions in the majority of cases. The major determinant of the number of aggressive interactions that individuals were involved in was time of year, with aggression increasing as the winter progressed and spring approached.

3.2 Introduction

3.2.1 Function of dominance hierarchies

Many species of animal that live in social groups for all or part of their lives form dominance hierarchies within their group as a means of reducing agonistic interactions (*e.g.* grey wolves *Canis lupus*: Mech 1991; great tits: Gosler 1993; Nubian ibex *Capra ibex nubiana*: Greenberg-Cohen, Alkon & Yom-Tov 1994). Dominance hierarchies initially result from repeated agonistic interactions between the same pair of individuals in a social group that result in a consistent outcome in terms of winner and loser, which is recognised by both individuals involved (Drews 1993). Because time and energy could be wasted on agonistic interactions that will always have the same outcome and because there is always a risk of injury (Kaufmann 1983), group members may avoid agonistic interactions with those individuals that are dominant over them. Dominance hierarchies therefore reduce the need for high numbers of agonistic encounters within a social group that may result in injuries arising from aggressive interactions (Kaufmann 1983).

Among social groups that implement dominance hierarchies, the highest-ranking individuals generally have priority of access to limited resources such as food, mates and territories (*e.g.* Kaufmann 1983; Ens & Goss-Custard 1984; Arcese & Smith 1985). Dominance status is therefore often used as an index of individual fitness, because these advantages lead to dominant individuals having higher survival rates and a higher probability of producing more recruits to the breeding population (Arcese & Smith 1985; Frank 1986).

3.2.2 Structure of dominance hierarchies

The way in which dominance status is achieved varies between animal taxa and in some cases dominance status may be heritable, as in Japanese quail *Coturnix japonica* (Nol, Cheng & Nichols 1996). In many species, particularly ungulates (fallow deer *Dama dama*: Jennings *et al.* 2002; Nubian ibex: Greenberg-Cohen, Alkon & Yom-Tov 1994; red deer *Cervus elaphus*: Freeman, Freeman & Romney 1992), dominance status is determined by fighting ability or resource holding potential (RHP). Under these circumstances, the animals in question often have weapons, which allow them to use their strength and fitness to their greatest potential during fighting (*e.g.* antlers, horns or sharp hooves).

Dominance, however, is not always a result of an individual's ability to defeat others. In many primate species, dominance depends on matrilineal lineage (*e.g.* female macques *Macaca* spp.: Chapais, Girard & Primi 1991; spotted hyenas *Crocuta crocuta*: Frank 1986). In other species, dominance rank depends on the length of time that an individual has been associated with a specific group, particularly if new group members automatically become the most subdominant animals (*e.g.* dark-eyed juncos *Junco hyemalis*: Cristol 1995a, 1995b; Cape Mountain zebras *Equus zebra*: Rasa & Lloyd 1994).

Among avian species that form dominance hierarchies within their groups, dominance status is frequently dependent on sex, although age and plumage characteristics can also determine dominance status to some extent (Arcese & Smith 1985; Lamprecht 1986; Järvi, Walso & Bakken 1987; Wagner & Gauthreaux 1990; Liker & Barta 2001). Overall, these characteristics are controlled or related to testosterone levels which influence almost all dominance hierarchies, since testosterone controls levels of aggression (Järvi, Walso & Bakken 1987; Vleck & Brown 1999; Deviche, Wingfield & Sharp 2000; Buchanan *et al.* 2001).

3.2.3 The dominance hierarchy of *Parus* species

For many *Parus* species where individuals live in non-kin flocks outside the breeding season, a dominance hierarchy is established during flock formation in late summer and early autumn (Hogstad 1989; Gosler 1993). In the majority of *Parus* species, it has been demonstrated that within conspecific flocks, males generally dominate females and within the sexes, adults usually dominate juveniles (Dixon 1965; Hogstad 1987d, 1992; Lahti *et al.* 1996; Barluenga, Moreno & Barbosa 2001). From species-specific studies, various other factors have been described as determining dominance status. Dominant willow tits are reported to be larger and heavier than subdominants (Hogstad 1987d) and great tit males with wider breast stripes and higher levels of testosterone are thought to be more dominant than those with lower testosterone and narrower breast stripes (Järvi & Bakken 1984; Røskaft *et al.* 1986; Järvi, Walso & Bakken 1987; Pöysä 1988). However, caution must be exercised when dealing with breast stripe measurements since recent work suggests that some measurements of breast stripe width in great tits may not be repeatable (See: Figuerola & Senar 2000).

This chapter aims to determine which factors are important in influencing dominance status in the populations of great tits, blue tits and coal tits at West Hollingside. Since little work has been published on the different behavioural traits of dominant and subdominant birds with regards to the way in which they interact, this study also hopes to determine whether dominant birds interact more often than subdominants and whether flock members tend to interact with birds of a particular dominance rank compared to their own rank. In addition, this study aims to determine whether temporal factors affect interaction rates and aggression.

3.3 Methods

3.3.1 Observations and data collection

Methods used for assigning the dominance ranks and measuring the biometrics of great tits, blue tits and coal tits are presented in Chapter 2. Data were collected during two winters, from December 2000 to March 2001 and from October 2001 to February 2002 both for behavioural observations that were used to construct the dominance hierarchies for each winter and for biometric measurements (these were collected separately for each year to account for changes in size with age).

3.3.2 Statistical analysis

In order to understand which factors contributed most to the dominance status of individuals, the effects of age, sex and body size were analysed. Scheirer-Ray-Hare tests (non-parametric equivalent of 2-way ANOVA) were used to test the influence of age and sex, and Spearman's rank correlations were used to test the effects of body size on dominance status.

The stability of a dominance hierarchy over the data collection period is essential if a single dominance index is to be used for each individual. Hierarchies may not be stable over an entire season if levels of aggression are likely to change as spring approaches particularly in species that become territorial with the onset of spring. The dominance hierarchies of great tits, blue tits and coal tits in this study were tested by splitting each field season into early and late winter (the halfway point was taken as the end of the first week in January) and calculating a dominance hierarchy for each species during both halves of the season. Because splitting the sampling season in two meant that some birds were only present in one of the time periods or that some birds interacted fewer than five times in one of the time periods, the sample size was considerably lowered. For each species, the two separate dominance hierarchies for early and late winter were compared using Wilcoxon's signed rank tests (Gosler & Carruthers 1999).

Spearman's rank-order correlations were used to test whether individual birds were interacting randomly or showing preference for conspecifics of a particular dominance rank when initiating aggressive interactions. These tested the relationship between the dominance status of an individual and the mean dominance status of the individuals with which it initiated aggressive interactions during the study period (See: Gosler & Carruthers 1999). Since sex was usually related to dominance status, the sexes were separated for those species and years that demonstrated a sex difference in dominance status and the analyses were carried out for males and females separately. This eliminated the possibility that any relationship between the dominance status of birds and the mean dominance status of their opponents was due to males and females selectively interacting or avoiding flock members of the same sex.

The frequency of aggressive interactions was calculated for each bird by dividing the number of overtly aggressive interactions (those that involved displaying or physical contests) by the number of times that the bird visited the feeders. To test whether the age or sex of birds influenced the frequency of aggressive interactions, GLMs were used. The relationship between the frequency of aggressive interactions and dominance status was tested using Spearman's rank-order correlations.

REMLs were used to test whether or not there was temporal variation in the number of visits to the feeders or in the number of those visits that resulted in aggressive interactions between conspecifics for each species during the 2000-2001 winter field season. The number of visits made by great tits to the feeders was not normally distributed and was therefore $\log_{10}$ transformed. The frequency of aggressive interactions of great tits and blue tits were not normally distributed and were therefore square root transformed for subsequent analysis. Data for visit rates and the frequency of aggressive interactions were only available for the season 2000 – 2001 when all visits to the feeding tables were recorded whether or not they resulted in an interaction between two birds.

3.4 Results

3.4.1 Dominance status with respect to sex and age

Males had higher dominance ranks than females in great tits and blue tits during both winters (Table 3.1, 3.2). Male coal tits were dominant to females during the winter 2001-2002 but there was no relationship between sex and dominance rank for coal tits in the previous winter. There was no difference in dominance status between adult and juvenile great tits, blue tits or coal tits (Table 3.2).

	2000-2001			**2001-2002**		
	Median (interquartile range)			**Median (interquartile range)**		
	n	**male**	**female**	***n***	**male**	**female**
Great tit	25	8.0 (8)	20.0 (5)	49	14.5 (15)	31.0 (12)
Blue tit	21	6.5 (10)	14.0 (5)	23	8.5 (11)	16.0 (10)
Coal tit	15	9.0 (10)	7.0 (9)	21	9.5 (9)	18.5 (10)

Table 3.1: The median dominance ranks with interquartile ranges of male and female great tits, blue tits and coal tits.

	Sex or age factor	**2000-2001**		**2001-2002**	
		$H_{d.f.}$	P	$H_{d.f.}$	P
Great tit	sex	$48.64_{1,33}$	<0.001	$72.46_{1,48}$	<0.001
	age	$10.10_{1,33}$	0.1	$0.01_{1,48}$	0.5
Blue tit	sex	$4.76_{1,20}$	<0.05	$5.72_{1,22}$	<0.05
	age	$0.05_{1,20}$	0.8	$0.00_{1,22}$	0.9
Coal tit	sex	$0.18_{1,14}$	0.7	$6.27_{1,20}$	<0.05
	age	$0.15_{1,14}$	0.5	$0.21_{1,20}$	0.1

Table 3.2: The results of the Scheirer-Ray-Hare-Tests on the effects of age and sex on the dominance ranks of great tits (*n* values 2000-2001: male = 23, female = 13, adult = 12, juvenile = 24; 2001-2002: male = 29, female = 20, adult = 32, juvenile = 17), blue tits (*n* values 2000-2001: male = 9, female = 12, adult = 7, juvenile = 14; 2001-2002: male = 12, female = 11, adult = 13, juvenile = 10) and coal tits (*n* values 2000-2001: male = 8, female = 7, adult = 5, juvenile = 10; 2001-2002: male = 11, female = 10, adult = 15, juvenile = 6).

3.4.2 Effect of body size on dominance status

Body size, which was represented by the first principal component from PCA of the biometrics taken in each year, was not related to dominance status in great tits, blue tits or coal tits (Table 3.3).

	2000-2001			2001-2002		
	r_s	*n*	*P*	r_s	*n*	*P*
Great tit	-0.08	30	0.7	0.16	41	0.3
Blue tit	0.15	26	0.5	-0.38	20	0.1
Coal tit	0.07	14	0.8	-0.18	18	0.5

Table 3.3: The results of Spearman's rank-order correlations between dominance status and body size (measured as the first principal component from a PCA of the biometrics described in Chapter 2) in great tits, blue tits and coal tits during both winters.

3.4.3 Stability of the dominance hierarchy

The dominance hierarchies of all three species were stable from early to late winter. Results of the Wilcoxon's signed rank tests demonstrated that there was no significant difference between the dominance hierarchies calculated for the first and second halves of the winter in either year (Table 3.4).

	2000-2001		2001-2002	
	$Z_{d.f.}$	*P*	$Z_{d.f.}$	*P*
Great tit	$74.5_{1,19}$	1.0	$185.5_{1,30}$	0.8
Blue tit	$47.5_{1,12}$	1.0	$97.0_{1,21}$	1.0
Coal tit	$13.0_{1,9}$	0.7	$66.5_{1,19}$	1.0

Figure 3.4: Results of Wilcoxon's signed rank tests of the difference between dominance ranks in the early and late periods of winter during both field seasons (*n* values 2000-2001: great tits = 20, blue tits = 13, coal tits = 8; 2001-2002: great tits = 31, blue tits = 22, coal tits = 20).

3.4.4 The randomness of interactions

Great tits were not interacting in a random manner during either winter (Table 3.5) and were more likely to initiate aggressive interactions with another great tit of similar or lower dominance status (Figure 3.1). When controlling for sex during the 2000-2001 field season, male great tits were initiating interactions with males of similar or lower dominance rank and there were insufficient data to analyse females separately. During the 2001-2002 field season, male great tits were initiating aggressive interactions with males of similar or lower dominance status (r_s = 0.46, n = 28, P<0.05) but females showed no preference with regards to the dominance status of their opponents (r_s = 0.07, n = 13, P = 0.8).

There were no significant correlations between blue tit dominance rank and the mean dominance rank of those blue tits that they initiated aggressive interactions with in either year. Coal tits showed no preference for their opponents' dominance rank during the winter of 2000-2001 but were more likely to initiate an aggressive interaction with coal tits of a similar or lower dominance status during the 2001-2002 field season (Table 3.5, Figure 3.2). When controlling for sex during the winter of 2001-2002, male coal tits were more likely to interact with males of a similar or lower dominance status (r_s = 0.87, n = 10, P<0.001) and female coal tits showed no such tendency (r_s = 0.48, n = 9, P = 0.2).

	2000-2001			**2001-2002**		
	r_s	n	P	r_s	n	P
Great tit	0.80	16	<0.001	0.70	41	<0.001
Blue tit	0.42	9	0.3	0.41	18	0.1
Coal tit	-0.40	14	0.1	0.72	19	<0.001

Table 3.5: The results of Spearman's rank-order correlations demonstrating the relationship between an individual's dominance status and the mean dominance status of the birds with which it initiated aggressive interactions.

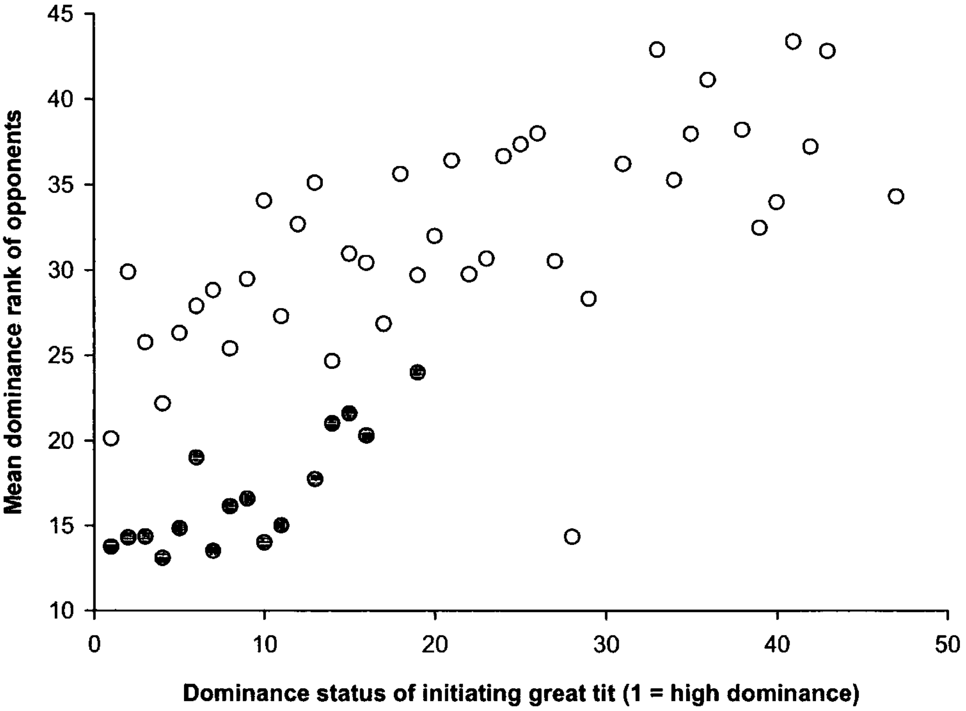

Figure 3.1: The relationship between an individual great tit's dominance rank and the mean dominance rank of the birds with which it initiated aggressive interactions (data for 2000-2001 (•) and 2001-2002(o)).

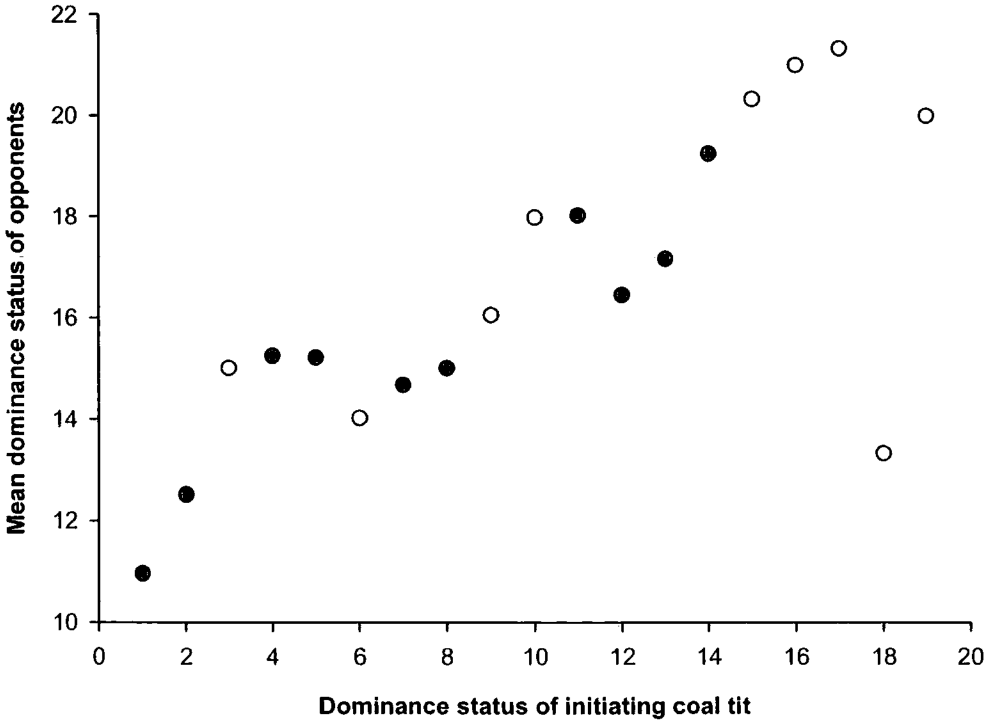

Figure 3.2: The positive relationship between the dominance status of coal tits and the mean dominance status of the coal tits with which they initiated aggressive interactions during the winter of 2001-2002 (male = •, female = o).

3.4.5 Temporal variation in aggression

The number of visits to the feeding tables per day increased from early to late winter in great tits (Figure 3.3), blue tits (Figure 3.4) and coal tits. The number of visits to the feeding tables increased with the time of day in coal tits but not great tits or blue tits (Table 3.6). The frequency of aggressive interactions (number of aggressive interactions per visit to the feeder) increased as the winter progressed in all three species (blue tits, Figure 3.5) and increased with the time of day in great tits and coal tits (Table 3.6). Figures are provided for those relationships that were not influenced by both temporal factors.

	Temporal factor	**Number of visits**		**Frequency of aggressive interactions**	
		Wald (χ^2) d.f.	***P***	**Wald (χ^2) d.f.**	***P***
Great tit	date	$92.74_{21,106}$	<0.001	$36.98_{20,102}$	<0.05
	time	$14.91_{8,106}$	0.1	$16.36_{8,102}$	<0.05
Blue tit	date	$105.97_{21,110}$	<0.001	$84.12_{19,103}$	<0.001
	time	$9.91_{8,110}$	0.3	$8.42_{8,103}$	0.4
Coal tit	date	$42.49_{21,112}$	<0.01	$49.02_{21,112}$	<0.001
	time	$18.30_{8,112}$	<0.05	$21.99_{8,112}$	<0.01

Table 3.6: Results of REML analysis of the relationship between date, time and the number of visits to the feeders per day or the frequency of aggressive interactions (the number of visits that resulted in aggressive interactions). Data are presented for great tits (*n* values: Number of visits = 107, Frequency of aggressive interactions = 103), blue tits (*n* values: Number of visits = 111, Frequency of aggressive interactions = 104) and coal tits (*n* values: Number of visits: = 113, Frequency of aggressive interactions = 113) in the 2000-2001 field season only.

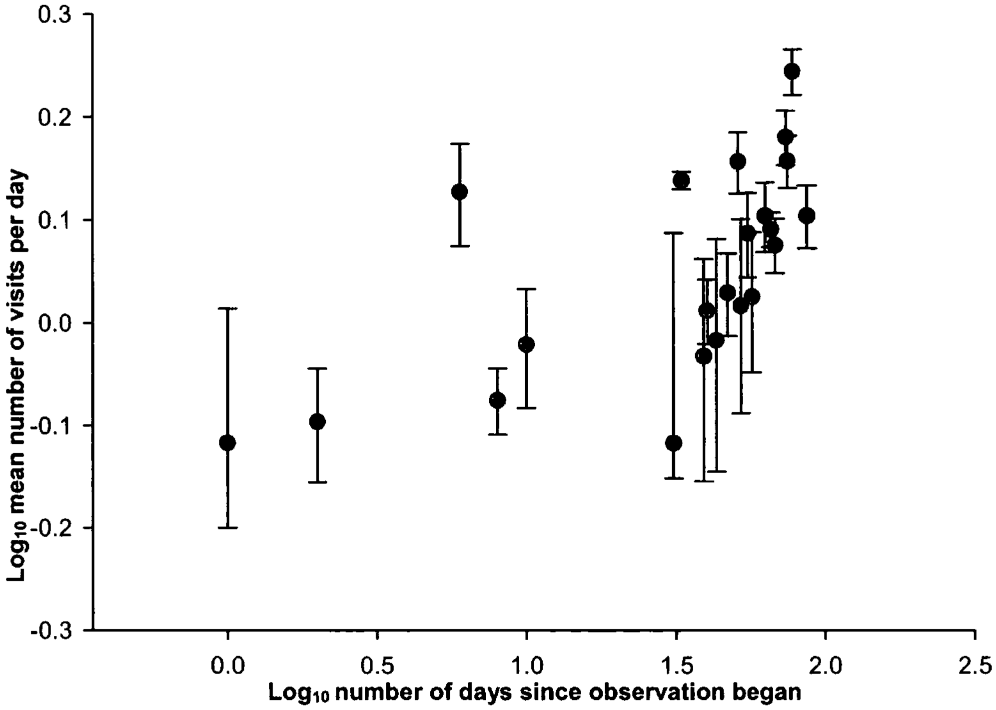

Figure 3.3: The relationship between the mean (s.e.) number of visits made by individual great tits to the feeders each day and the number of days since the observations began on December 13th 2000. All data $\log_{10}$ transformed.

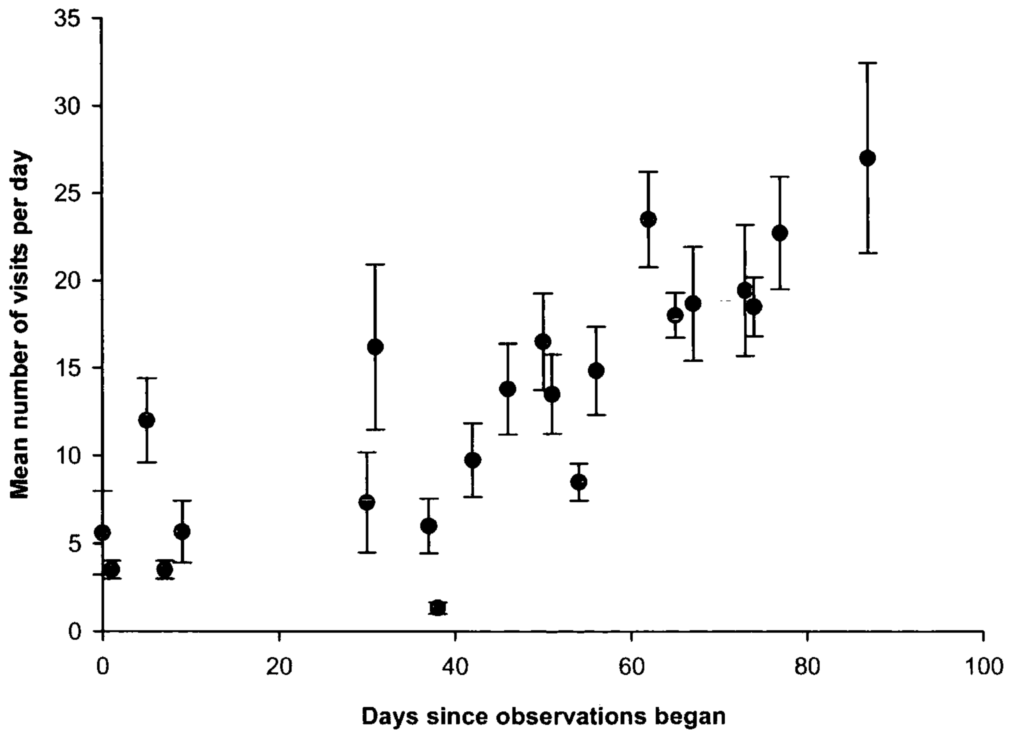

Figure 3.4: Relationship between the mean (s.e.) number of visits by individual blue tits to the feeders per day during 2000-2001 and date (number of days since the observations began on 13th December 2000).

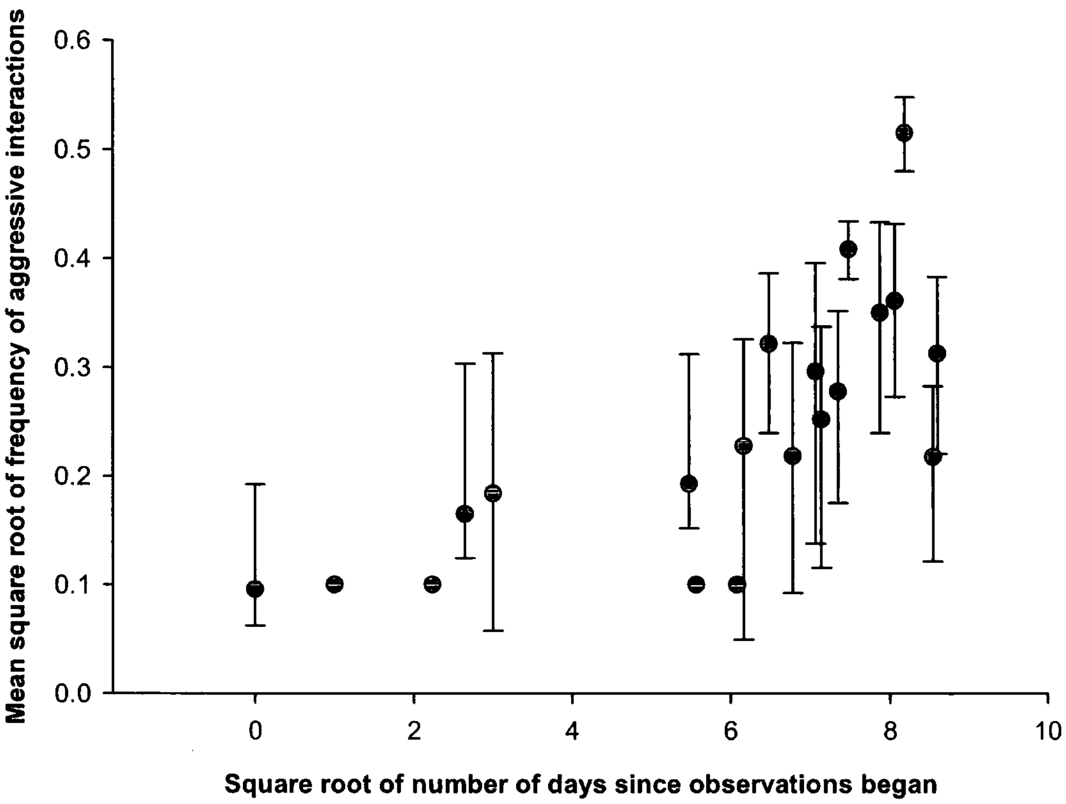

Figure 3.5: The relationship between the mean frequency of aggressive interactions (number of aggressive interactions per visit) that blue tits were involved in and date (number of days since observations began). All data are square root transformed.

3.4.6 Frequency of aggressive interactions

Juvenile great tits were involved in significantly more aggressive interactions per visit than were adults during the winter of 2001-2002 (mean: adult 0.54 aggressive interactions/visit; juvenile 0.64 aggressive interactions/visit; Table 3.7). There was no relationship between age and frequency of aggressive interactions in great tits during the winter of 2000-2001 or blue tits and coal tits in either winter. Sex did not influence the frequency of aggressive interactions in great tits, blue tits or coal tits (Table 3.7). Dominance status was not related to the frequency of aggressive interactions during either winter in great tits, blue tits or coal tits (Table 3.8).

	Sex or age factor	2000-2001		2001-2002	
		$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	sex	$0.38_{1,24}$	0.5	$0.23_{1,48}$	0.6
	age	$1.10_{1,24}$	0.3	$4.17_{1,48}$	<0.05
Blue tit	sex	$1.59_{1,14}$	0.2	$0.21_{1,21}$	0.7
	age	$2.00_{1,14}$	0.2	$0.00_{1,21}$	1.0
Coal tit	sex	$0.67_{1,14}$	0.4	$0.42_{1,20}$	0.5
	age	$0.14_{1,14}$	0.7	$2.11_{1,21}$	0.2

Table 3.7: Results of GLMs testing the relationship between sex (*n* values 2000-2001: great tits: male = 15, female = 10, blue tits: male = 7, female = 8, coal tits: male = 8, female = 7; 2001-2002: great tits: male = 29, female = 20, blue tits: male = 12, female = 10, coal tits: male = 11, female = 10) or age (*n* values 2000-2001: great tits: adult = 7, juvenile = 18, blue tits: adult = 6, juvenile = 9, coal tits: adult = 5, juvenile = 10; 2001-2002: great tits: adult = 34, juvenile = 15, blue tits: adult = 13, juvenile = 9, coal tits: adult = 14, juvenile = 8) and frequency of aggressive interactions.

	2000-2001			2001-2002		
	r_s	n	P	r_s	n	P
Great tit	0.20	24	0.4	-0.32	49	0.1
Blue tit	-0.31	15	0.3	-0.24	22	0.3
Coal tit	0.14	15	0.6	-0.30	22	0.2

Table 3.8: The results of Spearman's rank-order correlations between dominance status and the frequency of aggressive interactions.

3.5 Discussion

3.5.1 Stability of the hierarchy

The stability of a dominance hierarchy over an entire field season has important consequences for the extent to which the data can be analysed, particularly if one dominance index is to be used for each individual over the total time period of that field season (Gosler & Carruthers 1999). Unstable hierarchies, where the hierarchical order changes over the course of the winter, are more difficult to analyse because the dominance rank of any individual may not be static. Since the hierarchies in this study were shown to be stable between early and late winter, a single dominance index for each member of the dominance hierarchy was therefore sufficient to use for the duration of each field season (as also found by Gosler & Carruthers 1999).

3.5.2 Factors that determine dominance status

The dominance of males over females in social groupings is well recorded in many social taxonomic groups (Garnett 1981; Arcese & Smith 1985; Wagner & Gauthreaux 1990; Hogstad 1992; Tarvin & Woolfenden 1997) and may be due to the larger size and therefore greater strength of males compared to females in most species. The higher levels of circulating testosterone in males may also cause them to be dominant over females since testosterone has been shown to be linked to levels of aggression in some species (Harding 1981; Hau *et al.* 2000) though the amount of influence that testosterone has on aggression has been questioned (Canoine & Gwinner 2001; van Duyse, Pinxten & Eens 2002). Despite the physical and behavioural differences between males and females in many species, there are some social species where gender plays no part in the dominance hierarchy and the most dominant animal could easily be female *e.g.* the grey wolf (Mech 1991; Klinghammer pers. com). Less commonly, there are also some species (though limited) where females are usually dominant over males *i.e.* the spotted hyaena (Frank 1986).

The results of this study showed that males were dominant over females in all three species during both field seasons except for coal tits during the first field season (winter 2000-2001) and age was not related to dominance status in any of the species. Males have been shown to be dominant to females in some species of *Paridae*, particularly willow tits, which have featured in many studies of dominance relationships (Hogstad 1992; Koivula *et al.* 1995; Lahti *et al.* 1996; Barluenga, Moreno & Barbosa 2001; for review of earlier literature see Ekman 1989; Matthysen 1990). The relationship between age and dominance status in *Parus* species, though not uncommon, is less well documented that

that between dominance and sex (Hogstad 1992; Gosler 1993; Lahti *et al.* 1996; for review of *Parus* species see Ekman 1989; Matthysen 1990). Of the three species in this study, the relationship between age and dominance status has only been suggested for great tits in previous literature with adults usually, though not always, being dominant over juveniles (Gosler 1993).

The results from this study are similar to those of Wagner and Gauthreaux (1990) in that there was a relationship between dominance status and sex but not age. Wagner and Gauthreaux (1990) carried out studies on song sparrows *Melospiza melodia* and explained the relationship between dominance status and sex as being due to sexual size asymmetries that did not exist within the age categories (adults or juveniles). Of those studies that have found sex differences in Parids, none have provided evidence as to why the sexes differ in dominance status. In this study, body size was measured in males and females of all three species using the first principal component from a PCA of a number of biometrics (Chapter 2), and no relationship was found between body size and dominance status within the sexes. Though this suggests that differences were due to sexual factors rather than body size, it is possible that a lack of variation in body size within the sexes but not between the sexes may have produced this result. This is possible for great tits since the variance in body size of females was much less than that of the overall population (including both sexes) during both years (Appendix 3). There was no difference between the variances in body size within the sexes and that within the population in blue tits or coal tits.

Body size is important in determining dominance status in species that often resort to physical fights and tests of strength, such as the North American mountain sheep *Ovis canadensis* and *Ovis dalli* (Geist 1966). For the Paridae, which do not often participate in contests of strength but rather use posture displays (Hinde 1952; Gosler 1993) or attack by chasing their opponent (particularly in the coal tit), size or strength may not be as important and the results from all three species in this study support this view.

3.5.3 How random are interactions

Little work has been published on how flocking birds interact within a dominance hierarchy. Within grey wolf packs, interactions are non-random with individuals interacting in an agonistic manner with the animals immediately above and below them in the hierarchy, as well as with the omega wolf (the lowest ranking wolf), which is frequently attacked by all pack members (Busch, 1995; pers. obs.). Within red deer herds, animals are also more likely to interact with other deer that are of a similar dominance status in the hierarchy (Darling 1937; Freeman, Freeman & Romney 1992). It is most likely that great tits and coal tits interact with birds of similar or lower dominance status because those of similar status are the birds that pose the greatest threat and those of lower status can be easily displaced from a food resource. Within a dominance hierarchy such as those present in most Parids, all group members benefit from being higher up in the hierarchy (Ens & Goss-Custard 1984; Arcese & Smith 1985) so are more likely to challenge the individual immediately above them in rank and defend their position from the individual immediately below them. This will lead to all flock members interacting most with the animals directly above and below them in the hierarchy as well as with individuals of lower rank which they can displace from a food resource. Interactions between birds of similar status was probably most prominent in male great tits and coal tits but not females because of testosterone making males more competitive than females, especially in spring when males were competing for territories (Järvi, Walso & Bakken 1987; Silverin 1993; Wikelski, Hau & Wingfield 1999; Hau *et al.* 2000).

A similar study to this carried out by Gosler and Carruthers (1999), found that great tits from a population at Killarney National Park, Republic of Ireland, interacted in a random manner similar to the behaviour of blue tits in this study. It is possible that great tits interacted more with birds of a similar dominance status in this study because competition was high between great tits at West Hollingside due to the small number of territories containing nest boxes. Nest boxes were at a high density in West Hollingside allowing male great tits to have several nest boxes within their territory but overall, few boxes were available for use by great tits.

The higher proportion of blue tits nesting in boxes (from those males visiting the feeders in spring) at West Hollingside compared to that of great tits suggests that competition for territories with nest boxes was not as high as that experienced by great tits since a much smaller proportion of great tits were able to secure nest boxes (Table 3.9). This supports the previous theory that competition was high in great tits because the number of males visiting the feeders in spring was much higher than the number of territories with nest boxes available. The lack of relationship between blue tit dominance rank and the mean rank of the birds that each blue tit interacted with also suggests a less competitive dominance hierarchy in blue tits compared to great tits (Gosler & Carruthers 1999).

	Winter season 2000-2001 visiting	**Breeding season 2001** nesting	**Winter season 2001-2002** visiting	**Breeding season 2002** nesting
Great tit	18	6	26	8
Blue tit	18	17	18	23

Table 3.9: The numbers of male blue tits and great tits visiting the feeders during the late winter and the numbers of those species that subsequently secured nest boxes.

3.5.4 Frequency of aggressive interactions

The lack of relationship between dominance status and the frequency of aggressive interactions in all three species during both field seasons in this study does not support the work of Järvi and Bakken (1984). Since Järvi and Bakken (1984) also studied great tits, it is possible that environmental factors may be involved, such as food supply or flock structure.

The difference in the frequency of aggressive interactions between juvenile and adult great tits during the 2001-2002 field season may have reflected the higher levels of competition between juvenile birds at the feeding area compared to adults. Because juvenile birds have a lower probability of survival in winter than adults due to their lack of experience at finding food (Hogstad 1989; Gosler 1993; Carrascal *et al.* 1998) they may rely more heavily on a supplementary food source and therefore have more incentive than adults to interact over a food source that they are familiar with.

3.5.5 Temporal variations in activity

The increase in the number of all three species visiting the feeders as the season progressed was expected since the abundance of natural food diminishes over the course of the winter (Pulido & Diaz 2000) probably forcing more birds to rely on supplemental food. It is also possible that more birds, particularly juveniles that were not born in the study area, found the supplementary food supply as the winter progressed and they increased their search range for food. The increase in the frequency of aggressive interactions from early to late winter in all three species probably arises from the increased competition levels associated with a limited food resource during winter conditions when natural food supply is already reduced (Pulido & Diaz 2000). Aggression levels may also be caused to rise in all three species with the onset of spring and the acquisition of breeding territories and mates (Gosler 1993).

The reasons why coal tits and great tits (during 2001-2002) became more aggressive during the course of the day are not clear from this study, though since the visit rate also increased in coal tits, this seems to support the idea that coal tits were under added pressure compared to great tits and blue tits as the day progressed. Since coal tits are smaller than both blue tits and great tits and therefore need a greater amount of energy to maintain body temperature overnight (Kendeigh 1970, 1972), they may have to increase their food intake rate more than the other species as dusk approaches and competition may therefore be intense.

3.5.6 Conclusions

Males were generally dominant over females in all three study species. This coincided with males being larger on average than females in great tits but not in blue tits or coal tits. Thus other factors such as circulating testosterone levels are probably also important in determining sexual differences in dominance status in blue tits and coal tits. To test whether inter- or intraspecific variation in dominance status is related to circulating testosterone levels, birds of both sexes could have their testosterone levels experimentally increased or decreased and any change in dominance status observed. Similar studies of this type have recently been carried out using house sparrows *Passer domesticus*, which have found that testosterone is related to bib size which is associated with dominance status in this species (Evans, Goldsmith & Norris 2000; Buchanan *et al.* 2001).

Great tits and coal tits did not interact within their dominance hierarchy in a random manner, but were more likely to initiate aggressive interactions with birds of similar or lower dominance status, possibly because those are the birds that present the greatest threat and the birds that an individual might benefit most from confronting. There was only weak and inconsistent evidence for any relationship between dominance status and the frequency of aggressive interactions.

Chapter 4

Individual differences in seed handling time and vigilance: an effect of dominance?

4.1 Abstract

An individual's ability to forage efficiently may depend on several factors such as dominance status, experience, body size or strength and will have important consequences for winter survival, particularly in juveniles. Food handling time also contributes to foraging efficiency and may have different consequences depending on the species and type of prey involved. This study found that seed handling times and vigilance levels of great tits, blue tits and coal tits, were subject to temporal variation with regards to date and time of day. Differences in bill depth between male and female blue tits probably accounted for differences in their seed handling times, but there were insufficient data to test whether or not bill depth could explain differences in seed handling time within the sexes. Vigilance in coal tits was affected by body size and dominance status, with the latter being well represented in previous literature.

4.2 Introduction

Foraging efficiency has important consequences for energy acquisition, which can have profound effects on mating opportunities and territory defence. High foraging efficiency can result in a better body condition, which will increase the probability of an individual surviving the winter (Goss-Custard *et al.* 1995; Illius *et al.* 1995). The less time that an individual spends foraging, the more time is available for other activities such as finding a mate and territory acquisition, which can determine how many recruits an individual contributes into the breeding population. Foraging efficiency is determined by an individual's ability to locate prey items or a food patch (Day *et al.* 2001), the ability to manipulate that prey item quickly and to gain the maximum nutritional value from it (Vince 1964; Benkman 1987, 1988; Gosler 1987; Johnson, Giraldeau & Grant 2001), vigilance whilst searching for prey or handling prey (which can affect survival positively but foraging efficiency negatively) (Goss-Custard, Cayford & Lea 1999; Fritz, Guillemain & Durant 2002) and the susceptibility of that individual to interference competition from conspecifics or other species (which can reduce foraging efficiency) (Norris & Johnstone 1998; Leeman *et al.* 2001).

An individual's ability to find a food patch is difficult to measure in the Paridae because of their arboreal lifestyle and small size. Foraging efficiency is therefore best measured using the remaining factors that contribute to an individual's ability to forage effectively: food handling time, vigilance and susceptibility to interference competition (See: Chapter 5).

4.2.1 Importance of food handling times

Birds with long food handling times need to spend more time foraging to acquire the same energy as individuals with shorter food handling times leaving less time for interacting with conspecifics and defending territories (Benkman & Pulliam 1988). Since long food handling times and therefore low foraging efficiency means that birds may have to feed in the open for longer, birds with longer food handling times may also be at a higher risk from predation (Lendrem 1984; Popp 1988; Fritz, Guillemain & Durant 2002).

Among seed-eating birds, the variation in the time spent handling a food item between and within species has been demonstrated to be dependent on the musculature surrounding the bill (Benkman & Pulliam 1988; Marchetti & Price 1989), the technique of extracting the seed from the husk (Vince 1964) and the time spent being vigilant during the food handling process (Popp 1988). Seed-eating birds often have bill specializations allowing them to concentrate their efforts on seed types that are most profitable to them, and this controls resource partitioning. For instance Crossbills *Loxia* sp. have a bill structure where the upper and lower mandibles are crossed allowing them to successfully extract seeds from conifer cones (Snow & Perrins 1998), which other species only achieve with great difficulty. Slight variations in the structure of bill allow different species of crossbill to be more specialized for feeding on conifer cones from different tree species (Benkman 1987). Compared to other seed-eating birds such as tits (which feed on insects during the summer) finches (*e.g.* greenfinches *Carduelis chloris* and hawfinches *Coccothraustes coccothraustes*) have stout bills for manipulating extremely hard seeds that other groups of birds find impossible to handle (Snow & Perrins 1998). Hawfinches, which have the most powerful bills within the finches, can use their bills to exert a force of 50Kg (Snow & Perrins 1998).

4.2.2 Factors affecting foraging efficiency and food handling times

Though numerous studies have considered how foraging efficiency or overall intake rate are affected by factors such as age, sex and dominance status, few studies have considered food handling times of individuals with respect to these factors (Greig, Coulson & Monaghan 1983; Stevens 1985; Gosler 1987; Goss-Custard & Durell 1987a; Pöysä 1988; Marchetti & Price 1989; Caldow *et al.* 1999). The lack of published literature regarding food handling times may reflect a difficulty of measuring food handling times in many species.

There is only one published account to suggest that a difference in foraging efficiency exists between males and females (Gosler 1987), but juveniles have often been reported to have lower foraging efficiency compared to adults, particularly in those species where food is difficult to find or to manipulate (Greig, Coulson & Monaghan 1983; Goss-Custard & dit Durrell 1987a; Caldow *et al.* 1999). Variation in food handling times has generally only been compared between similar bird species, and has usually been attributed to differences in ability to manipulate food items relating to differences in body size or bill structure (Grant 1981; Pulliam 1985; Benkman 1987, 1988; Benkman & Pulliam 1988). Bird species that have greater muscle mass surrounding the bill are generally faster at seed handling than those with less musculature (Pulliam 1985; Benkman & Pulliam 1988). Within species, it is not known whether differences in the musculature surrounding the bill or body size cause variation in seed handling ability. With regards to the three species in this study, the differences in body size between individuals within species are small (Svensson 1992) compared to those in previous studies that have looked at differences in seed handling times between closely related species (Pulliam 1985; Benkman & Pulliam 1988).

Great tits and blue tits feed on insects during the breeding season and switch to a seed dominated diet during the winter months when insect abundance is much reduced (Perrins 1979; Gosler 1993; Harrap & Quinn 1996; Snow & Perrins 1998). They feed on seeds by clamping them to a branch with both feet and hammering them until a hole is made, allowing the seed contents to be extracted and consumed (Vince 1964). Because of the specialized way in which tits feed and the manipulation that is required, it has been reported that although seed handling technique is innate in great tits, it can be improved by practice (Vince 1964). Thus differences in seed handling times are likely to be especially pronounced between adults and juveniles.

With regards to dominance status, it has been reported that dominant individuals tend to have higher intake rates and foraging efficiencies than subdominant conspecifics (Goss-Custard, Durell & Ens 1982; Pöysä 1988).

This could arise from dominant individuals excluding subdominant birds from the most profitable feeding areas in terms of high productivity or reduced predation rates (Alatalo & Moreno 1987; Grubb & Woodrey 1990; Suhonen 1993; Barbosa, Barluenga & Moreno 2000; Revilla & Palomares 2001) or from subdominants having to increase their vigilance levels (discussed in Section 4.2.3). The exclusion of subdominants from the more profitable areas has been recorded in tits when foraging in trees (Hogstad 1988; Brotons *et al.* 2000). In this study, birds visited a supplementary food source where they were subject to the same food profitability and predation risks regardless of their dominance status, allowing me to examine effects of dominance status *per se* as opposed to indirect effects related to foraging location.

4.2.3 Vigilance behaviour

In flocking birds such as the majority of *Parus* species, where individuals feed in close proximity to each other and dominance hierarchies exist, there have been conflicting results as to the relationship between dominance status and vigilance. Krams (1998b) provided evidence that dominant great tits benefited from their own vigilance and did not rely on that of subdominant birds. In contradiction to this, other studies on both homospecific and heterospecific flocks have found that dominant birds reduce their vigilance and benefit from the vigilance of subdominants whilst subdominants need to have higher vigilance in order to monitor conspecifics when feeding within flocks (Ekman 1987; Waite 1987a, 1987b; Pravosudov & Grubb 1999; Smith, Ruxton & Cresswell 2001). The explanation for dominants having lower vigilance than subdominants may stem from the fact that dominant birds need only to be vigilant in order to detect predators, whereas subdominant birds need to be vigilant in order to detect predators but also to monitor other birds within the group that may try to displace them because of their lower social status (Waite 1987a, 1987b; Pravosudov & Grubb 1999).

The principal aim of this study was to test whether seed handling times and vigilance levels differed within species in great tits, blue tits and coal tits. I hoped to find how seed handling times and vigilance levels were governed in these species and to examine the role of age, sex, body size and dominance status.

4.3 Methods

The methods for calculating the dominance hierarchies are explained in Chapter 2 and the methods of testing the dominance hierarchies are presented in Chapter 3.

4.3.1 Food handling observations

Colour-ringed great tits and blue tits (see Chapter 2 for details of how the birds were captured and the biometric data that were collected) were observed visiting an artificial feeder supplemented with black sunflower seeds on 52 days between November 2001 and February 2002, amounting to 172 hours of observations. When great tits or blue tits arrived at the feeder they would remove one seed and then retreat to a nearby bramble *Rubus fruticosus* patch approximately 1.5 metres high and 1 metre in length, situated approximately four metres from the field station where all observations took place. On some occasions, individuals would leave the observation area and handle the seed elsewhere, in which case, seed handling times could not be recorded.

The seed handling times of the individual birds, identifiable from their colour rings, were measured to the nearest second whilst they were in the bramble patch. Timing commenced when the bird made its first attempt to crack open the seed husk and was continuous throughout feeding on that particular food item including during periods of vigilance. Timing stopped when the bird dropped the bottom half of the husk indicating that it had eaten the seed (pers.

obs), which was usually followed by bill cleaning or a change in the direction that the bird was facing.

Food handling data that were collected in the presence of another bird and hence may have been affected by interference competition, were distinguished from data gathered when a bird was feeding alone (and the data are presented in Chapter 5). The bramble patch that was used by birds whilst handling seeds was isolated from other suitable perches so that interference could be quantified. In the instances when a bird left the area without finishing its food item or if it accidentally dropped the seed it was handling, the data were eliminated from all further analysis.

Food handling behaviour was not observed in coal tits because they tended to remove seeds from the feeder and fly out of the observation area either to consume the seeds, or to hoard them for consumption later. Coal tits did not remain in the vicinity of the observation area to consume sunflower seeds often enough to produce adequate data for analysis. Any birds that did remain in view were usually too high up in the canopy for me to accurately determine when seed handling began or was completed.

4.3.2 Vigilance Observations

Vigilance behaviour was observed from the same observation point as the food handling behaviour over 26 days (on different days from the seed handling observations) between November 2001 and February 2002, amounting to 83 hours of observations. Because measuring vigilance behaviour required a good view of the feeding birds so that every vigilance event could be recorded, vigilance observations could not be carried out on birds that were feeding in the bramble patch because the density of vegetation made it difficult to see the entire bird. The feeders were therefore supplemented with bird cake (lard mixed with black sunflower seeds) rather than sunflower seeds on days that vigilance observations were carried out. Bird cake encouraged birds to remain on the feeders for longer whilst food handling due to the consistency of lard, which does not allow large pieces to be broken off and carried off to be consumed elsewhere. It was therefore most profitable for birds to remain on the feeder breaking off small pieces of bird cake and consuming them in situ.

Great tits, blue tits and coal tits were timed whilst consuming bird cake on the feeders and the number of vigilance behaviours was documented for each feeding observation. Vigilance behaviours were identified as the periods when the bird raised its head so that it was higher than the horizontal plane of the body; which may or may not have been followed by the bird scanning the vicinity (Beveridge & Deag 1987). A vigilance rate (per minute) was then calculated for each feeding bout by dividing the number of vigilance behaviours by the time spent feeding (*i.e.* when the bird started eating until it left the feeder). A mean vigilance rate was calculated for each bird after controlling for temporal factors (time of day and date of year). Food handling behaviour could not be considered at this time because there was no way of knowing how much food had been taken during each feeding bout.

4.3.3 Statistical Analysis

For all statistical analysis, data for individual birds were used only if the bird had been timed handling a seed more than five times or been observed for vigilance behaviour more than five times. REMLs were used to determine the effects of time of day and date (days since the observations began) on seed handling times and vigilance. Residuals from those results that were significant were used as data from then onwards to control for these effects.

A Pearson's correlation was used to test the significance of the relationship between vigilance and seed handling time in great tits and blue tits (because seed handling times were not collected for coal tits, this was not possible for the species). GLMs were used to test the effects of sex and age on seed handling times and vigilance levels, and in order to test for a relationship between body size and seed handling time or vigilance, the first principal component from a PCA of the biometrics described in Chapter 2 was used as the independent variable in a linear regression. Spearman's rank-order correlations were used to test the significance of the relationship between dominance status and seed handling time or vigilance.

4.4 Results

4.4.1 Temporal variation

The results from REML analysis using date and time as fixed factors and individual bird as a random factor, demonstrated that the seed handling times of great tits varied with date but those of blue tits did not (Table 4.1). There was no distinct pattern as to how great tit seed handling times varied with date. Seed handling times of both great tits and blue tits varied with time of day and those of both species tended to decrease with increasing time of day (Figure 4.1). Residuals from the REML models of great tit and blue tit seed handling times were used to measure the seed handling times from this point onwards, with a single mean residual calculated for each bird.

	Date		**Time**	
	Wald $(\chi^2)_{d.f.}$	***P***	***Wald*** $(\chi^2)_{d.f.}$	***P***
Great tit	$20.92_{11,1441}$	<0.05	$2240.39_{1109,1441}$	<0.001
Blue tit	$57.34_{48,419}$	0.2	$814.15_{327,419}$	<0.001

Table 4.1: REML analysis results of the effects of date (days since the observations began) and time of day (proportion of daylight hours) on the seed handling times of great tits (*n* = 55) and blue tits (*n* = 34).

REML analysis, producing a model in the same way as was done for seed handling times, indicated that great tit vigilance was not affected by temporal factors during this study. Vigilance in blue tits and coal tits however, was affected by both date and time of day (Table 4.2). The vigilance of coal tits tended to increase with date (Figure 4.2) but there was no pattern in the variation of the vigilance of blue tits with date. The vigilance of both species decreased with time of day (Figure 4.3). Residuals from the blue tit and coal tit vigilance models when testing the effects of date and time of day were used to measure vigilance for the rest of the study, after calculating a mean vigilance for each bird.

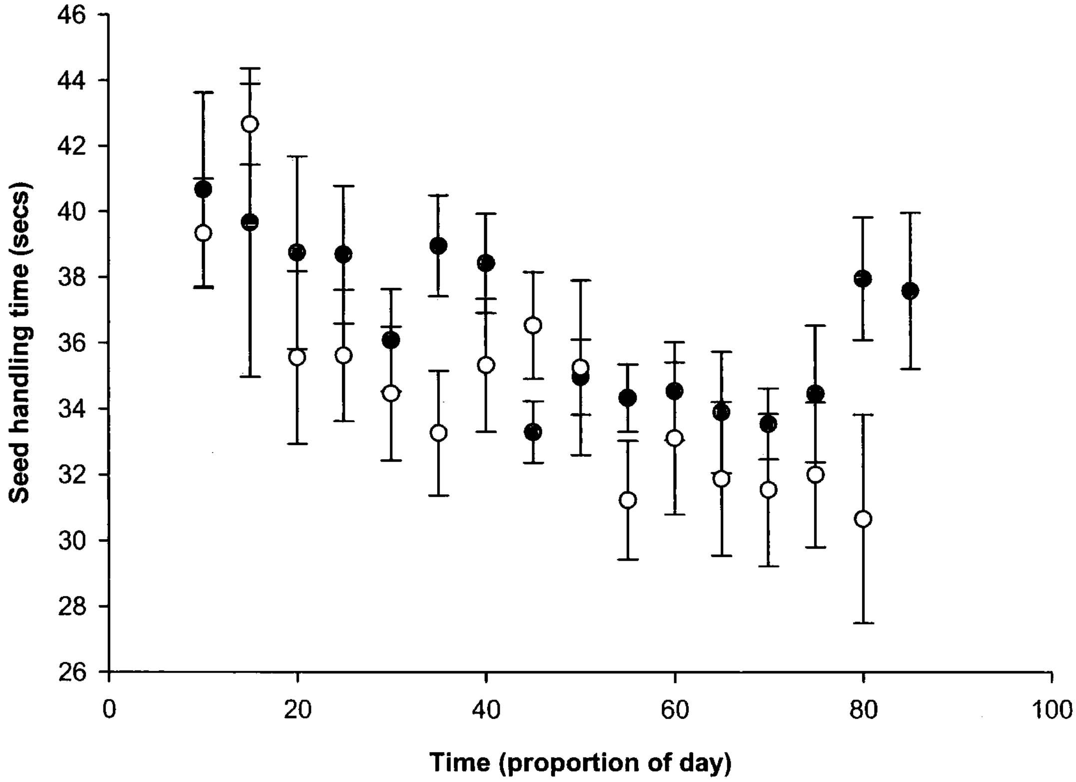

Figure 4.1: The negative relationship between the seed handling times of great tits (•) and blue tits (o) and time of day (proportion of daylight hours).

	Date		Time	
	Wald (χ^2)$_{d.f.}$	*P*	*Wald* (χ^2)$_{d.f.}$	*P*
Great tit	$10.77_{6,312}$	0.1	$187.05_{283,312}$	1.0
Blue tit	$13.04_{6,148}$	<0.05	$527.36_{137,148}$	<0.001
Coal tit	$154.80_{17,490}$	<0.001	$1510.49_{461,490}$	<0.001

Table 4.2: REML analysis results of the effect of date (number of days since observations began) and time of day (proportion of daylight hours) on the vigilance of great tits (*n* = 38), blue tits (*n* = 20) and coal tits (*n* = 26).

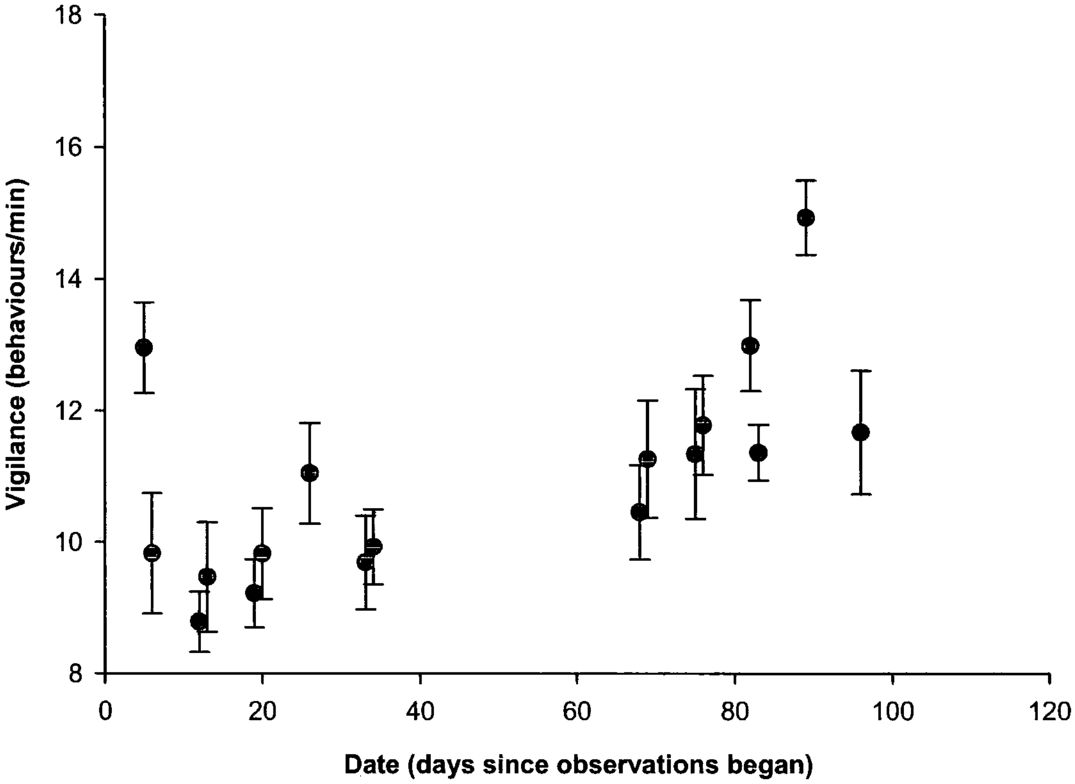

Figure 4.2: The positive relationship between the vigilance of coal tits and date (days since observations began on 1st November 2001).

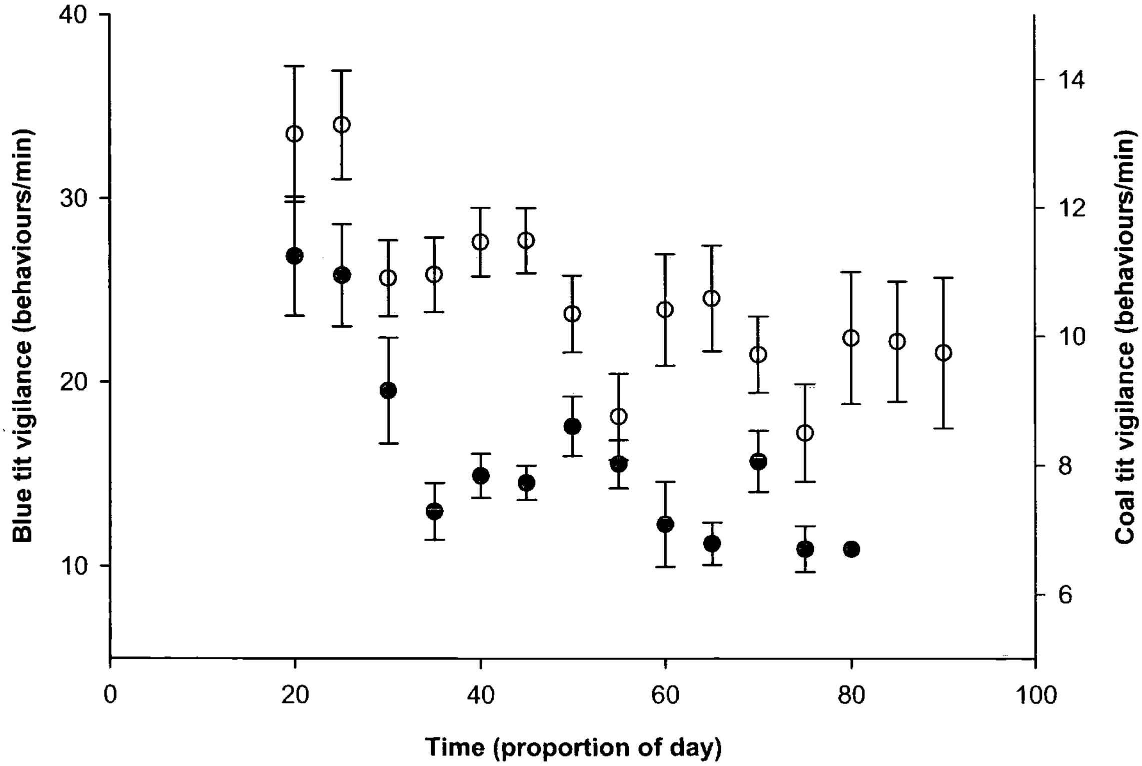

Figure 4.3: The negative relationship between vigilance and time of day (proportion of daylight hours) in blue tits (•) and coal tits (o).

4.4.2 Relationship between seed handling time and vigilance

There was a positive relationship between the seed handling times of great tits when feeding on sunflower seeds in the bramble and their vigilance when feeding on bird cake in the open (Figure 4.4) (r = 0.66, n = 24, P<0.001) but there was no relationship between the seed handling times of blue tits in the bramble and their vigilance levels whilst foraging on the feeders (r = -0.24, n = 21, P = 0.4).

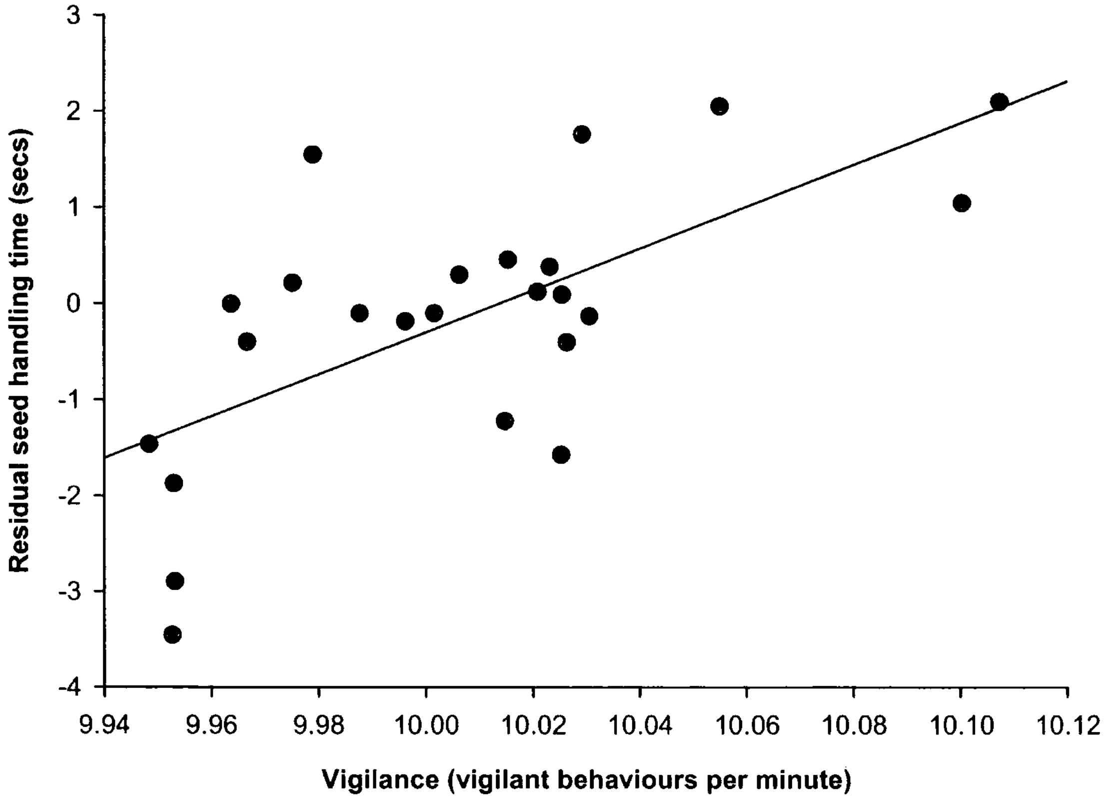

Figure 4.4: The positive relationship between the vigilance of great tits and their residual seed handling times (corrected for date and time of day).

4.4.3 Effects of age and sex

The seed handling times or vigilance levels of great tits were not affected by the age or sex of individuals (Table 4.3). Seed handling times were not related to age but were significantly related to sex in blue tits, with males having shorter seed handling times than females (Figure 4.5). Vigilance levels of both blue tits and coal tits were not related to age or sex (Table 4.3).

	Sex		Age	
	$F_{d.f.}$	*P*	$F_{d.f.}$	*P*
Seed handling times				
Great tit	$2.16_{1,31}$	0.2	$1.60_{1,31}$	0.2
Blue tit	$8.91_{1,22}$	<0.01	$2.32_{1,22}$	0.2
Vigilance				
Great tit	$1.04_{1,28}$	0.3	$0.78_{1,28}$	0.4
Blue tit	$0.20_{1,17}$	0.7	$0.35_{1,20}$	0.6
Coal tit	$0.95_{1,16}$	0.3	$0.32_{1,16}$	0.6

Table 4.3: Results of GLMs showing the effect of age and sex on seed handling times (*n* values: great tits: male = 20, female = 12, adult = 23, juvenile = 9; blue tits: male = 12, female = 11, adult = 14, juvenile = 9) and vigilance (*n* values: great tits: male = 20, female = 9, adult = 19, juvenile = 10; blue tits: male = 9, female = 9, adult = 13, juvenile = 8; coal tits: male = 9, female = 8, adult = 10, juvenile = 7) of all three species (coal tits have vigilance data only).

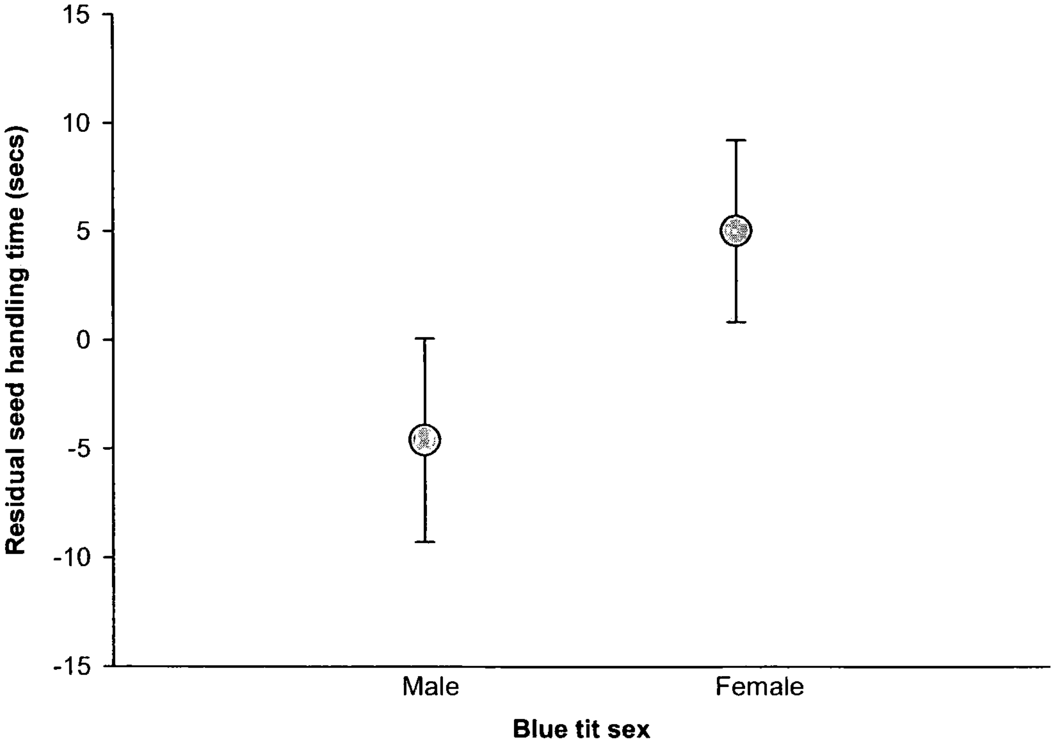

Figure 4.5: The effect of sex on the mean (with 95% confidence intervals) residual seed handling times of blue tits (corrected for time of day).

4.4.4 Effect of body size

Seed handling times of great tits and blue tits were not related to their body size as represented by PC1 (great tit: $r^2 = 0.02$, $F_{1,27} = 0.41$, $n = 28$, $P = 0.5$; blue tit: $r^2 = 0.05$, $F_{1,19} = 0.86$, $n = 20$, $P = 0.4$). There was no relationship between the vigilance levels of great tits or blue tits and body size (great tit: $r^2 = 0.05$, $F_{1,23} = 1.34$, $n = 24$, $P = 0.3$; blue tit: $r^2 = 0.08$, $F_{1,13} = 1.0$, $n = 14$, $P = 0.3$). Coal tit vigilance levels were related to body size ($r^2 = 0.45$, $F_{1,15} = 11.53$, $n = 16$, $P<0.01$) in that larger coal tits were less vigilant (Figure 4.6).

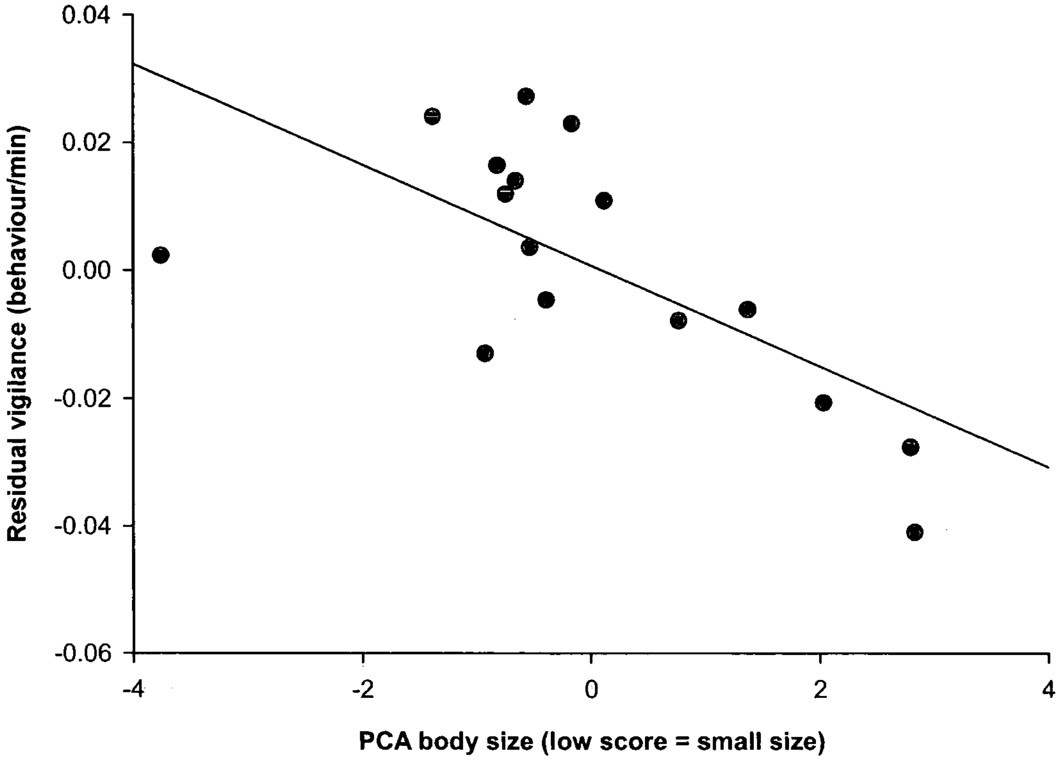

Figure 4.6: The relationship between body size (PCA of wing length, body mass, bill length, head plus bill length, tarsus length and tail length) and residual vigilance (controlled for date and time) in coal tits.

4.4.5 Effect of dominance status

There was no relationship between dominance status and seed handling times in great tits ($r_s = 0.07$, $n = 30$, $P = 0.7$) or in male or female blue tits (male: $r_s = 0.64$, $n = 12$, $P = 0.1$; female: $r_s = 0.25$, $n = 7$, $P = 0.5$). Dominance status was not related to vigilance in great tits (r_S = -0.04, n = 29, P = 0.8) or blue tits (r_S = -0.10, n = 15, P = 0.7). Coal tit vigilance levels were positively correlated with dominance status (Figure 4.7; r_S = 0.64, n = 16, P<0.01): subdominant coal tits spent more time being vigilant than dominant birds.

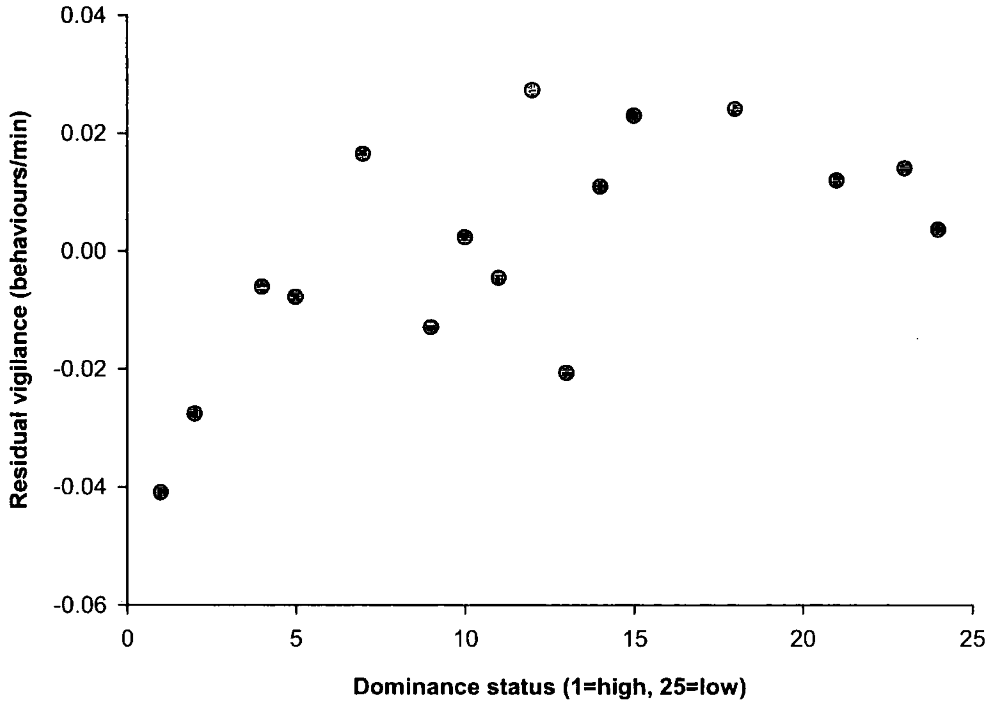

Figure 4.7: Positive relationship between the dominance status of coal tits and their residual vigilance (controlled for date and time).

4.5 Discussion

4.5.1 Temporal effects on seed handling time and vigilance

There is little published literature to suggest why the seed handling times or vigilance rates of flocking passerines may vary systematically with time of day or date of year (Gosler 2001). The increase in vigilance with date in coal tits may have resulted from increased predation risk since the numbers of birds within a particular flock are likely to decrease over the course of the winter as juvenile birds die (Hogstad 1989; Gosler 1993; Carrascal *et al.* 1998). Many studies on other species have highlighted a decrease in vigilance with increasing flock size and also vice versa (Blumstein, Evans & Daniel 1999; Lima, Zollner & Bednekoff 1999; Boysen, Lima & Bakken 2001). The reported decrease in vigilance with time of day in blue tits and coal tits may result from these birds taking more risks later in the day by reducing their vigilance as they try to find and consume enough food to provide them with the energy resources needed to survive the night.

4.5.2 Seed handling times and vigilance in relation to each other

Great tits with longer seed handling times were more vigilant when feeding in the open than those birds with short seed handling times. This supports studies that have demonstrated that higher vigilance has a negative effect on intake rates in both mammals (Underwood 1982; Baack & Switzer 2000) and birds (Lendrem 1984; Fritz, Guillemain & Durant 2002). However, in this study, seed handling times and vigilance rates were measured at different times and in different areas (*i.e.* seed handling times were measured in a sheltered area and vigilance was measured in an open area, though the areas were only 3m apart). Because seed handling times and vigilance were measured at different times, and a relationship was apparent such that would be expected if both were measured together, this strongly suggests that longer seed handling times are caused by birds having higher vigilance and that the vigilance of an individual may not change between a covered and an open site. Vigilance data would however need to be collected from the covered site to confirm this.

4.5.3 The effects of sex and age on seed handling times

The lack of relationship between seed handling times and sex in great tits supports the results of most previous work comparing intake rates and handling times of male and female animals (Fritz, Durant & Guillemain 2001; Gillingham, Parker & Hanley 1997). The difference in seed handling times between male and female blue tits is similar to the results of one previous study great tits which also found that males had shorter food handling times than females (Gosler 1987) and this was attributed to bill index (the relationship between bill length and depth). Bill strength has been shown to be important in seed handling and therefore, it is possible that the difference arose due to males being stronger than females and having more muscle around the bill allowing them to handle sunflower seeds more efficiently (Benkman & Pulliam 1988; Marchetti & Price 1989). Further data are required to test this hypothesis.

Another factor that could cause differences in seed handling times between males and females is a difference in bill depth. It has been established that bill depth is important in dehusking large seeds when similar species have been compared (Grant 1981; Benkman 1987). In this study, males had deeper bills than females in February 2003 (Appendix 5). Differences in the bill proportions of males and females have also been noted in oystercatchers *Haematopus ostralegus* (Durrell, Goss-Custard & Caldow 1993), serins *Serinus serinus* (Björklund & Senar 2001), great tits (Gosler 1987) and many sexually monomorphic seabirds (Vanfraneker & Terbraak 1993; Palomares *et al.* 1997). Though bill depth could not be related to seed handling times in this study because the comparison of bill depths was measured one year after the seed handling observations were completed, it is likely that bill depth accounts for the difference in seed handling times because of the evidence from past studies linking handling times to bill depth.

It has been reported in many avian species that adults have higher intake rates than juveniles (Greig, Coulson & Monaghan 1983; Stevens 1985; Goss-Custard & dit Durrell 1987a, 1987b), which could lead to higher juvenile mortality in winter (Hogstad 1989). The higher mortality of juveniles in winter is thought to arise from juveniles' inexperience at finding food rather than from longer food handling times (Verhulst 1992). Though it has been found that great tits improve their seed handling techniques with time (Vince 1964), there was no difference between the seed handling times of adult and juvenile great tits or blue tits in this study. An explanation for this may be that sunflower seeds had been provided continuously from the breeding season throughout autumn and winter, and therefore juvenile birds were likely to have had sufficient time to become experienced at manipulating the seeds before the observations for this study began in October 2001.

4.5.4 Dominance and seed handling times

Cook and Cockrell (1978) proposed that subdominant birds would take longer to handle seeds if they spent more time cleaning the husk in order to maximise their energy gain from each seed since they may be prevented from obtaining more food by higher ranking birds. It is known that in some *Parus* species, dominant individuals do prevent subdominants from obtaining the most profitable food resources (Ekman & Askenmo 1984; Ekman 1986, 1987; Hogstad 1988). The higher vigilance of subdominant birds brought about by their need to observe more dominant individuals (Waite 1987a, 1987b; Goss-Custard, Cayford & Lea 1999; Pravosudov & Grubb 1999; Smith, Ruxton & Cresswell 2001) could also lead to a relationship between seed handling time and dominance status. However, the seed handling times of great tits and blue tits were not significantly related to dominance status in this study, possibly as a result of the observations being made during feeding bouts when no other birds were nearby. Dominance status may therefore only influence seed handling times when other birds are in the vicinity of the feeding bird.

4.5.5 Correlates of vigilance

Although no relationship was apparent between body size and vigilance in great tits or blue tits, larger coal tits were less vigilant than their smaller conspecifics. Since body size is not related to dominance status (See: Chapter 3), the lower vigilance of larger birds could not have been brought about by a higher dominance status (see below). It is therefore unclear why larger birds should be less vigilant.

The negative relationship between vigilance and dominance rank has been well documented (Goss-Custard, Cayford & Lea 1999; Pravosudov & Grubb 1999; Smith, Ruxton & Cresswell 2001) and is supported by the results from coal tits in this study. The explanation that has been proposed for this relationship is that dominant animals use vigilance to detect predators whereas subdominant animals also use vigilance as a means of monitoring more dominant animals since they are more likely to be subject to kleptoparasitism or displaced from a feeding perch (Waite 1987a, 1987b; Pravosudov & Grubb 1999; Blumstein, Daniel & Evans 2001). Although subdominant coal tits in this study were not subject to kleptoparasitism whilst feeding, they were often displaced from the feeding tables, thus making it profitable for them to remain vigilant in order to detect these attacks and so avoid them.

A relationship between dominance status and vigilance was not detected in great tits or blue tits. It is probable that subdominant blue tits did not increase their vigilance because blue tits usually visited the feeders alone and therefore interactions were not as frequent as in great tits and coal tits (per. obs.), making it more profitable for blue tits to spend most of their time feeding or being vigilant only for predators. The differences in the types of interactions most common in great tits and coal tits may account for the lack of relationship between dominance status and vigilance in great tits. During interactions between great tits on a feeder, the dominant bird approached the subdominant bird and displayed for a few seconds before the subdominant bird left the feeder. This allowed the subdominant individual to hold onto the food item that it was eating as it flew away. Dominant coal tits however, ambushed subdominants as soon as they arrived in the vicinity of a feeding subdominant bird and therefore subdominants usually dropped the food item that they were eating and may have been chased for some distance. Because coal tits were more likely to loose their food and may be denied access to the resource for some time, it is probably more profitable for them to be vigilant for dominant birds so that they can leave the feeder with a food item before being attacked.

4.5.6 Conclusions

This study provided evidence that temporal factors (both date and time of day) were important in determining seed handling times and vigilance to some extent in Parids. Male and female blue tits differed in their ability to handle seeds, which was not explained by differences between sexes in body size, bill length or dominance status, but may have been related to differences in bill depth.

Dominance status and body size were both important in determining vigilance levels in coal tits. The relationship between dominance status and vigilance is well documented in previous studies (Pravosudov & Grubb 1999; Smith, Ruxton & Cresswell 2001) and has been attributed to subdominants needing to be vigilant for predators as well as for more dominant birds that may displace them.

Chapter 5

The incidence of interference competition in great tits: the costs of flocking

5.1 Abstract

The presence of competitors can have an adverse effect on the foraging efficiency or intake rates of foraging birds despite individuals choosing to forage within social groups. The decrease in foraging efficiency caused by the presence of conspecifics or heterospecifics is termed interference competition and is thought to result primarily from individuals increasing their personal vigilance to monitor dominant flock members. Most evidence for interference competition has come from studies of oystercatchers *Haematopus ostralegus* (where interference is related to kleptoparasitism) or blackbirds *Turdus merula*, but has not been quantified in the Paridae. Great tits were found to suffer from interference competition when feeding with another conspecific and with at least one other titmouse. The change in foraging efficiency due to interference competition was related to the dominance status of individual great tits when feeding with at least one other titmouse but not when great tits were feeding with a conspecific. Despite the results of previous studies, juvenile great tits did not suffer from interference competition to any greater extent than adults. Foraging efficiency decreased with increasing group size, from one to four individuals.

5.2 Introduction

5.2.1 Costs and benefits of social foraging

The mechanisms underlying social foraging have been a popular topic for research, principally because awareness of the factors that underpin such activities can help scientists to understand and develop optimal foraging models. For species that are involved in social foraging, per capita food intake rate increases to a higher level than that which can be achieved when foraging alone (Pulliam 1985; Grubb 1987; Ranta *et al.* 1996; Beauchamp 1998). Despite the increase in intake rate that individuals benefit from when foraging in groups, any food resources that are located have to be shared amongst more foragers. When this occurs, individuals benefit from group foraging to different degrees, usually dependent on either social dominance within the group or the strategies adopted by certain individuals (*e.g.* producers vs. scroungers) (Baker *et al.* 1981; Ekman 1987; Hogstad 1988; Pöysä 1988; Ranta *et al.* 1996). Evidence to support the producer-scrounger theory comes from studies which show that some individuals consistently find food that is then consumed by other group members, whilst other individuals spend their time exploiting food found by others rather than attempting to find food by themselves (Ranta *et al.* 1996; Barta & Giraldeau 1998; Marchetti & Drent 2000).

5.2.2 Interference competition defined

An individual's competitive ability in social foraging populations is important in determining its reproductive success and probability of survival (Dhondt & Eyckerman 1980; Gustafsson 1988; Norris & Johnstone 1998; Oddie 2000). The energy intake rate of an individual and the way in which this is altered by the presence of group members is governed by that individual's ability to compete for resources (Caldow *et al.* 1999). The temporary decline in intake rate that is often reported to occur when individuals feed in close proximity to each other has been defined as interference competition (Stillman, Goss-

Custard & Caldow 1997; Caldow *et al.* 1999). The variation in susceptibility to interference between individuals contributes to the distribution of foragers across a patchy food supply (van der Meer & Ens 1997; Sutherland & Parker 1998; Tregenza & Thompson 1998). This variation differs with respect to particular factors such as dominance status, food type, patch size and competitor density (Ens & Goss-Custard 1984; Cresswell 1998; Norris & Johnstone 1998; Stillman *et al.* 2000). Studies that look at the factors governing interference supply valuable data that assist in our understanding of the foraging distributions of individuals with differing competitive ability.

Interference competition can be classified as one of two types: active or passive. Active interference competition includes aggression between two individuals which forces one of the individuals to leave that particular patch, kleptoparasitism (the stealing of one individual's food by another) or avoidance of competitors in an attempt to reduce these encounters (Krebs & Davies 1993; Sutherland & Parker 1998). Passive interference competition may occur without an individual trying to cause the reaction *e.g.* through resource depletion resulting in longer search times (this is often termed exploitation competition), through prey disturbance when an individual disturbs prey which another forager would otherwise have found or through changes in the direction of the search path of one individual to avoid collisions with another (Charnov, Orians & Hyatt 1976). Active interference competition is more easily observed and measured than passive interference since there is often no interaction visible during passive interference competition and no way of predicting what the outcome would have been with no disturbance.

5.2.3 Previous studies

Many of the studies that have investigated interference competition in birds have concentrated on the effects of conspecific group size on the intake rates of individuals (Ens & Goss-Custard 1984; Cresswell 1997, 1998; Stillman, Goss-Custard & Caldow 1997). They have focused mainly on relatively few avian species, in particular oystercatchers *Haematopus ostralegus* (Ens & Goss-Custard 1984; Goss-Custard & dit Durrell 1987b; Norris & Johnstone 1998) and blackbirds *Turdus merula* (Cresswell 1997, 1998, 2001; Cresswell, Smith & Ruxton 2001; Smith, Ruxton & Cresswell 2001). Though much has been discovered about interference competition from studies on oystercatchers, the results may not be applicable to *Parus* species because the feeding method and food types of oystercatchers are different from that of passerines. Additionally, interference in oystercatchers is largely driven by kleptoparasitism that is not common among many other species (Ens & Goss-Custard 1984; Sutherland & Parker 1998). As a result of oystercatchers having long prey handling times and short attack distances during aggressive interactions, they are prone to kleptoparasitism and therefore interference is more pronounced than that which occurs in most other species (Sutherland & Parker 1998). Though kleptoparasitism rarely occurs in feeding great tits, they do become involved in aggressive interactions over food resources (pers. obs). Therefore, it is expected that interference will occur through individuals using feeding time to monitor conspecifics that may try to displace them from their feeding perch.

5.2.4 Factors that may affect susceptibility to interference

Previous studies have found that age is a major determinant of how susceptible individuals are to interference competition because juveniles tend to have a lower foraging efficiency and are more prone to kleptoparasitism than adults (Greig, Coulson & Monaghan 1983; Goss-Custard & dit Durrell 1987a, 1987b; Caldow *et al.* 1999). The relationship between age and susceptibility to interference competition has not been well studied in species that do not suffer from kleptoparasitism, with contradictory evidence reported by Cresswell (2001), who demonstrated that susceptibility to interference competition did not change between years in blackbirds (which do not exhibit kleptoparasitism).

In some species, dominance status is important in determining the effect of conspecific flock members on the feeding rate of other foraging birds (Ens &

Goss-Custard 1984; Smith, Ruxton & Cresswell 2001). Dominant individuals tend to be less prone to interference probably because they are unlikely to be kleptoparasitised or attacked by another bird in the vicinity due to their high social status. As a result, they do not have to avoid conspecifics that are feeding in the vicinity and can reduce their vigilance, thus benefiting from the vigilance of others (Smith, Ruxton & Cresswell 2001). Subdominant individuals may be more prone to interference, because they spend time avoiding other flock members and being vigilant for conspecifics that may attack them. It is predicted that the presence of other great tits will have a greater adverse effect on subdominant great tits compared to dominant great tits in the population at West Hollingside.

5.2.5 Heterospecific interference competition

Although interference competition has been well studied amongst avian homospecific foraging flocks, the effects of interference competition have not been well studied within the heterospecific flocks that are common in most Parids (Beveridge & Deag 1987). Though some work has been carried out on interference competition in heterospecific wader flocks (Barnard, Thompson & Stephens 1982), it is more difficult to study interference competition in free-living Paridae since they have very short food handling times and typically take food away from the feeding area to a safer place for handling. Previous studies have indicated that heterospecific exploitation competition does occur for food and nest sites between blue tits and great tits (Dhondt & Eyckerman 1980; Minot 1981; Torok & Toth 1999). It has also been reported that when coal tits and willow tits are foraging together, coal tits will use the outer branches of trees rather than the safer inner branches caused by the dominance of willow tits over coal tits (Alatalo & Moreno 1987). The opposite is true for willow tits foraging with crested tits *Parus cristatus*, where willow tits are forced to use the outer branches because of their subdominance in the presence of crested tits (Suhonen 1993; Krams 1998a). A study investigating vigilance in heterospecific flocks found that individuals of the most dominant species (great tits) decreased their vigilance in the presence of the subdominant species (blue tits, coal tits and crested tits) (Carrascal & Moreno 1992). Since great tits are dominant to both blue tits and coal tits (Dhondt & Eyckerman 1980; Carrascal & Moreno 1992; pers. obs), they are likely to decrease their vigilance in the presence of these species. A decrease in vigilance in the presence of the lower ranking species should then result in individual great tits having shorter seed handling times in the presence of blue tits and coal tits compared to their seed handling times when conspecifics are present.

5.2.6 Vigilance behaviour in the group context

Of the studies that focus on the benefits of group foraging, many concentrate on the vigilance of individuals foraging within groups. It is well documented that as group size increases, individual vigilance decreases (Krebs, MacRoberts & Cullen 1972; Beauchamp 1998; Lima, Zollner & Bednekoff 1999; Blumstein, Daniel & Evans 2001). Two hypotheses have been put forward to explain why individuals would decrease their vigilance in the presence of conspecifics. It is possible that a decrease in vigilance could occur when there are more individuals to detect predators, and therefore flock members' benefit from the vigilance of others (Lima, Zollner & Bednekoff 1999; Boysen, Lima & Bakken 2001). A decrease in vigilance with increasing group size could similarly arise from the occurrence of scramble competition in that individuals may be less vigilant simply because they are trying to get a larger share of the food and as a result have less time to be vigilant (Lima, Zollner & Bednekoff 1999; Blumstein, Daniels & Evans 2001). Although all individuals within a flock can reduce their vigilance to some extent, it has been shown that some flock members decrease their vigilance more than others *i.e.* dominant birds decrease their vigilance more compared to the subdominants, which maintain a higher level of vigilance in order to monitor dominant conspecifics.

The main aim of this study was to determine whether great tits are affected by interference competition whilst feeding. I hope to determine whether the magnitude of the effect of other birds on a feeding great tit is determined by factors such as sex, age, body size or dominance status. The effect of flock size on seed handling times and vigilance will also be considered using flock sizes of up to five individuals. The effects of the presence of lower ranking species on the food handling times of great tits will be investigated.

5.3 Methods

A dominance hierarchy was calculated for colour-ringed great tits, as described in Chapter 2. Great tits were aged, sexed and a measure of body size was obtained from principal components analysis using the methods described in Chapter 2.

Interference competition was not investigated in blue tits and coal tits because of the lack of data recorded for these species as a result of their behaviour at the feeders. Blue tits tended to visit the feeding area alone and therefore rarely fed in the presence of another blue tit. Coal tits were intolerant of any other coal tits in their vicinity and the most dominant coal tit would chase away any subdominant birds near to the feeders.

5.3.1 Seed handling observations and interference levels

The methods for making seed handling observations are described in Chapter 4. Great tits that were observed fewer than five times were excluded from the analysis so that outliers would not bias the data. During seed handling observations on a focal bird located in the bramble patch, other birds were visiting the feeders and bringing seeds back to the bramble (the visiting birds were always within one metre of the feeding bird if they were perched in the bramble patch). From past studies on the hoarding behaviour of coal tits

(Brotons 2000a), this is a distance that should cause interference competition to the feeding bird and therefore all birds visiting the bramble patch were recorded. Whilst timing a great tit handling a seed, the numbers as well as the species of birds visiting the bramble were recorded. Individual colour ring combinations of visiting birds were not recorded so that observer attention could be concentrated on the focal bird and the numbers of other birds visiting the immediate area. The species of birds that were recorded within the vicinity of a feeding great tit were: blue tits, coal tits, chaffinches *Fringilla coelebs*, wrens *Troglodytes troglodytes*, robins *Erithacus rubecula*, willow tits and blackbirds *Turdus merula*.

5.3.2 Vigilance observations and interference levels

The methods for observing and recording vigilance are described in Chapter 4. Whilst observing each focal bird at the feeder, the numbers and species of birds visiting the same feeder were also recorded. As with seed handling observations, individual colour ring combinations of visiting birds were not recorded so that observer attention could remain on the focal bird. The feeders were small (200 x 200mm) so that the arrival of another bird at the feeder could not go unnoticed by the focal bird or by the observer.

Statistical analyses were carried out on great tit data when comparing vigilance rates both when feeding alone and when at least one other *Parus* species (great tit, blue tit or coal tit) was present. The presence of other *Parus* species could not be divided into different species categories and numbers of birds present because the sample size was small, probably as a result of the feeders being small and therefore birds being reluctant to feed in such close proximity to another individual.

5.3.3 Statistical analysis of general interference

Seed handling times and vigilance were corrected for date and time of day by using the residuals from REMLs (See: Chapter 4 for the effects of date and time of day on seed handling times and individual vigilance).

Paired t-tests were used to examine whether there was a difference in the seed handling times of great tits feeding alone and when at least one other titmouse (great tit, blue tit or coal tit) was present. GLMs were used to detect whether the percentage change in seed handling time or vigilance in the presence of at least one titmouse was related to an individuals age or sex. Regression analysis was used to test for the presence of a relationship between the percentage change in seed handling times or vigilance levels and body size. Finally, Spearman's rank-order correlations were used to test for a relationship between dominance status and the percentage change in seed handling times or vigilance in the presence of at least one other titmouse.

5.3.4 Statistical analysis of heterospecific interference

In order to determine whether great tits reacted differently to another feeding great tit or a lower ranking species (*i.e.* blue tit or coal tit) a paired t-test was carried out to compare the differences in seed handling times between a great tit feeding in the presence of another great tit or with a lower ranking heterospecific. Further statistical analyses were carried out to determine whether differences were related to age, sex, body size or dominance status of great tits. These statistical methods followed those for overall interference levels described previously (Section 5.3.3).

5.3.5 Statistical analysis of group size effects

As in Chapter 4, REMLs were used to obtain residual seed handling times controlling for date and time. However, for this analysis the numbers of birds present during any one feeding event was the main focus. Identification numbers were therefore given to each bird and entered as a random factor with the numbers of other birds present entered as a fixed factor. The other bird species that were present in the bramble patch (within 1 metre) during the feeding of great tits are discussed in Section 5.3.1.

Great tits were recorded feeding with up to six other individuals, but data were only used when up to four individuals plus the focal bird were present because of the small sample size for additional birds within the flock. REMLs were used to test for a relationship between the seed handling times of great tits feeding with increasing numbers of other birds in the vicinity. The relationship between great tit dominance status and the change in seed handling time with an increasing group size was determined using a Spearman's rank-order correlation of dominance status and the slope of the relationship between seed handling time when feeding alone and with increasing numbers of birds.

5.4 Results

5.4.1 The effects of other titmice on feeding great tits

Great tits had longer seed handling times when feeding in the presence of one or more titmice including other great tits than when they were feeding alone (Figure 5.1; $t_{22} = -5.71$, $n = 23$, $P<0.001$). Great tits were also less vigilant in the presence of other titmice (Figure 5.2; $t_{19} = 2.27$, $n = 20$, $P<0.05$).

Figure 5.1: The difference in residual seed handling time (corrected for date and time of day) between great tits feeding alone and in the presence of at least one other titmouse (mean and 95% confidence intervals).

Figure 5.2: The decrease in vigilance of great tits when feeding in the presence of at least one other titmouse compared to when feeding alone (mean and 95% confidence intervals). Data were paired and significant at P<0.05.

5.4.2 Effects of age, sex and body size on sensitivity to interference

There was no significant effect of an individual's age or sex on the percentage change in seed handling time (sex: $F_{1,22} = 1.89$, male $n = 15$, female $n = 8$, $P = 0.2$, age: $F_{1,22} = 0.01$, adult $n = 16$, juvenile $n = 7$, $P = 0.9$) or vigilance (sex: $F_{1,20} = 0.00$, male $n = 13$, female $n = 8$, $P = 1.0$, age: $F_{1,20} = 0.00$, adult $n = 15$, juvenile $n = 6$, $P = 1.0$) between great tits feeding alone and feeding in the presence of other titmice. Body size was not related to the change in seed handling times ($r^2 = 0.03$, $F_{1,19} = 0.58$, $n = 20$, $P = 0.5$) or vigilance ($r^2 = 0.05$, $F_{1,17} = 0.86$, $n = 18$, $P = 0.4$) between great tits feeding alone and feeding in the presence of other titmice.

5.4.3 Dominance status and interference from other titmice

Low-ranking great tits increased their seed handling times to a greater extent than high-ranking birds in response to other titmice being present (Figure 5.3; $r_s = 0.68$, $n = 21$, $P<0.001$). However, dominance rank had no effect on the percentage change in the vigilance of great tits when feeding in the presence of other titmice ($r_s = -0.014$, $n = 21$, $P = 1.0$).

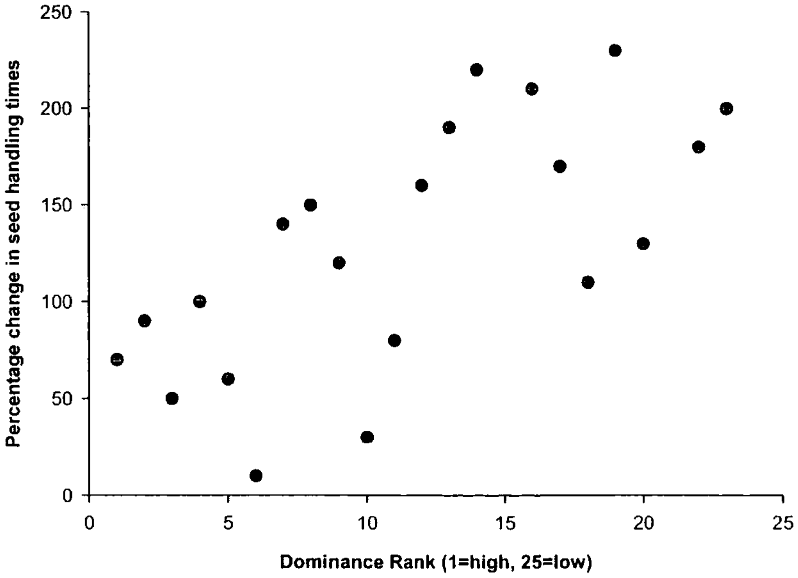

Figure 5.3: The effect of the dominance status of great tits on the percentage change in their seed handling times as a result of at least one other titmouse being present.

5.4.4 The effect of different species on seed handling times

There was a significant difference between the seed handling times of great tits when they were feeding in the presence of another great tit or in the presence of a lower ranking heterospecific (blue tit or coal tit) (t_{17} = 4.23, *n* = 18, *P*<0.001). Great tits had longer seed handling times when feeding in the presence of a conspecific than when they were feeding with a blue tit or coal tit (Figure 5.4).

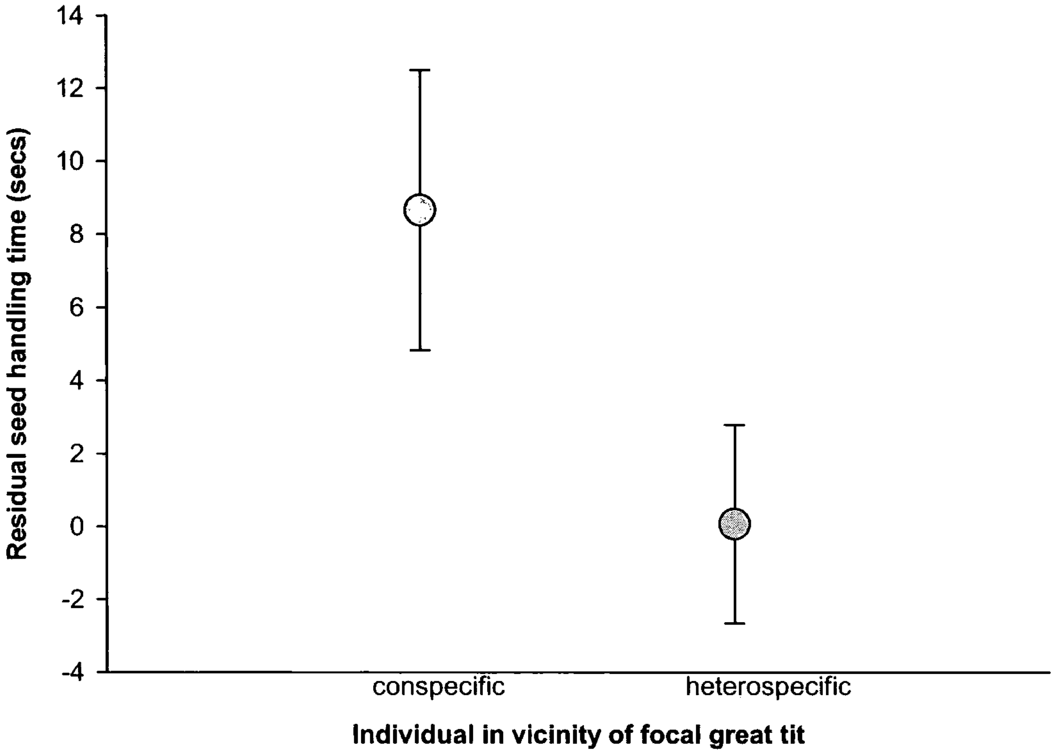

Figure 5.4: A comparison of the seed handling times of great tits when feeding with another great tit and when feeding with a lower ranking species (blue tit or coal tit) (mean and 95% confidence intervals).

5.4.5 The effects of other feeding great tits

The presence of a conspecific in the vicinity of a feeding great tit caused an increase in seed handling times (t_{23} = 5.44, *n* = 24, *P*<0.001: mean (s.d.) alone 3.16 (1.43); great tit present 8.17 (3.21)). There was no relationship between the percentage change in seed handling times due to the presence of another great tit and sex ($F_{1,15}$ = 0.07, male n = 10, female n = 6, P = 0.8) or age ($F_{1,15}$ = 0.98, adult n = 9, juvenile n = 7, P = 0.3). Body size had no effect on the percentage change in the seed handling times of great tits when they were feeding with a conspecific (r^2 = 0.09, $F_{1,14}$ = 0.1, n = 15, P = 0.8). The percentage change in seed handling time due to another great tit was not related to dominance status (r_s = 0.30, n = 15, P = 0.3).

5.4.6 The significance of flock size

The seed handling times of great tits increased as the number of other birds present in the flock increased (Figure 5.5; Wald $\chi^2_{4,32}$ = 71.01, n = 33, P<0.001), though there was no increase in seed handling time when the group size increased from four to five birds including the focal bird.

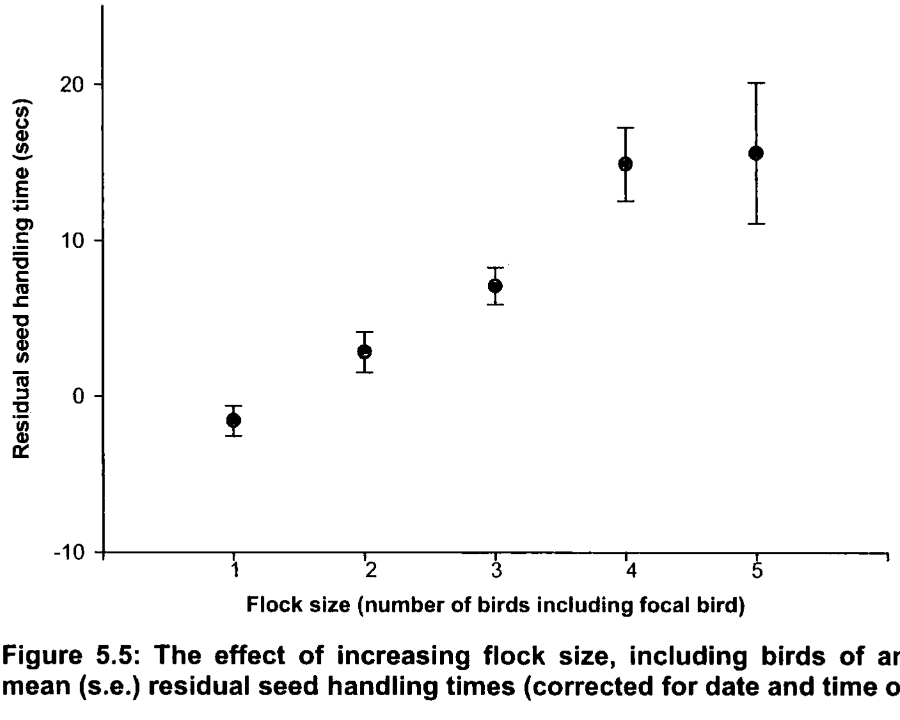

Figure 5.5: The effect of increasing flock size, including birds of any species, on the mean (s.e.) residual seed handling times (corrected for date and time of day) of great tits.

There was no relationship between dominance status and the effects of increasing group size on the seed handling times of great tits (r_s = 0.22, n = 33, P = 0.2).

5.5 Discussion

5.5.1 Interference competition in great tits

Great tits experienced interference competition, which was established both from their seed handling times during foraging with other titmice (this did not take account of the number of competitors) and foraging with one other conspecific. Interference competition may have serious implications for the time and energy budgets of great tits since seed handling times almost tripled on average when one other great tit was in the vicinity. Though interference competition has been reported in oystercatchers and blackbirds, the published changes in intake rates, feeding rates or foraging efficiencies have not been as large as those reported in the current study (Goss-Custard & dit Durrell 1987b; Cresswell 1997), suggesting that great tits are more severely affected by the presence of competitors than either oystercatchers or blackbirds. This may be the result of the great tits in this study being forced to feed in very close proximity to each other because of the small size of the feeding tables and thus experiencing an artificial situation.

In previous studies, increases in seed handling times in the presence of other birds have been due to an increase in vigilance in order to monitor flock members (Lendrem 1984; Fritz, Guillemain & Durant 2002). However in this study, vigilance decreased in the presence of other birds. Such a decrease has been explained by the fact that there are more individuals being vigilant for predators so that each individual can decrease its personal vigilance and benefit from the vigilance of others (Grubb 1987; Hogstad 1987c; Boysen, Lima & Bakken 2001; Barbosa 2002). The combination of increased seed handling times but decreased vigilance in this study may have arisen because of the different conditions under which seed handling times and vigilance were measured. Because vigilance was measured in the open, where birds were at greater risk of predation, it is not known how vigilance would change in relation to other birds in a more sheltered site where predation risk is low. Vigilance data would have to be collected from the covered site to test this.

5.5.2 Age and its consequences for interference competition

Although previous studies have documented a difference between the effects of interference competition on the intake rates of adult and juvenile oystercatchers (Goss-Custard & dit Durrell 1987a, 1987b), the results from this study do not support this for great tits. It is notable however, that the only studies to find that adult and juvenile birds react differently to the presence of competitors have been carried out on the oystercatcher where kleptoparasitism is common. Because juvenile oystercatchers take time to learn how to forage efficiently and have a lower foraging efficiency compared to adults (Goss-Custard & dit Durrell 1987a), losing a prey item would cost them more than adults in energy terms since they will take longer to regain the lost energy. It would probably therefore be beneficial for juvenile oystercatchers to increase their vigilance thus decreasing their foraging efficiency further but being able to avoid encounters that could lead to kleptoparasitism. Because great tits are not subject to kleptoparasitism, and juveniles do not have longer food handling times than adults in this population (see Chapter 4), juveniles have nothing to benefit from increasing their vigilance above that of adults since they are subject to the same risks and costs.

5.5.3 Dominance status and its consequences for interference competition

As was established from studies on oystercatchers and blackbirds (Ens & Goss-Custard 1984; Smith, Ruxton & Cresswell 2001), dominant great tits were less susceptible to general interference (the presence of one or more other titmice) than subdominants. Despite the relationship between dominance status and interference caused by other titmice (of which the heterospecifics were lower ranking), this study found that dominant and subdominant great tits were affected to the same extent by the presence of one other great tit. This contradicts previous studies on oystercatchers and blackbirds since they were carried out on conspecific flocks and a relationship between the effects of interference competition and dominance status was apparent (Ens & Goss-

Custard 1984; Smith, Ruxton & Cresswell 2001). The current results indicate that a mixed species group affects subdominant great tits more even though the other species are lower ranking whereas the effect of one other conspecific is the same for both dominants and subdominants. These results are not due to subdominants reacting more to larger group sizes since there was no relationship between group size and dominance status (discussed later).

The effect of dominance status on the severity of interference is also apparent at the species level within heterospecific flocks: a foraging great tit had a significantly greater adverse effect on the seed handling times of great tits than a foraging heterospecific (blue tit or coal tit). It is well known that great tits are dominant to blue tits and coal tits when feeding (Perrins 1979; Dhondt & Eyckerman 1980; pers. obs) as well as when competing for nest sites (Perrins 1979). There is no published literature regarding species dominance and its affect on interference competition but it was expected that the presence of a blue tit or coal tit in this study would have a reduced effect on the seed handling times of great tits compared to the presence of a conspecific. This was predicted because blue tits or coal tits were unlikely to attempt to displace a feeding great tit, therefore vigilance would not have to be increased to monitor them.

5.5.4 The importance of group size

The evidence from this study, which indicates an increase in the seed handling times of great tits with increasing numbers of competitors of a range of species, supports the results from previous studies of both passerines and non-passerines. A decrease in feeding rate with increasing flock size has been described in studies of oystercatchers where kleptoparasitism is common (Stillman *et al.* 1996; Stillman, Goss-Custard & Caldow 1997; Triplet, Stillman & Goss-Custard 1999). Kleptoparasitism does not occur in great tit populations, which displace each other during feeding but do not steal the food items being handled (pers. obs), similar to the types of interactions that have been observed in blackbirds which have been found to decrease their feeding rate as flock size increases (feeding rate incorporates many prey handling events and produces a measure of prey items eaten per unit time) (Cresswell 1998). The increase in seed handling time with increasing group size is likely to be caused by an increase in vigilance to match the increase in group size since the presence of more competitors lead to a higher probability of being displaced.

However, many studies have also reported an increase in intake rate with increasing group size (Lendrem 1984; Boysen, Lima & Bakken 2001; for review see: Beauchamp 1998). This is more likely to happen when food is patchy and unpredictable so that birds will benefit from flock members finding food (Grubb 1987; Ranta *et al.* 1996; Lima, Zollner & Bednekoff 1999; Marchetti & Drent 2000), from copying the foraging techniques or locations from flock members (Morse 1978; Waite & Grubb 1988; Sasvári & Hegyi 1998) or because personal vigilance is reduced since there are more animals searching for predators (Grubb 1987). Since food was provided and was therefore predictable during this study, the presence of other birds would not benefit a feeding great tit, particularly when foraging in close proximity to a potential competitor.

Most studies that have investigated interference competition have concentrated on intake rates rather than food handling times (Ens & Goss-Custard 1984; Goss-Custard & dit Durrell 1987b; Beauchamp 1998; Cresswell 1998; Cresswell, Smith & Ruxton 2001). However, Johnson, Giraldeau and Grant (2001) demonstrated that a decrease in intake rate with increasing group size in the house sparrow *Passer domesticus* was primarily due to an increase in their seed handling times. The work of Johnson, Giraldeau and Grant (2001) and the results from the current study, show that interference competition is important after prey capture in these species and that increases in food handling times may account for previously reported relationships between interference competition and intake rates.

5.5.5 Conclusions

Great tits are susceptible to interference competition from mixed-species flocks as well as from homospecific great tit flocks. The observed increase in seed handling times due to interference competition was not related to sex, age or body size but was determined by dominance status in mixed-species flocks (regardless of group size). The seed handling times of great tits in a heterospecific flock were affected more by the presence of a conspecific than by either a blue tit or a coal tit reflecting the dominance hierarchy between the species. Increasing heterospecific flock size was a major determinant of the increase in seed handling time due to interference in great tits.

Although the seed handling times of great tits were negatively affected by the presence of competitors, they continued to form heterospecific foraging flocks in winter where they presumably benefited from increased foraging efficiency through consuming food found by other group members that they themselves may not have found and through a reduction in predation risk through other flock members' vigilance. The benefits presumably outweigh the costs for all individuals within a flock, though subdominants may not benefit to the same extent as dominant birds. Subdominants foraging in a flock probably have higher intake rates overall than if they foraged alone because they have better protection from predation and have access to more food than they would if searching alone (Hogstad 1987, 2003).

Chapter 6

Variation in the nutritional condition of titmice during winter flocking: a study using ptilochronology

6.1 Abstract

The nutritional condition of birds during winter can be important in determining their likelihood of survival particularly in small passerines that are sensitive to harsh winter conditions. Ptilochronology is an accurate method used to produce a long-term estimate of a bird's nutritional condition spanning the number of days that it takes to grow a new feather. Feathers can be induced during periods when birds are not normally moulting to provide estimates of nutritional condition for these times by measuring 10 daily growth bars along the feather. Ptilochronology was used during this study to estimate the nutritional condition of great tits, blue tits and coal tits during two winters and the factors that may influence nutritional condition were investigated. The density of induced great tit feathers was affected by the age of individuals, with juvenile birds producing feathers of lower density. The nutritional condition of coal tits was affected by dominance status in that dominant birds had lower quality feathers and produced them at a slower rate and with higher levels of fluctuating asymmetry in the growth rate than did subdominant conspecifics. This study highlights a nutritional cost to high dominance status that could have long-term consequences.

6.2 Introduction

The winter body condition of small European passerines has important consequences for their survival and can be dependent on climate, food availability and dominance status (Piper & Wiley 1990; Gosler & Carruthers 1999). High dominance status can reduce the effects of climate and food supply on body condition since most of the time dominant birds have priority of access with regards to roosting sites and food resources (Kaufmann 1983; Ens & Goss-Custard 1984; Arcese & Smith 1985; Pöysä 1988). Through gaining access to the highest quality resources, dominant birds benefit from their social status by being in better body condition (Carrascal *et al.* 1998; Gosler & Carruthers 1999).

6.2.1 Difficulties of measuring body condition

Several methods of assessing body condition in small passerines have been employed in the past and involve estimating or measuring the extent of the muscle reserves or how much fat individuals are storing. Fat scoring (Fry, Ash & Ferguson-Lees 1970) and muscle scoring (Gosler 1991) have been used in the past as a means of estimating fat reserves and muscle mass. Scoring fat or muscle is advantageous in that they are both easy estimates to make in the field since they do not require additional equipment. However their use is limited (Greenwood 1992) on the grounds that scores have a maximum value and the change in fat levels between each score may be different at the top and bottom ends of the scale (this must be considered during analysis and interpretation of data). Other more accurate methods of assessing body condition by measuring fat and muscle have proved unreliable in studies involving small passerines because the errors associated with these methods are often large *e.g.* Total Body Electrical Conductivity (TOBEC: Roby 1991; Kaiser 1993; Selman & Houston 1996), ultrasound (Selman & Houston 1996; Dietz *et al.* 1999) and near-infrared interactance (IRI: Roby 1991). These methods have been designed with larger birds in mind where errors are negligible, but are therefore unsuitable for small passerines. Ptilochronology is a more recent technique used to measure average body condition over longer periods (the length of time that it takes to grow a new feather) and can be applied to birds of any size (Grubb 1989; Grubb & Cimprich 1990; Grubb 1991; Grubb, Waite & Wiseman 1991; Brown 1996; Carrascal *et al.* 1998).

6.2.2 Ptilochronology and its applications

When a feather is accidentally lost any time outside the moulting period, it is replaced over the course of several weeks or more, depending on environmental conditions (Grubb 1989). Moult itself is thought to be undertaken at times that are not energetically stressful (Ginn & Melville 2000), but a feather can be lost at any time and birds can therefore be forced to replace lost feathers at times when food resources and energy reserves are low. In order to compensate for low energy reserves during feather growth, many birds will slow feather growth rate when resources are limited so that they can produce high quality feathers but at a slower growth rate (Grubb 1989).

The rate of feather growth has been found to be relatively similar during the day and night despite the fact that most birds are fasting during the night (Murphy & King 1986). It is thought that cystine, the essential amino acid in keratin, is stored in the liver during the day, and can be activated for feather synthesis during the night when birds are fasting (Murphy & King 1990). However a difference does exist between the feather material that is deposited during the day and night and this is reflected in dark and light bands respectively along the feather web (Wood 1950; Murphy & King 1986; Jenni & Winkler 1994). The difference in colour between feather produced during the day and night, is not a reflection of feather quality but is a result of the different optical properties of the pigments integrated into the keratin matrix of the feather during the day and night (Wood 1950). One pair of light and dark bands is termed a growth bar and is equivalent to 24 hours growth. It has been demonstrated that under unfavourable conditions, feather growth is slowed resulting in narrower growth bars and if such disturbance of feather growth is persistent, the resulting bars are called fault bars (Jenni & Winkler 1994; Ginn & Melville 2000).

Ptilochronology is a powerful tool for assessing the body condition of free ranging or captive birds (Grubb 1989; Grubb & Cimprich 1990; Grubb 1991; Grubb, Waite & Wiseman 1991; Hogstad 1992; Carrascal *et al.* 1998; Keyser & Hill 1999). It involves measuring the width of the growth bars on induced flight feathers and hence producing a measure of growth rate per day for individuals (Grubb 1989; Brown 1996). The method is based on the general assumption that narrower growth bars reflect periods of low nutrition and that any change in nutritional status is mirrored in the width of the growth bars (Grubb 1989, 1991, 1992). Because ptilochronology can provide an average measure of body condition spanning a number of weeks if necessary, it eliminates the problem of short term temporal variation in body condition, as occurs with body mass over time of day (Gosler 1996), and hence it gives a more representative estimate. Usually ten growth bars are measured since this number of growth bars can usually be seen on most feathers (sometimes the growth bars can be difficult to see along the whole feather length: pers. obs.) and amounts to more than one third of the length of the feather web in great tits and coal tits.

Several studies have used ptilochronology to investigate the effect of dominance status on the feather growth rates of passerines (Grubb 1989; Hogstad 1992; Carrascal *et al.* 1998). These studies have found that dominant individuals tend to grow an induced tail feather at a faster rate than subdominants. In two of these studies (Grubb 1989; Carrascal *et al.* 1998), it was highlighted that the difference in feather growth only occurred during harsh periods and did not occur when food was supplemented or climate was milder. This suggests that dominant birds benefited most from their high status during harsh conditions when competition was likely to be greatest. However, in both of these studies, dominance was fully or partially measured from sex or age differences with males being assumed to be dominant to females and within the sexes, adults assumed to be dominant over juveniles (the dominance hierarchies of great tits and coal tits in these populations are not structured in this way: Chapter 3). These dominance categories are somewhat general, and so reported differences in feather growth could have been due to other confounding factors related to age or sex, such as body size, morphology and habitat usage, which may have been correlated with both dominance status and the growth rate of induced feathers. It is expected that dominant great tits and coal tits in this study will replace their feathers at a faster rate than subdominant birds and they may also produce longer and denser feathers.

6.2.3 Use of fluctuating asymmetries when assessing body condition

Fluctuating asymmetries are thought to be related to stress and result from an individual's inability to develop a bilateral trait so that it is identical on either side of the body (Palmer & Strobeck 1986; Parsons 1990). Fluctuating asymmetries in the lengths of the primary feathers of captive starlings *Sturnus vulgaris* have been related to nutritional stress (Swaddle & Witter 1994; Witter & Swaddle 1994). Asymmetries in feather lengths can also occur due to differential amounts of wear on the tips of the feathers due to asymmetries in feather quality (*i.e.* density) and therefore resistance to wear (Carbonell & Tellería 1999). However, different amounts of wear on the feather tips could also be brought about by other means that are difficult to measure *e.g.* differential wear on the two sides of the body caused by the bird constantly leading with one wing during flight.

The levels of fluctuating asymmetry in feathers can be used as a measure of condition in certain bird species that show symptoms of stress when in poor condition (Palmer & Strobeck 1986; Parsons 1990). However it must be remembered when interpreting the data, that degrees of fluctuating asymmetry represent body condition when the feathers were produced rather than current condition (which is also the case for ptilochronology). Because fluctuating. asymmetry can be related to nutritional stress, it is a useful tool that can be used alongside ptilochronology to assess body condition through traits in induced tail feathers. If fluctuating asymmetry can be used as a measure of stress in free-living passerines, this study predicts that subdominant birds will demonstrate higher levels of fluctuating asymmetry in their induced tail feathers compared to dominant birds.

This study aims to test how the growth rate of induced feathers may differ between individual great tits, blue tits and coal tits. The effect of age, sex and body size on induced feather growth rate will be tested, as well as their effects on feather quality (length, linear density and fluctuating asymmetry). This study also tests whether dominance plays a role in the production of induced tail feathers in winter with regards to feather growth rate, length, linear density and fluctuating asymmetry.

6.3 Methods

This study was carried out on great tits and blue tits during both the winters of 2000-2001 and 2001-2002 and was carried out on coal tits in the winter of 2000-2001 only. Though attempts were made to include coal tits in the preceding winter, sample sizes were too small to allow accurate analysis. Because birds had to be captured on two separate occasions, to remove the original feathers and to collect the induced feathers, sample sizes were considerably reduced (Appendix 6) because birds either died between the two sampling periods or in the case of blue tits and coal tits there was often some localised migration during January which meant that many of the birds left the study area.

The methods for calculating dominance indices, ageing and sexing the birds and measuring body size are presented in Chapter 2.

6.3.1 Feather collection

During a two-week period in January 2001, the two central tail feathers were removed from 40 great tits, 40 blue tits and 18 coal tits. This procedure was repeated during the second field season in December 2001, when the two central tail feathers were removed from 54 great tits and 66 blue tits. The sampling period of two weeks each year allowed adequate sample sizes to be obtained with minimal temporal variation in environmental conditions.

Six weeks after the initial feather removal period, intensive mist netting commenced in an attempt to recapture those birds with induced central tail feathers, which were normally regrown within approximately 5 weeks. This was carried out from March - June 2001, and February - June 2002. During spring 2001, 30 great tits, 14 blue tits and 13 coal tits that had previously been captured for the removal of their tail feathers, were recaptured and during spring 2002, 24 great tits and 14 blue tits were recaptured. Before the induced feathers were removed, they were checked for the absence of sheath at the base of the feather to ensure that they were fully grown.

6.3.2 Ptilochronology and feather quality indices

Feather length was measured to the nearest 0.5mm in 2001 using a stopped rule and to the nearest 0.1mm using dial callipers in 2002. To control for possible effects of body size, feather length was calculated as a proportion of the length of the original feathers that had been removed from each bird. Feather mass was measured with a precision of four decimal places using an A.N.D electronic balance and an index of linear density was calculated by dividing feather mass by feather length. The real density of the feathers could not be calculated since the volume of the feathers was unknown.

Daily growth rate was calculated for each feather (two feathers from each bird) by taking the average width of ten growth bars measured to the nearest 0.5mm. Growth bars were difficult to measure on the feather itself because light reflectance could make the distinction between light and dark bands difficult (Murphy 1992). Photographs were therefore taken with a Nikon 801s 35mm camera and enlarged to 230 x 150mm which made accurate measurement possible. To take account of the fact that different parts of the feather may grow at different rates (Ginn & Melville 2000), five growth bars were measured at each of one third of the way along the feather length and three-quarters of the way along the feather shaft from the proximal end (Plate 6.1).

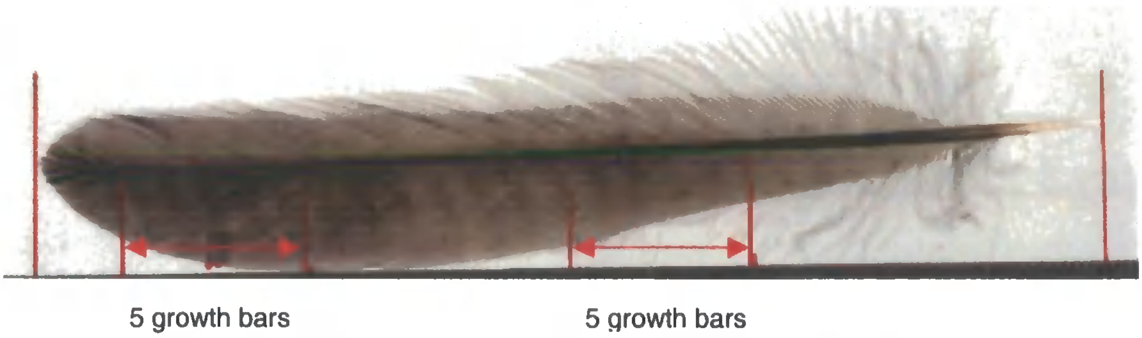

Plate 6.1: Great tit central tail feather displaying daily growth bars (one light and one dark band) and the two areas that were measured on each feather.

For each individual bird, a mean was taken from its left and right central tail feathers for measurements of feather length, linear density and growth rate. These means were used in all further analysis. Fluctuating asymmetry was measured by calculating the difference in length, linear density and growth rate between the induced left and right central tail feathers.

6.3.3 Statistical analysis

Since feather length, linear density and growth rate are all essentially measures of feather quality, Pearson's correlations were carried out to test whether they were correlated with each other.

Regression analysis was carried out to determine whether the date on which the original feathers were removed had an effect on the growth rates of the induced feathers (*i.e.* if variation in the weather conditions or resource availability over the growing period due to the two week feather removal period could account for changes in feather quality). Since the distal ends of feathers can become worn and abraded over time, regression analysis was used to determine whether the length of time taken to recapture the study birds and remove their induced feathers when they were fully grown (*i.e.* the age of the induced feather) was related to the length of the induced feathers. Residuals were used from the regressions of feather length against time for both the original feather removal date and induced feather retrieval time when necessary to control for these effects. The feather growth rates of great tits for the winter 2000-2001 were also standardised to control for feather length.

GLMs were used to test for the effects of age and sex on induced feather length, linear density and growth rate. Regression analysis was used to test whether apparent feather quality was affected by body size. Spearman's rank-order correlations were used to test the relationship between dominance status and apparent feather quality. Because of the small sample size of blue tits with known dominance rank and also ptilochronological information during the 2000-2001 field season, statistical analysis could not be carried out on these data.

Regression analysis was used to determine the relationship between date and fluctuating asymmetry in induced feather length, linear density and growth rate. Residuals were used from those results that were significant in subsequent analysis involving fluctuating asymmetry. The effect of age and sex on fluctuating asymmetry was tested using GLMs and the effect of dominance status on the fluctuating asymmetry in feathers was tested using Spearman's rank-order correlations.

6.4 Results

6.4.1 Relationships between feather length, density and growth rate

There was a relationship between the induced feather lengths of great tits and their growth rates (Table 6.1). The induced feathers of great tits that had the greatest feather lengths also had the fastest growth rates in both winters. The induced feather lengths of coal tits and blue tits were not related to their growth rates. Longer feathers also had a higher density index in great tits than shorter feathers but a relationship did not exist between feather length and density index in blue tits or coal tits (Table 6.1).

	Length and growth rate			Length and density		
2000-2001	*r*	*n*	*P*	*r*	*n*	*P*
Great tit	0.84	25	<0.001	0.55	25	<0.01
Blue tit	0.14	8	0.8	-0.19	11	0.6
Coal tit	0.30	13	0.3	0.37	13	0.2
2001-2002						
Great tit	0.81	24	<0.001	0.80	24	<0.001
Blue tit	0.49	13	0.1	0.32	14	0.3

Table 6.1: Results of Pearson's correlations demonstrating the relationships between induced feather lengths and growth rate or linear density.

6.4.2 Effect of sampling time period on feather growth rate

The final lengths of the induced feathers were not affected by wear since there was no relationship between the age of the induced tail feathers and their length in great tits, blue tits or coal tits (Table 6.2). The standardised feather growth rates of great tits during 2000-2001 were affected by the date on which the original feathers were removed. The growth rates of induced tail feathers were not related to the original feather removal date during the winter 2001-2002 for great tits, for blue tits during either winter or for coal tits (Table 6.2).

	Age of induced feather and feather length			Date of original feather removal and standardised growth rate		
2000-2001	r^2	$F_{d.f.}$	P	r^2	$F_{d.f.}$	P
Great tit	0.02	$0.49_{1,24}$	0.5	0.25	$7.67_{1,24}$	<0.05
Blue tit	0.00	$0.00_{1,13}$	1.0	0.25	$1.55_{1,8}$	0.3
Coal tit	0.07	$0.87_{1,11}$	0.4	0.35	$4.39_{1,11}$	0.1
2001-2002						
Great tit	0.02	$0.46_{1,23}$	0.5	0.02	$0.34_{1,23}$	0.6
Blue tit	0.02	$0.25_{1,13}$	0.6	0.16	$2.32_{1,13}$	0.2

Table 6.2: Results of regression analysis testing whether temporal variation affected feather wear (*n* values: 2000-2001: great tits = 25, blue tits = 14, coal tits = 12; 2001-2002: great tits 24, blue tits = 14) or growth rates (*n* values: 2000-2001: great tits = 25, blue tits = 9, coal tits = 12; 2001-2002: great tits = 24, blue tits = 14).

6.4.3 Age, sex and feather quality

Induced feather length, linear density and growth rate were not related to sex in either great tits, blue tits or coal tits. The age of great tits had an effect on the proportional lengths of the induced central tail feathers during both winters (Figure 6.1) and also affected feather density during the winter 2001-2002 (Table 6.3; Figure 6.2). Juvenile great tits produced tail feathers that were longer than those of adults (as a proportion of their original length) and juveniles also produced feathers that were less dense than those of adults. The age of blue tits or coal tits did not affect feather length, linear density or growth rate.

	Feather parameter	2000-2001				2001-2002			
		Sex		Age		Sex		Age	
		$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	**length**	$0.67_{1,30}$	0.4	$8.48_{1,30}$	<0.01	$0.58_{1,23}$	0.5	$6.53_{1,23}$	<0.05
	linear density	$2.13_{1,24}$	0.2	$2.22_{1,24}$	0.2	$2.63_{1,23}$	0.1	$8.31_{1,23}$	<0.01
	growth rate	$0.00_{1,24}$	1.0	$0.19_{1,24}$	0.7	$0.71_{1,23}$	0.4	$0.09_{1,23}$	0.8
Blue tit	**length**	$1.62_{1,13}$	0.2	$0.11_{1,13}$	0.7	$0.63_{1,13}$	0.4	$4.88_{1,13}$	0.1
	linear density	$0.65_{1,10}$	0.4	$0.01_{1,10}$	0.9	$3.67_{1,13}$	0.1	$3.38_{1,13}$	0.1
	growth rate	$0.79_{1,8}$	0.4	$0.13_{1,8}$	0.7	$0.10_{1,13}$	0.8	$0.92_{1,13}$	0.4
Coal tit	**length**	$2.6_{1,11}$	0.1	$0.1_{1,11}$	0.4				
	linear density	$0.77_{1,11}$	0.4	$0.03_{1,11}$	0.9				
	growth rate	$0.42_{1,11}$	0.4	$0.55_{1,11}$	0.6				

Table 6.3: Results of GLMs investigating the effects of age and sex on feather growth rate (*n* values: 2000-2001: great tits male = 11, female = 14, adult = 8, juvenile = 17; blue tits male = 4, female = 5, adult = 4, juvenile = 5; coal tits male = 7, female = 5, adult = 5, juvenile = 7; 2001-2002: great tits male = 16, female = 8, adult = 14, juvenile = 10; blue tits male = 6, female = 8, adult = 5, juvenile = 9), length (as a proportion of the original length) (*n* values: 2000-2001: great tits male = 14, female = 17, adult = 11, juvenile = 20; blue tits male = 6, female = 8, adult = 5, juvenile = 9; coal tits male = 8, female = 4, adult = 4, juvenile = 8; 2001-2002: great tits male = 16, female = 8, adult = 14, juvenile = 10; blue tits male = 7, female = 7, adult = 6, juvenile = 8) and linear density (*n* values: 2000-2001: great tits male = 11, female = 14, adult = 8, juvenile = 17; blue tits male = 4, female = 7, adult = 4, juvenile = 7; coal tits male = 8, female = 4, adult = 4, juvenile = 8; 2001-2002: great tits male = 16, female = 8, adult = 14, juvenile = 10; blue tits male = 6, female = 8, adult = 6, juvenile = 8).

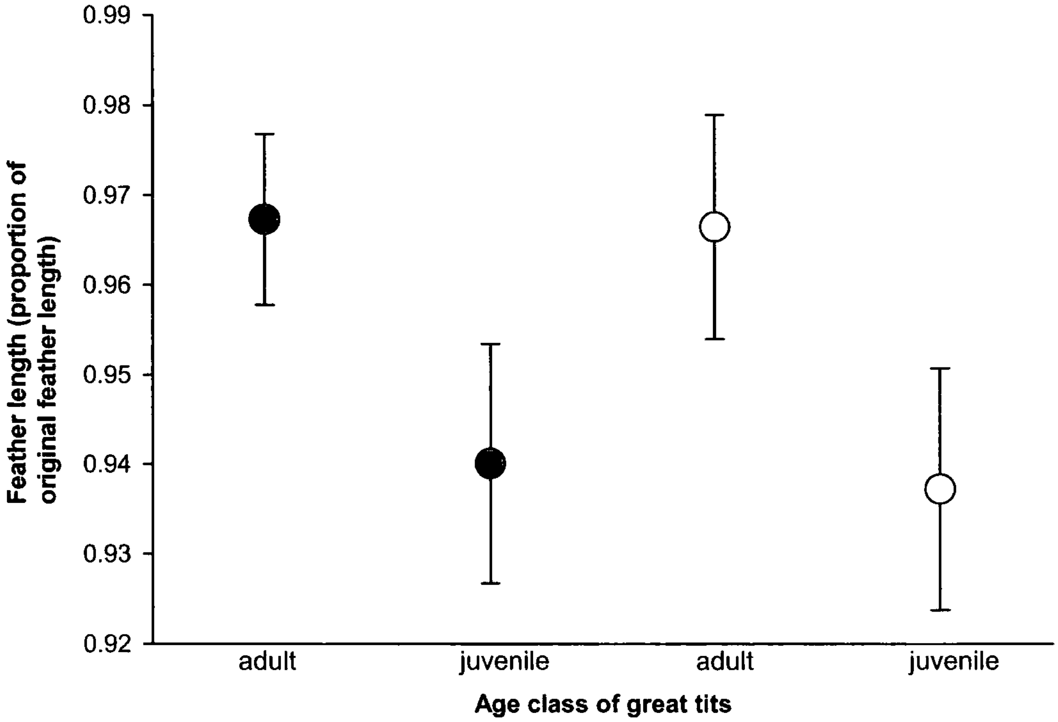

Figure 6.1: The effect of age class on the length of the induced central tail feathers (as a proportion of their original feather length) in great tits during 2000-2001 (•) and 2001-2002 (o) (mean and 95% confidence intervals).

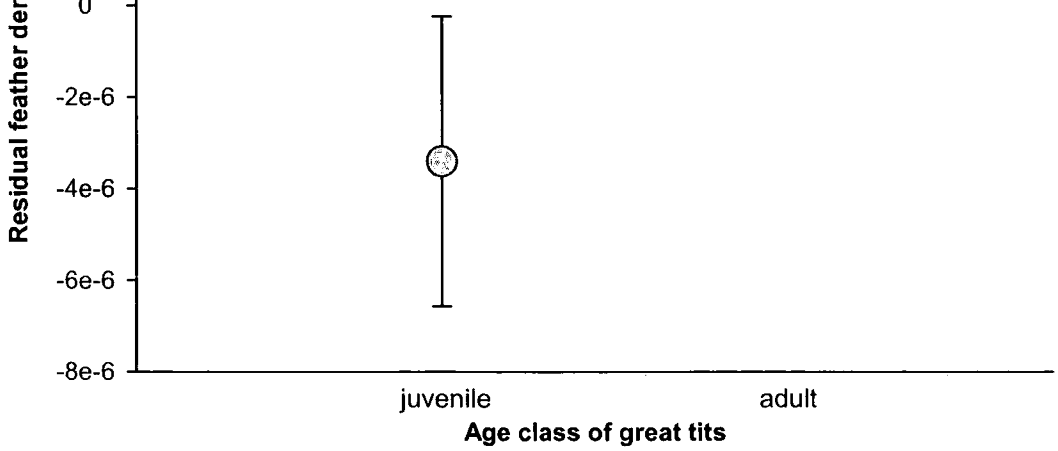

Figure 6.2: The effect of age on the linear density of induced central tail feathers in great tits during the 2001-2002 field season (mean and 95% confidence intervals).

6.4.4 Body size and feather quality

Body size did not have an effect on the lengths (as a proportion of the original feather length), linear densities or growth rates of the induced central tail feathers of great tits, blue tits or coal tits during either winter (Table 6.4).

	Feather parameter	2000-2001			2001-2002		
		r^2	$F_{d.f.}$	P	r^2	$F_{d.f.}$	P
Great tit	**length**	0.01	$0.29_{1,25}$	0.6	0.10	$2.11_{1,19}$	0.2
	linear density	0.05	$0.96_{1,19}$	0.3	0.07	$1.50_{1,19}$	0.2
	growth rate	0.02	$0.48_{1,19}$	0.5	0.05	$1.03_{1,19}$	0.3
Blue tit	**length**	0.06	$0.72_{1,13}$	0.4	0.10	$1.25_{1,12}$	0.3
	linear density	0.06	$0.58_{1,10}$	0.5	0.29	$4.38_{1,12}$	0.1
	growth rate	0.05	$0.30_{1,8}$	0.6	0.09	$0.10_{1,12}$	0.8
Coal tit	**length**	0.04	$0.44_{1,11}$	0.5			
	linear density	0.00	$0.10_{1,11}$	0.8			
	growth rate	0.23	$2.95_{1,10}$	0.1			

Table 6.4: Results of regression analysis on the effects of body size (calculated from PCA: Chapter 2) on feather length (as a proportion of the original feather length) (*n* values 2000-2001: great tit = 26, blue tit = 14, coal tit = 12; 2001-2002: great tit 20, blue tit = 13), linear density (*n* values 2000-2001: great tit = 20, blue tit = 11, coal tit = 12; 2001-2002: great tit = 20, blue tit = 13) and growth rate (*n* values 2000-2001: great tit = 20, blue tit = 9, coal tit = 11; 2001-2002: great tit = 20, blue tit = 13.

6.4.5 Dominance status and feather quality

The dominance status of great tits or blue tits was not related to the length, linear density or growth rate of the induced central tail feathers (Table 6.5). There was a relationship between dominance status and feather quality in coal tits in that dominant birds had the lowest quality feathers (Table 6.5; Figure 6.3). Dominant coal tits grew their induced tail feathers at a slower growth rate and produced feathers that were proportionally shorter and less dense than those of subdominants.

	Feather parameters	2000-2001			2001-2002		
		r_s	*n*	*P*	r_s	*n*	*P*
Great tit	**length**	0.26	14	0.3	-0.23	24	0.3
	linear density	-0.14	14	0.6	0.06	24	0.8
	growth rate	0.04	14	0.9	0.16	24	0.5
Blue tit	**length**				0.16	13	0.6
	linear density				-0.13	13	0.7
	growth rate				-0.07	12	0.8
Coal tit	**length**	-0.72	10	<0.05			
	linear density	-0.88	10	<0.001			
	growth rate	-0.78	9	<0.05			

Table 6.5: Results of Spearman's rank-order correlations between dominance status and feather length, linear density and growth rate.

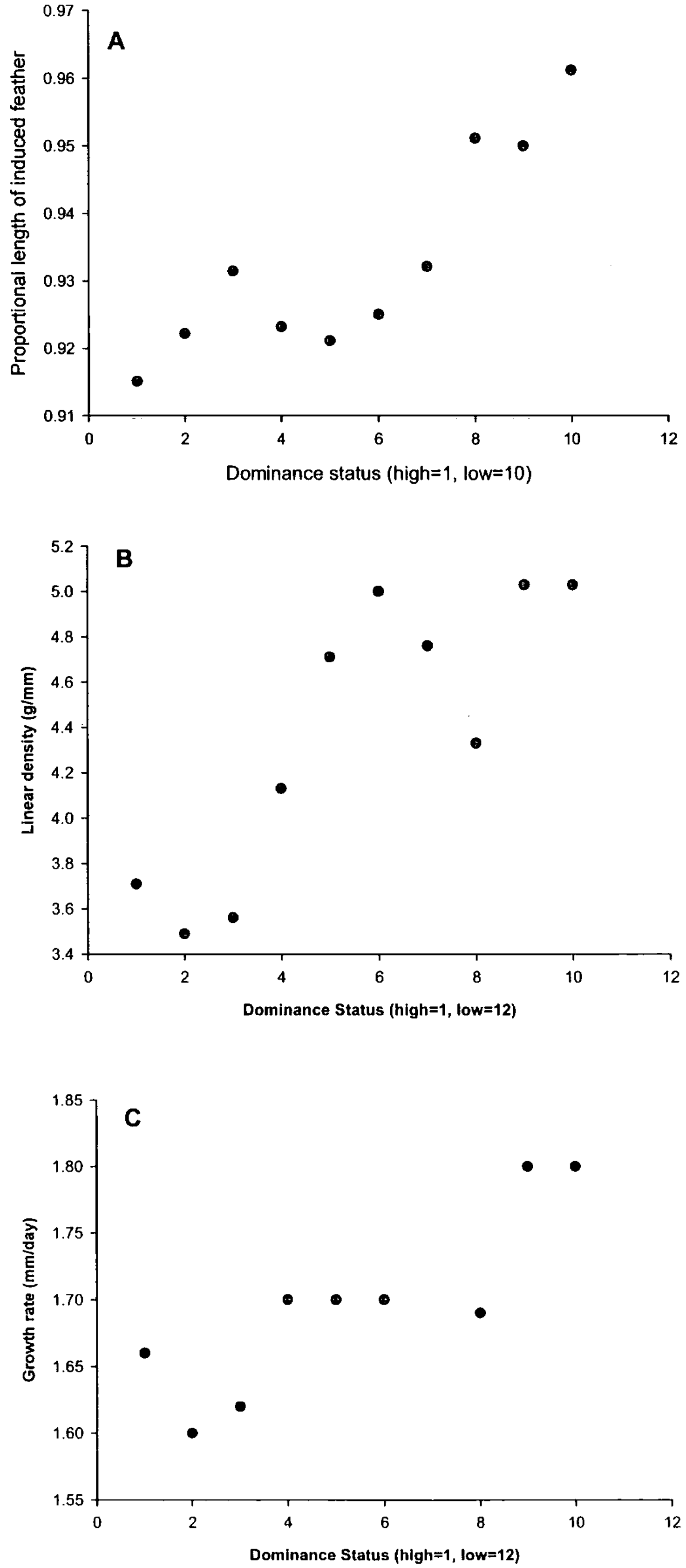

Figure 6.3: The relationship between the dominance status of coal tits and induced tail feather (A) length (as a proportion of the original feather length), (B) linear density and (C) growth rate during the 2000-2001 field season.

6.4.6 Fluctuating asymmetries in induced feather parameters

The date on which the original tail feathers were removed was not related to the amount of fluctuating asymmetry displayed in the proportional length or linear density of great tit, blue tit or coal tit tail feathers during either year. Fluctuating asymmetry in the growth rates of left and right feathers was related to date in great tits during the winter of 2000-2001 with asymmetry in growth rates increasing over the removal period. The degree of fluctuating asymmetry in growth rate was not related to date in blue tits or coal tits or in great tits during the 2001-2002 field season (Table 6.6).

	Feather parameter	2000-2001			2001-2002		
		r^2	$F_{d.f.}$	P	r^2	$F_{d.f.}$	P
Great tit	**length**	0.08	$2.34_{1,28}$	0.1	0.03	$0.58_{1,22}$	0.5
	linear density	0.00	$0.01_{1,24}$	0.9	0.00	$0.16_{1,22}$	0.7
	growth rate	0.14	$4.40_{1,28}$	<0.05	0.15	$3.77_{1,21}$	0.1
Blue tit	**length**	0.01	$0.01_{1,13}$	0.9	0.00	$0.00_{1,12}$	0.9
	linear density	0.06	$0.61_{1,10}$	0.5	0.70	$0.08_{1,12}$	0.8
	growth rate	0.22	$1.74_{1,8}$	0.2	0.27	$0.36_{1,14}$	0.6
Coal tit	**length**	0.05	$0.49_{1,10}$	0.5			
	linear density	0.03	$0.34_{1,11}$	0.6			
	growth rate	0.08	$0.72_{1,9}$	0.4			

Table 6.6: The effect of feather collection date on the level of fluctuating asymmetry in length (*n* values 2000-2001: great tits = 29, blue tits = 14, coal tits = 11; 2001-2002: great tits = 23, blue tits = 13), linear density (*n* values 2000-2001: great tits = 25, blue tits = 11, coal tits = 12; 2001-2002: great tits = 23, blue tits = 13) and growth rate (*n* values 2000-2001: great tits = 29, blue tits = 9, coal tits = 10; 2001-2002: great tits = 22, blue tits = 15) between the left and right feathers.

The levels of fluctuating asymmetry demonstrated by the induced central tail feathers of great tits, blue tits or coal tits with regards to proportional length, linear density or growth rate were not affected by the age or sex of individuals in either winter (Table 6.7).

	Feather parameter	2000-2001				2001-2002			
		Sex		Age		Sex		Age	
		$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	length	$0.20_{1,29}$	0.7	$0.91_{1,29}$	0.9	$0.00_{1,23}$	1.0	$0.72_{1,23}$	0.4
	linear density	$0.08_{1,25}$	0.8	$0.10_{1,25}$	0.8	$0.97_{1,23}$	0.3	$0.76_{1,23}$	0.4
	growth rate	$0.19_{1,29}$	0.7	$0.00_{1,29}$	1.0	$0.02_{1,22}$	0.9	$0.98_{1,25}$	0.3
Blue tit	length	$0.02_{1,13}$	0.9	$0.24_{1,13}$	0.6	$0.97_{1,13}$	0.3	$0.07_{1,12}$	0.8
	linear density	$0.05_{1,10}$	0.8	$0.77_{1,10}$	0.4	$0.41_{1,12}$	0.5	$0.09_{1,12}$	0.8
	growth rate	$0.72_{1,8}$	0.4	$0.46_{1,8}$	0.5	$0.49_{1,14}$	0.5	$0.22_{1,14}$	0.7
Coal tit	length	$1.69_{1,11}$	0.2	$4.19_{1,11}$	0.1				
	linear density	$0.01_{1,12}$	0.9	$3.30_{1,12}$	0.1				
	growth rate	$0.20_{1,9}$	0.7	$0.05_{1,9}$	0.8				

Table 6.7: Results of GLMs testing the effects of age and sex on the fluctuating asymmetry associated with feather growth rate (*n* values: 2000-2001: great tits male = 13, female = 17, adult = 8, juvenile = 22; blue tits male = 4, female = 5, adult = 4, juvenile = 5; coal tits male = 6, female = 4, adult = 3, juvenile = 7; 2001-2002: great tits male = 15, female = 8, adult = 13, juvenile = 13; blue tits male = 7, female = 8, adult = 6, juvenile = 9), length (as a proportion of the original length) (*n* values: 2000-2001: great tits male = 13, female = 17, adult = 8, juvenile = 22; blue tits male = 6, female = 8, adult = 5, juvenile = 9; coal tits male = 8, female = 6, adult = 6, juvenile = 8; 2001-2002: great tits male = 16, female = 8, adult = 14, juvenile = 10; blue tits male = 6, female = 8, adult = 5, juvenile = 9) and linear density (*n* values: 2000-2001: great tits male = 12, female = 14, adult = 8, juvenile = 18; blue tits male = 4, female = 7, adult = 4, juvenile = 7; coal tits male = 8, female = 5, adult = 5, juvenile = 8; 2001-2002: great tits male = 16, female = 8, adult = 14, juvenile = 10; blue tits male = 6, female = 7, adult = 5, juvenile = 8).

Dominance status was not related to the degree of fluctuating asymmetry in the length or linear density of the induced central tail feathers of great tits, blue tits or coal tits (Table 6.8). Dominance status was however, related to the amount of fluctuating asymmetry in the feather growth rate of coal tits during the 2000-2001 field season but not great tits or blue tits in either field season.

	Feather parameters	2000-2001			2001-2002		
		r_s	*n*	*P*	r_s	*n*	*P*
Great tit	**length**	0.06	30	0.8	0.18	24	0.1
	linear density	-0.07	15	0.8	-0.38	23	0.1
	growth rate	-0.21	16	0.4	0.09	22	0.7
Blue tit	**length**	0.18	9	0.6	-0.24	13	0.5
	linear density	-0.37	6	0.5	-0.18	12	0.6
	growth rate	-0.07	8	0.9	0.10	12	0.7
Coal tit	**length**	-0.31	12	0.4			
	linear density	0.63	9	0.1			
	growth rate	-0.86	9	<0.05			

Table 6.8: Results of Spearman's rank-order correlations testing the relationship between dominance status and the level of fluctuating asymmetry in induced tail feathers.

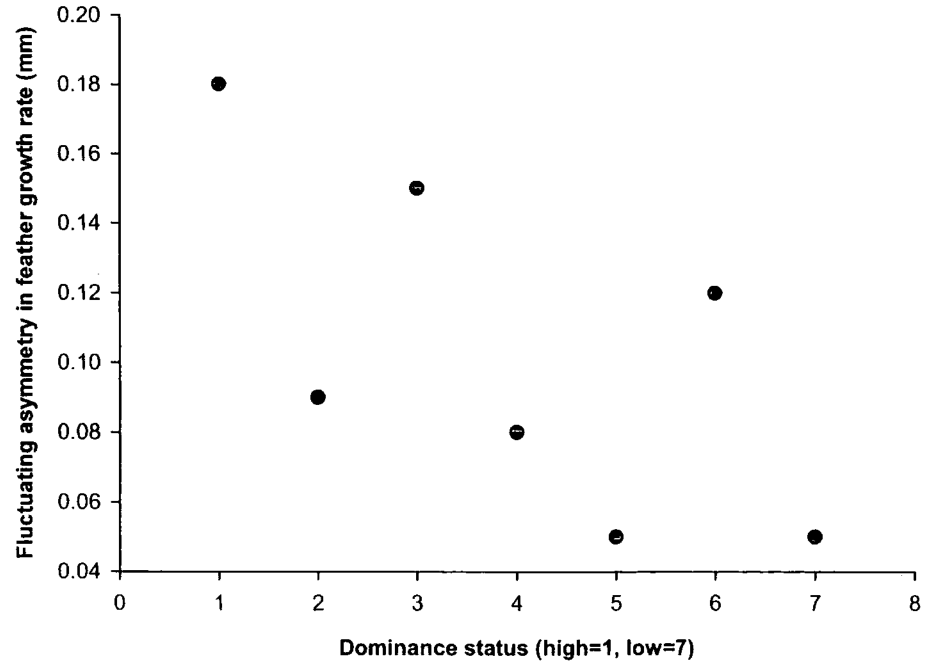

Figure 6.4: The negative relationship between dominance rank and the degree of fluctuating asymmetry in the growth rates of tail feathers induced in coal tits.

6.5 Discussion

6.5.1 Temporal Considerations

The induced central tail feathers of great tits had a faster growth rate if the original feathers were removed later in the two-week removal period during the winter of 2000-2001. A change in weather or environmental conditions probably caused this relationship between growth rate and removal date through conditions improving later in the feather growth period. The difference in growth rate between those feathers induced at the beginning and end of the removal period highlights the need for all feathers to be removed during the shortest possible time span when studying ptilochronology.

6.5.2 Relationship between feather growth rate and quality

During both winters, great tits with the fastest feather growth rates produced feathers that were longer and with a higher linear density than those feathers with slow growth rates. These results demonstrate that birds with better body condition can produce higher quality feathers (using length and density) and are able to do so without compromising growth rate. These results contradict those of some recent studies (Dawson *et al.* 2000; Hall & Fransson 2000), which have shown that feathers which grow more quickly are often shorter, lighter in weight or more asymmetrical than those that are grown more slowly. However, previous studies have generally been carried out under time-constrained conditions where birds have been forced to moult rapidly, so may represent situations where the need to grow the feathers rapidly is greater than the need for feathers of higher quality *i.e.* when energy is needed for migration (Dawson *et al.* 2000; Hall & Fransson 2000). It is probable that the main reason for the differences between the results found in this study and those of past studies arise from birds only replacing two feathers during this study whereas in previous studies, birds have been completing a full body moult and doing so under time-constraint so that there is greater pressure on individual birds.

6.5.3 Effects of sex and age on growth rate and quality

Though sex did not influence the lengths, linear densities or growth rates of induced tail feathers in great tits, blue tits or coal tits, previous studies have found that males and females do differ in their feather growth rate or quality when feathers are induced. The final lengths and masses of tail feathers induced in northern cardinals *Cardinalis cardinalis* have been reported to differ between the sexes, with males having better quality tail feathers than females (Grubb, Waite & Wiseman 1991). Within Parids, adult male great tits have been shown to grow induced feathers more quickly than females under harsh climatic conditions but not under milder conditions (Carrascal *et al.* 1998) suggesting that harsher climates cause a difference to occur between the sexes because of differing abilities to cope with poor environmental conditions. It is possible that during this study, the environmental conditions were not harsh enough to cause differences in the nutritional status of male and female Parids.

The age class (adult or juvenile) of great tits was related to induced tail feather length in both years and induced linear density during the winter of 2001-2002. Juvenile great tits produced longer feathers than adults suggesting that they were in better nutritional condition. However, these results are probably the consequence of juvenile great tits having shorter original tail feathers (Appendix 7) because they were either grown in the nest (~10%) or grown during post-juvenile moult (~90%) (Jenni & Winkler 1994) when juvenile birds are under greater pressure than adults to find enough resources because of their lack of experience in foraging. During winter, though conditions were more harsh overall, juvenile great tits could produce tail feathers that are almost as long as those that they were capable of producing when carrying out their partial moult. Adult great tits however, that produced high quality feathers during their annual moult, demonstrated a larger difference between those feathers and the feathers induced during winter.

Juvenile great tits were unable to produce such high-density tail feathers as adults during the 2001-2002 field season. This was probably a result of juvenile birds having greater difficulty meeting their daily energy requirements, which often leads to juvenile birds having lower survival rates (Hogstad 1989; Gosler 1993; Carrascal *et al.* 1998). These results support evidence from studies on northern cardinals and great tits that have shown that juvenile birds produce lower quality feathers than adults when feathers are induced (Grubb, Waite & Wiseman 1991; Carrascal *et al.* 1998). It is possible that differences between the age classes were not observed during the 2000-2001 field season because of the higher daily temperatures during the feather growth period in that year (Appendix 8). Higher daily temperatures allow birds to survive on fewer resources since less energy is needed for thermoregulation.

6.5.4 Effects of dominance status on induced tail feather growth rate and quality

Though no relationship was apparent between the dominance status of great tits or blue tits and feather growth rate or quality, dominant coal tits produced poorer quality induced tail feathers (as measured by length and density) that had slower growth rates than those of their subdominant conspecifics. These results imply a cost to high dominance status in coal tits but not great tits or blue tits. Costs of high dominance status have been reported previously and have usually been measured as an increase in the metabolic rates of dominant birds (Røskaft *et al.* 1986; Hogstad 1987; Bryant & Newton 1994), though a study has also reported greater levels of fluctuating asymmetry in the primary feathers of dominant starlings (Swaddle & Witter 1994) (discussed later). Reduced feather growth rate and quality (as measured by length and density) have not been suggested as a cost to high dominance status before and these results imply that dominant individuals are undergoing longer term costs associated with their dominance status, unlike those of high metabolism since metabolism returns to normal levels at night (Hogstad 1989).

The results obtained for coal tits in this study are contrary to those of previous studies, which reported that dominant individuals grow induced tail feathers at a faster rate than subdominant conspecifics (Grubb 1989; Hogstad 1992; Carrascal *et al.* 1998). However, Grubb (1989) applied a dominance hierarchy to downy woodpeckers *Picoides pubescens* based on two dominance levels (male = dominant, female = subdominant). This type of dominance hierarchy would not differentiate between differences that are due to dominance and those due to sex. Since differences in feather growth rate and quality have been reported between males and females in the past, it is likely that sex effects may bias the data (Grubb, Waite & Wiseman 1991; Carrascal *et al.* 1998). The contrast between the results from this study and those of Hogstad (1992), which provided evidence demonstrating that dominant willow tits can grow an induced tail feather at a faster rate than subdominants, could reflect the difference in the type of social system between the willow tit, which has a stable flocking system and the coal tit, which has an unstable flocking system though individual dominance ranks are stable (See Chapter 3; Brotons 2000b). The instability of the coal tit system forces individuals to interact more frequently because they meet unfamiliar birds more often, though dominant and subdominant birds are involved in a similar number of aggressive interactions (See: Chapter 3). However, given that dominant birds are less likely to retreat during an interaction, they will expend more energy chasing or interacting with an opponent. This could account for the difference in nutritional state between dominant and subdominant coal tits with dominant individuals spending more time on intense aggressive interactions. However, since great tits also form unstable flocks, this does not explain why great tits and coal tits should differ in the effects of dominance status on feather growth rates and feather quality. It is possible that because coal tits are at the bottom of the inter-specific dominance hierarchy (Gosler 1990; Gosler & Carruthers 1994, pers. obs), their intra-specific dominance status may not be as important in determining the allocation of resources as it is in the great tit. Therefore although dominant coal tits may expend more energy than subdominants during interactions, the benefits in terms of nutrition may be limited.

6.5.5 Fluctuating asymmetries in growth rate and quality

Dominant coal tits demonstrated higher levels of fluctuating asymmetry in feather growth rate compared to subdominant conspecifics (but not fluctuating asymmetry in length or linear density) suggesting that they had poorer nutritional condition during feather growth. Swaddle and Witter (1994) reported that fluctuating asymmetries in the length of the primaries of moulting starlings could be caused by nutritional stress. It is unclear however whether fluctuating asymmetries in growth rates are as important as those displayed in feather length and density, which have more permanent consequences. The results obtained from coal tits in this study with regards to dominance status and fluctuating asymmetry in growth rates agree with previous results (Swaddle & Witter 1994) that provided evidence that dominant starlings displayed higher levels of fluctuating asymmetry in feather length than subdominant starlings under low levels of competition. Under low competition levels *i.e.* when the starlings were housed alone, the dominant birds paid the costs of being dominant but did not benefit since there were no conspecifics competing for food. However, when the study was repeated (Witter & Swaddle 1994) it was found that when birds were kept under high competition levels, there was no difference between the levels of fluctuating asymmetry in dominant and subdominant birds. Since the present study was carried out on free-living coal tits, and food was not available *ad libitum*, the previous explanation is not sufficient to justify these results since competition would have occurred for food. Why fluctuating asymmetry was not represented in feather length is not clear but may demonstrate lower levels of stress that are corrected later when one feather stops growing.

6.5.6 Conclusions

Care must be taken when using ptilochronology as a measure of body condition when feathers have been induced over a time period rather than on one day. This study has demonstrated the importance of this even over the short time period of two weeks. The sampling of induced feathers which involves re-capturing the birds is not as time constrained since feather wear seems to be negligible but must still be considered in every study.

In many avian species, high ranking individuals are more frequently involved in aggressive encounters which can result in elevated metabolic rates (Røskaft *et al.* 1986; Hogstad 1987; Bryant & Newton 1994) and impaired immunocompetence (Folstad & Karter 1992; Barnard *et al.* 1998), especially in territorial species and those that are involved in lengthy interactions involving aggressive physical interactions or displays (Järvi & Bakken 1984; Bryant & Newton 1994). However, these apparent costs of high dominance status may not necessarily be expensive to high-ranking birds, because they may be fitter individuals, and data on the subject are lacking. The data from this study suggest that there may be a nutritional cost to dominance in coal tits, because it is important to have a full compliment of high quality feathers (Dawson *et al.* 2000) and in this study, high dominance status was associated with impaired feather growth and reduced quality. Such costs of high dominance status are presumably offset by other advantages, for instance better territories, mates and feeding sites.

Though fluctuating asymmetry is considered to be a measure of stress, fluctuating asymmetry in the growth rates of feathers does not produce a lasting effect since it does not necessarily lead to fluctuating asymmetry in feather length or density. Though the higher levels of fluctuating asymmetry in the feather growth rates of dominant coal tits backs up the results from ptilochronology of dominant coal tits, interpretation must be cautious until further work is done to assess the disadvantages of fluctuating asymmetry in growth rates.

Chapter 7

The health status of great tits and blue tits: an immunological study

7.1 Abstract

The immunocompetence or health status of individuals can have important consequences for their survival and reproduction. However, having high immunocompetence can be costly since it competes for resources with other energetically demanding processes such as thermoregulation, moult and reproduction. Therefore only particular individuals may be capable of maintaining high immunocompetence. This study considered which factors might determine the health status of individual great tits and blue tits using blood parameters (number of reticulocytes in 10 000 erythrocytes, number of lymphocytes in 10 000 erythrocytes and the H/L ratio) and parasite prevalence. The health status of neither species was related to dominance and neither age nor sex had an effect on the measured blood parameters. However, contrary to previous results, males were found to have fewer parasites than females, which may have resulted from differences in foraging habitats between the sexes or from the effects of sex hormones.

7.2 Introduction

Due to the increasing numbers of studies on free living birds which have found that the evaluation of immunocompetence provides important information on individual health and physiological well being, the estimation of immunocompetence is now considered to be a valuable and accurate tool for use in the assessment of individual fitness (Sorci, Soler & Møller 1997; Hõrak, Ots & Murumägi 1998; Ots, Murumägi & Hõrak 1998; Hõrak *et al.* 1999; Dubiec & Cichon 2001). Because immunocompetence competes for resources with other important activities such as growth, reproduction and moult (Ots & Hõrak 1996; Saino, Calza & Møller 1997; Hõrak *et al.* 1998; Hõrak, Ots & Murumägi 1998; Brinkhof *et al.* 1999; Moreno *et al.* 2001), the majority of studies concentrating on immune function and health status in birds have been carried out on nestlings (Saino, Calza & Møller 1997; Brinkhof *et al.* 1999; Hõrak *et al.* 1999; Dubiec & Cichon 2001) or on adult birds during the breeding season when they also have the prospect of moult (Ots & Hõrak 1996; Hõrak *et al.* 1998; Hõrak, Ots & Murumägi 1998; Ots, Murumägi & Hõrak 1998; Williams *et al.* 1999; Moreno *et al.* 2001), thus allowing measurements to occur at times when the greatest variation is likely to be present between individuals.

7.2.1 Estimation of immunocompetence

The estimation of immunocompetence has usually been carried out using one of several established methods. The most commonly employed method involves the interpretation of the body's response to an artificially administered antigen (Cheng & Lamont 1988; Moreno *et al.* 2001; Barbosa & Moreno 2002), which often involves measuring the inflammatory response. The calculation of the parasite load of an individual's blood or intestine (Ots & Hõrak 1996; Hõrak *et al.* 1998; Lindström *et al.* 2001) can also provide an estimate of health status or parasite resistance and involves collecting blood or faecal samples from individuals. The measurement of certain haematological parameters *e.g.* the heterophil to lymphocyte ratio (H/L) or the numbers of each type of leucocyte (white blood cells), (Merilä & Svensson 1995; Hõrak, Ots & Murumägi 1998; Ots, Murumägi & Hõrak 1998) is also useful in providing estimates of individual health status. This study uses two of these methods for estimating an individual's immunocompetence and health status *i.e.* parasite prevalence and haematological parameters.

7.2.2 The function of the immune system

The successful immune function of an individual relies on the performance of its antibodies and leucocytes, which offer its main protection against pathogenic antigens (Alberts *et al.* 1994). Since the numbers and types of leucocytes can be affected by factors such as nutrition, stress, toxins and season (Gross & Siegel 1983; Grasman, Scanlon & Fox 2000), with careful interpretation, they are well suited for estimating individual fitness within populations.

There are several different types of leucocyte circulating within the peripheral blood of birds, but two types, lymphocytes and heterophils dominate numerically and are responsible for the majority of immunological responses (Alberts *et al.* 1994). Heterophils have been found to be non-specific immune cells concerned with phagocytosis of bacteria (Maxwell 1993; Alberts *et al.* 1994). They enter tissues during the inflammatory response and enhance resistance to bacterial infections though they are known to have a detrimental effect on the host tissue (Fulton *et al.* 1996). The immune response of lymphocytes is thought to be more specific and has little negative effect on the host (Maxwell 1993; Fulton *et al.* 1996).

7.2.3 Applications of blood parameters

It has been reported that the numbers of lymphocytes and heterophils circulating in the peripheral blood can give an indication of the likelihood of infection or stress (Gross & Siegel 1983; Ots, Murumägi & Hõrak 1998). Lower than normal numbers of lymphocytes signals immunosuppression with an increase in the likelihood of contracting viral infections (Siegel 1985; Fitzgerald 1988). However, because high numbers of lymphocytes can indicate either high immunocompetence or previous exposure to high levels of infection, interpretation of data indicating high numbers of lymphocytes is difficult.

It is now widely accepted that the H/L ratio from the blood of birds indicates stress levels with the highest H/L ratios indicating birds that are experiencing the greatest stress (Gross & Siegel 1983; Hõrak, Ots & Murumagi 1998). In a study assessing the accuracy and usefulness of various methods of estimating immunocompetence, the H/L ratio was reported to be one of the most accurate methods since measurement errors were shown to be small compared with the total variation between individuals (Ots, Murumägi & Hõrak 1998). The H/L ratio has also been shown to be sensitive to stressors such as infectious diseases, starvation and psychological disturbance (Gross & Siegel 1983; Maxwell 1993; Ots & Hõrak 1996; Hõrak, Ots & Murumagi 1998) making it ideal for comparisons of health status between individuals. Because of the difficulty in interpreting the cause of high lymphocyte numbers, the H/L ratio is most useful when high. When the H/L ratio is low, it is not known whether this is due to high immunocompetence or recent exposure to infection.

The numbers of immature red blood cells (reticulocytes) circulating in the bloodstream have not previously, to my knowledge, been used in avian studies to determine health status. However, the numbers of reticulocytes can be used to estimate the rate of red blood cell production. Polychromatophilia (an increase in the numbers of reticulocytes) is usually caused by normal marrow function in response to anaemia (Sodikoff 2002). Normally, reticulocytes make up around 1% of the circulating red blood cells but during anaemia they can increase to 4%. Reduced numbers of reticulocytes suggest that an individual is experiencing anaemia but that its body is not responding (Sodikoff 2002). Like the usefulness of lymphocyte counts, that of reticulocytes is limited to the idea that low numbers indicate poor quality birds that are not capable of responding to anaemia, but high numbers may indicate high quality birds or birds that have anaemia and but are responding in a healthy manner.

7.2.4 Factors affecting the health status of avian populations

The majority of studies that have made a comparison of the immune function of male and female animals, have found that females typically have the capabilities of mounting a greater immune response than males (Zuk & McKean 1996; Klein, Gamble & Nelson 1999; Klein 2000; Barbosa & Moreno 2002), which has been explained either by the immunosuppressive nature of the sex hormone testosterone in males (Alexander & Stimson 1988; Evans, Goldsmith & Norris 2000) or by differences in the reproductive costs affecting each sex (Hõrak *et al.* 1998; Moreno, Sanz & Arriero 1999). However, because some studies have been carried out during winter when reproductive costs are not an issue and differences in immunocompetence between males and females have been reported, the differing costs of reproduction between the sexes cannot account for all the variation in immunocompetence (Barbosa & Moreno 2002). Moreover, the effect of testosterone on immunity is not easily understood (Sheldon & Verhulst 1996; Peters 2000; Lindström *et al.* 2001): some studies have found that high testosterone suppresses the immune response (Saino & Møller 1994; Zuk, Johnsen & Maclarty 1995), whilst others found that it has no effect or may even enhance immunocompetence (Weatherhead *et al.* 1993; Klein, Gamble & Nelson 1999; Hasselquist *et al.* 1999).

Few studies have considered age-specific variation in immunocompetence of birds post-fledging, though many studies have been carried out on the effect of nestling age on immunocompetence within broods (Saino *et al.* 2002; Roulin *et al.* 2003) and between broods (Sorci, Soler & Møller 1997; Dubiec & Cichon 2001) (See: Chapter 8). In a study that did involve post-fledging birds, juvenile magpies *Pica pica* were found to harbour a greater number of parasite species and to have a higher parasite prevalence than adults (Blanco *et al.* 2001). In contrast to the results of Blanco *et al.* (2001), hooded crows *Corvus corone* *cornix* demonstrated no age class differences in their immunocompetence when blood parameters were considered (Acquarone, Cucco & Malacarne 2002). In titmice, juveniles have higher winter mortality than adults, due to the lack of resources (Hogstad 1989; Gosler 1993; Carrascal *et al.* 1998), therefore juveniles may also have lower immunocompetence, but this has not previously been examined.

With regards to dominance status, it has been reported that male laboratory mice (*Mus musculus*) with low social status have a greater immune function than do mice of higher social status, possibly due to the immunosuppressive effects of testosterone in high-ranking individuals (Barnard *et al.* 1998). Using the size of the bib as an indicator of dominance status in house sparrows *Passer domesticus*, Gonzalez, Sorci & de Lope (1999) reported that males with high dominance status had lower levels of immunocompetence during the breeding season as predicted by the immunocompetence handicap hypothesis. However, during November, the opposite was true possibly reflecting the better access to resources experienced by dominant birds. It is unclear how dominance rank will affect immune function in Parids since the higher testosterone levels of birds with high dominance status may negatively affect immunocompetence or dominant birds may just as likely experience a net benefit from their high dominance status through being in better body condition.

In this study I aim to determine whether a difference exists in the immunocompetence and parasite loads of the sex and age classes in great tits and blue tits. The purpose of this study is also to determine whether immunocompetence and parasite load are related to dominance status by using the H/L ratio, lymphocyte counts and reticulocyte counts as estimates of immunocompetence.

7.3 Methods

The methods for determining age, sex and dominance status are described in Chapter 2.

7.3.1 Collection of blood samples

Great tits and blue tits were captured between February and April 2002 for blood sampling under Home Office licence. Approximately 5-10µl of blood was collected from the brachial vein of each bird by first piercing the area with a sterile needle and then collecting the blood in a heparinised capillary tube. The area around the brachial vein where blood collection took place was sterilised with 70% ethanol before the insertion of the needle. Since most of the birds had been captured previously, biometrics were not measured during blood collection so that the birds could be released immediately after bleeding stopped.

7.3.2 Blood smears and cell counts

Immediately following blood collection, one drop of blood approximately 6mm in diameter was blown by mouth from the capillary tube onto a clean microscope slide. Using the short edge of another microscope slide at a 30-45° angle to the original slide, the blood droplet was pulled across the length of the slide to make a blood smear approximately one cell thick (Bennett 1970; Canfield 1998). The blood smear was air dried and then fixed in absolute methanol for 5 minutes before being stained with Giemsa stain (1:20; BDH) for 30 minutes. The slide was then rinsed with distilled water and air-dried.

The three blood cell parameters that were used to estimate the health status of great tits and blue tits were: the number of reticulocytes in 10 000 erythrocytes, the number of lymphocytes in 10 000 erythrocytes and the heterophil lymphocyte (H/L) ratio. Reticulocytes were recognised by their blue cytoplasm and less dense chromatin than mature red blood cells (erythrocytes) (Alberts *et al.* 1994) (Plate 7.1). Blood smears were examined under x100 using oil immersion and the number of reticulocytes were counted in approximately 10 000 erythrocytes. The numbers of white blood cells were estimated by counting the numbers of each type of white blood cell per 10 000 red blood cells under x100 using oil immersion. The different types of white blood cells were classified according to Alberts *et al.* (1994) (Plate 7.1). The heterophil lymphocyte ratio was calculated by counting approximately 100 white blood cells (the majority of which were heterophils and lymphocytes) and dividing the number of heterophils by the number of lymphocytes.

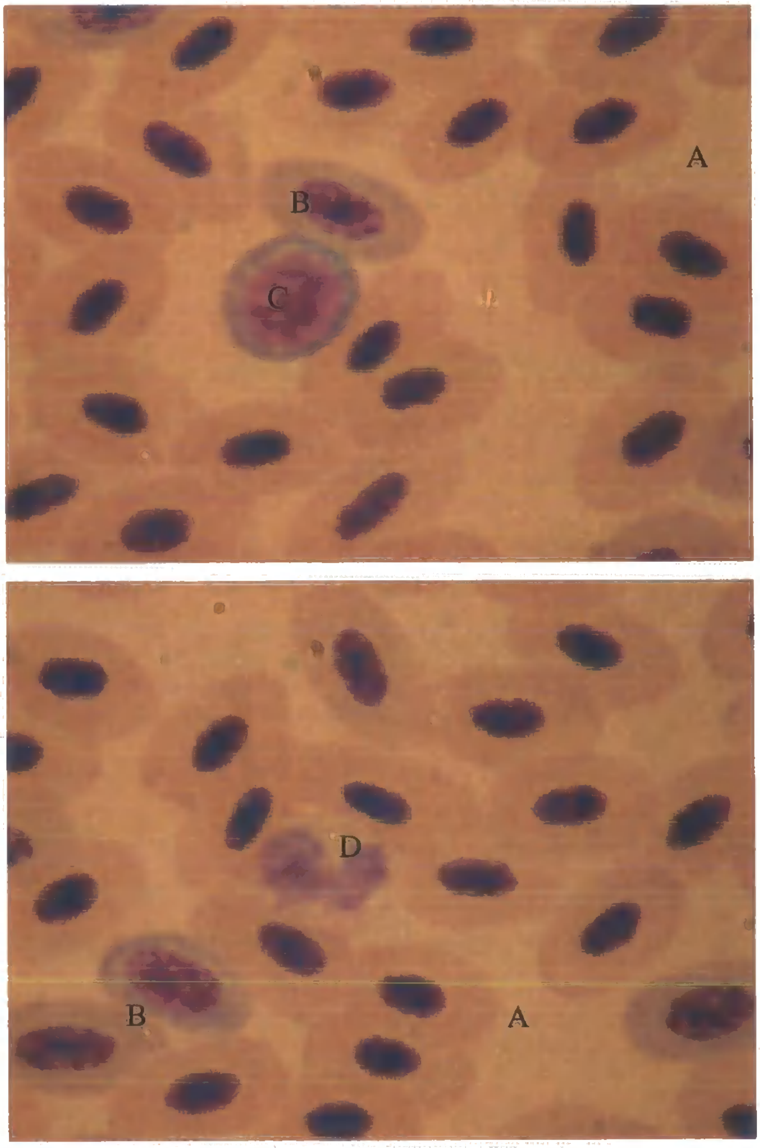

Plate 7.1: Avian erythrocytes (A), reticulocytes (B), lymphocytes (C) and heterophils (D) as viewed on blood smears at x100 with oil immersion.

7.3.3 Faeces collection and parasite counts

When great tits and blue tits had been extracted from mist nets, traps or nest boxes (See: Chapter 2) during February – April 2002, they were placed in a specially constructed compartmentalised box rather than in conventional bird bags. Each compartment of the box was lined with foil so that faeces could be collected once the birds had been removed from the box. Birds were not kept in the box for any longer than they would be kept in bird bags during the processing of other species (other species were processed first to allow the birds time to defecate). Faeces were stored on ice and refrigerated for no longer than 24 hours before being analysed.

Each faecal sample was weighed, combined with 2ml of saturated salt solution (to allow flotation of the eggs) and shaken until the faeces had broken up to produce an opaque solution. This solution was then immediately injected into both chambers of a McMaster egg counting slide with a syringe whilst taking care not to produce air bubbles (for further information on preparing faecal material for egg counting, See: Sloss, Kemp & Zajac 1994). The slide was allowed to stand for two minutes so that the flotation process could take place. Oocysts of parasites within each lane of both chambers were then counted and identified according to Sloss, Kemp and Zajac (1994).

The majority of parasites that were identified, according to Soulsby (1968), were Coccidians, which were either *Isospora* or *Eimeria.* Many of the Coccidian oocysts were unsporulated so they could not be identified as either *Isospora* or *Eimeria.* Those that were sporulated were classified depending on whether they contained two sporocysts indicative of *Isospora* or three sporocysts indicative of *Eimeria* (Soulsby 1968). Since the majority of parasites were one of these two species and because parasite numbers could be extremely variable (numbers in one faecal sample may not reflect intensity of infection (S. Lyndsey pers. comm)), parasite presence or absence was used as the parasite prevalence variable.

7.3.4 Statistical analysis

GLMs were used to compare the blood parameters between great tits and blue tits and were used to determine the relationships between the presence of parasites and blood parameters. Temporal variation in the health status (number of reticulocytes, numbers of lymphocytes and the H/L ratio) of great tits and blue tits was analysed using REML analysis with date (number of days since the first blood sample was taken) and time (proportion of daylight hours).

The effects of age and sex on the presence or absence of parasites was analysed using Chi-squared tests and their effects on the blood parameters of individuals were analysed using GLMs. A Mann-Whitney U test was used to determine whether dominance status affected the presence or absence of parasites in great tits and blue tits. Paired t-tests were used to determine whether the five most dominant birds or the five most subdominant birds in great tits (out of 20) or the three most dominant and subdominant birds in blue tits (out of 13) differed in their health status from that of the rest of the population.

7.4 Results

7.4.1 Blood parameters in great tits and blue tits: a comparison

Great tits and blue tits had similar densities of reticulocytes (Table 7.1; $F_{1,59}$ = 0.95, P = 0.3) and lymphocytes ($F_{1,59}$ = 0.23, P = 0.6) but blue tits had higher H/L ratios than great tits ($F_{1,59}$ = 5.70, P<0.05).

	Num. Reticulocytes	Num. Lymphocytes	H/L Ratio
Great tit	341.21 (92.19)	10.85 (7.16)	0.38 (0.26)
Blue tit	364.75 (95.99)	10.04 (5.99)	0.60 (0.42)

Table 7.1: The mean (s.d.) of the blood parameters of great tits (*n* = 33) and blue tits (*n* = 28) used to assess immunocompetence or health status.

7.4.2 Temporal variation in the health status of Parids

The number of lymphocytes in 10 000 erythrocytes did not vary temporally in great tits but increased with date though not time of day in blue tits (Figure 7.1). The numbers of reticulocytes in 10 000 erythrocytes and the H/L ratios of great tits and blue tits did not vary with date or time of day (Table 7.2).

	Blood parameters	**Date**		**Time**	
		Wald $(\chi^2)_{d.f.}$	***P***	***Wald $(\chi^2)_{d.f.}$***	***P***
Great tit	lymphocytes	$14.53_{11,42}$	0.2	$13.50_{19,42}$	0.8
	reticulocytes	$10.48_{11,42}$	0.5	$11.25_{22,42}$	1.0
	H/L ratio	$10.20_{11,42}$	0.5	$26.17_{22,42}$	0.3
Blue tit	lymphocytes	$34.77_{13,28}$	<0.001	$9.53_{22,28}$	1.0
	reticulocytes	$4.19_{13,28}$	1.0	$7.94_{12,28}$	0.8
	H/L ratio	$9.14_{13,28}$	0.6	$8.33_{12,28}$	0.8

Table 7.2: Results of REML analysis on the temporal changes that take place in the health status of great tits (n = 33) and blue tits (n = 28) over a ten-week period.

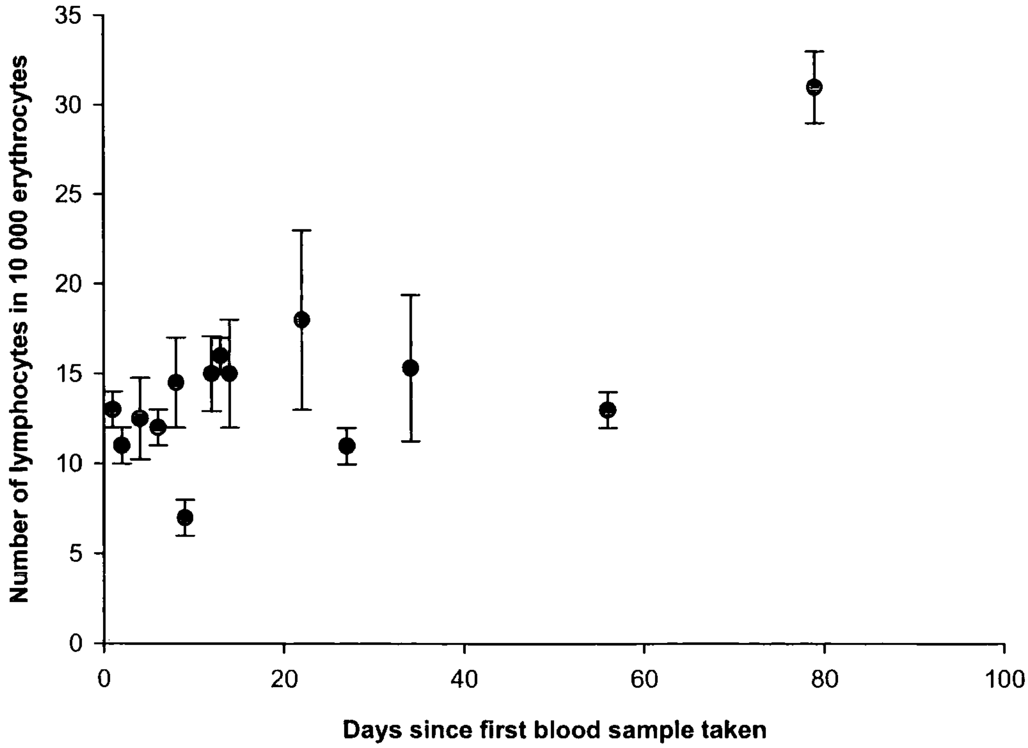

Figure 7.1: The increase in the lymphocyte counts of blood taken from blue tits between mid-February 2002 and the end of April 2002.

7.4.3 Immunocompetence and the presence of faecal parasites

There was no relationship for either species between blood parameters and the presence of *Isospora* or *Emeria* in faeces (Table 7.3).

	lymphocytes		reticulocytes		H/L ratio	
	$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	$0.01_{1,19}$	0.9	$0.46_{1,19}$	0.5	$0.03_{1,19}$	0.9
Blue tit	$0.80_{1,18}$	0.4	$0.01_{1,18}$	0.9	$0.00_{1,18}$	1.0

Table 7.3: GLM results showing the lack of relationship between blood parameters and the presence of faecal parasites (*n* values: great tits = 20, blue tits = 19).

7.4.4 Age, sex and health status

There was no difference between the age or sex classes with regards to blood parameters in either species (Table 7.4) or in the prevalence of intestinal parasites in blue tits (Table 7.5). However, there was significant variation with regards to the presence of parasites among great tits (Table 7.5) with adult females having the highest prevalence of parasites (Figure 7.2).

	Blood parameter	Sex		Age	
		$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	lymphocytes	$0.75_{1,32}$	0.4	$2.04_{1,32}$	0.2
	reticulocytes	$1.71_{1,32}$	0.2	$0.38_{1,32}$	0.5
	H/L ratio	$0.00_{1,32}$	1.0	$0.77_{1,32}$	0.4
Blue tit	lymphocytes	$0.97_{1,23}$	0.3	$0.03_{1,23}$	0.9
	reticulocytes	$3.30_{1,23}$	0.1	$2.77_{1,23}$	0.1
	H/L ratio	$3.00_{1,23}$	0.1	$0.64_{1,23}$	0.4

Table 7.4: GLM results demonstrating no effect of age or sex on the health status of great tits (*n* values: male = 20, female = 13, adult = 15, juvenile = 18) or blue tits (*n* values: male = 10, female = 14, adult = 8, juvenile = 16).

	Sex		Age		Age*Sex	
	$\chi^2_{d.f.}$	*P*	$\chi^2_{d.f.}$	*P*	$\chi^2_{d.f.}$	*P*
Great tit	$7.54_{1,29}$	<0.01	$0.22_{1,29}$	0.6	$10.11_{3,29}$	<0.05
Blue tit	$0.14_{1,29}$	0.7	$0.15_{1,29}$	0.7	$0.31_{3,29}$	1.0

Table 7.5: Chi-squared results testing the effects of age, sex and their interaction on the prevalence of intestinal parasites (*n* values: great tits: adult males = 12, adult females = 6, juvenile males = 13, juvenile females = 14; blue tits: adult males = 6, adult females = 5, juvenile males = 9, juvenile females = 8).

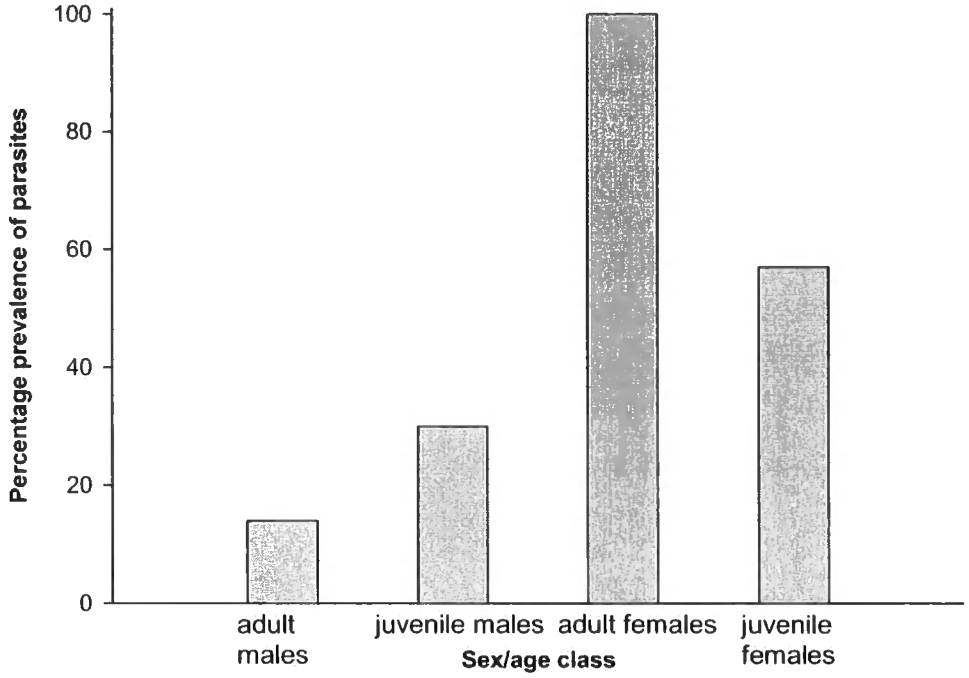

Figure 7.2: The difference in the prevalence of intestinal parasites (Coccidians) in the age and sex classes of great tits between mid-February 2002 and the end of April 2002.

7.4.5 The effects of dominance status on health status

There was no relationship between dominance status and the prevalence of intestinal parasites in great tits (Mann-Whitney U: W_{16} = 75.0, n = 17, P = 0.3) or blue tits (Mann-Whitney U: W_{12} = 49.0, n = 13, P = 1.0). Neither the most dominant nor the most subdominant birds differed from the rest of the population in their health status as measured by the three blood parameters (Table 7.6).

	Lymphocyte Count				Reticulocyte Count				H/L Ratio			
	Dominants		Subdominants		Dominants		Subdominants		Dominants		Subdominants	
	$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	$1.96_{1,18}$	0.2	$2.83_{1,18}$	0.1	$0.14_{1,18}$	0.7	$0.35_{1,18}$	0.6	$0.29_{1,18}$	0.6	$0.00_{1,18}$	1.0
Blue tit	$0.09_{1,11}$	0.8	$3.37_{1,11}$	0.1	$0.28_{1,11}$	0.6	$0.11_{1,11}$	0.7	$0.53_{1,11}$	0.5	$3.89_{1,11}$	0.1

Table 7.6: The significance of the differences between the health status of the most dominant or subdominant birds and the rest of the population (five and three birds at either end of the hierarchy were used for great tits and blue tits respectively) (total *n* values: great tits = 20, blue tits = 13).

7.5 Discussion

Great tits and blue tits differed in their H/L ratios but not in their lymphocyte and reticulocyte counts. However, since there is no published literature on the expected values for each species and how they are likely to differ, it is not possible to conclude whether the differences in the H/L ratios are due to blue tits being under greater stress than great tits or whether the differences are simply due to the species having differing numbers of lymphocytes or heterophils.

7.5.1 Temporal changes in health status

Many populations of birds and mammals are subject to seasonal cycles of disease with a higher death rate evident in winter and some animals cope with this by increasing their immune function during stressful times (McDonald, Lee, Than & Martin 1988; Nelson & Demas 1996; Merino, Møller & de Lope 2000). In this study, between mid-February 2002 and the end of April 2002, the number of lymphocytes in 10 000 erythrocytes increased with date in blue tits, though there was no other temporal variation in health status or immunocompetence in great tits or blue tits during the same period. Many of the previous studies that have reported temporal variation in the imunocompetence of birds have been carried out over the breeding season when there is greater pressure on birds (Zuk & Johnsen 1998; Christe, Møller & de Lope 2002) or over a longer time scale *i.e.* one full year (Mann *et al.* 2000). The progressive increase in the number of lymphocytes in blue tits may have resulted from individuals preparing their immune system for the stress of the breeding season but because high lymphocyte counts can also be caused by recent exposure to infection, it could equally as likely be caused by an increase in the exposure to infection as the year progressed. This result should, however, be viewed with some caution, because the relationship depends heavily on a single sample (Figure 7.2).

7.5.2 The effects of sex, age and dominance status on the health status of Parids, as measured by blood parameters

Despite many studies highlighting differences in the immune responsiveness of male and female animals (Alexander & Stimson 1988; Zuk & McKean 1996; Klein, Gamble & Nelson 1999; Klein 2000; Barbosa & Moreno 2002), the health status of the blood of great tits and blue tits did not vary between age or sex classes during this study. Blood samples were collected from mid-February until the end of April when testosterone levels should have been high as males compete for territories and mates, and so these results do not appear to support the notion that testosterone acts as an important immunosuppresent during this period. Immunocompetence was not related to dominance status since the most and least dominant birds did not differ from the rest of the population in their blood parameters.

Differences in immunocompetence and health status due to age in birds and mammals have been given little attention compared to sexual differences. Although differences were found in the immunocompetence of adult and nestling great tits and blue tits in this study (See: Chapter 8), by the time juvenile birds are setting up territories of their own (*i.e.* in their first spring), they have similar health status to that of adult birds (*i.e.* second spring and older).

7.5.3 The effects of age and sex on parasite prevalence

Despite the absence of a relationship between the health status of individuals (measured by blood parameters) and the sex or age classes, both age and sex had an effect on the presence of Coccidians (*Eimeria* and *Isospora*) in great tits. Females were more likely to have parasites than males though within the sexes, the age classes affected parasite prevalence in the opposite way. Adult females were more likely to harbour parasites than juvenile females and juvenile males were more likely to have parasites than adult males. Previous studies have typically found that males harbour more parasites than females (for reviews see: Zuk & McKean 1996; Klein 2000), which is the opposite result to that of the current study. The greater susceptibility of female great tits to parasites could result from a variety of factors relating to the birds' internal and external environments. For instance, differences in the microhabitats or diets of males and females may affect exposure to intestinal parasites, especially if males use their higher dominance status (See: Chapter 3) to push females into feeding areas that may be infected with sporulated oocysts. It is also possible that females may put less effort than males into fighting parasites during February and April so that reserves can be channelled into preparing the body for reproduction.

7.5.4 Conclusion

The lack of relationship between immunocompetence or intestinal parasite presence or absence and date in great tits during the build up to the breeding season suggests that the stress undergone during this time was not sufficient to inhibit immunocompetence. Though blue tits demonstrated an increase in the number of lymphocytes in their blood, this seemed to be heavily influenced by one sample taken late in the season.

Though past studies have suggested that testosterone may have an immunosuppressive effect causing differences in the immunocompetence of male and female animals, this study suggested that there was no sex or age difference in blood parameters of great tits or blue tits. The prevalence of *Isospora* and *Eimeria* differed between the sexes in great tits, possibly because males have higher resistance to these parasites than females or because males encounter the parasites less often. Parasite prevalence varied with age in opposite ways in male and female great tits.

High social status did not enhance or inhibit immunocompetence during the build up to the breeding season in great tits or blue tits. Therefore, there was no evidence that dominant individuals benefited from better health when blood parameters and parasite prevalence were considered.

Chapter 8

The health status and immunocompetence of nestlings: hierarchies within broods

8.1 Abstract

The immunocompetence of nestlings can be affected by a variety of factors including hatching date, environmental conditions and body condition. Hatching asynchrony can lead to large amounts of variation in body size between the first hatched and last hatched nestlings. During food provisioning by parent birds, the largest nestlings can bias the allocation of resources towards themselves, leading to a competitive hierarchy within a brood with the largest most competitive nestlings having the best body condition and therefore the most developed immune system. The immunocompetence of great tit nestlings in this study was affected by hatching date and both great tit and blue tit nestlings were affected by brood size. Within broods, the competitive hierarchy did not cause the smallest nestlings to have the least developed immune system. Differences in blood parameters existed between nestlings from different broods suggesting that parental quality or environmental conditions affected immunocompetence.

8.2 Introduction

The trade off that exists between quality and quantity of offspring is an important consideration in current theories of life history evolution. Parents must choose between producing a few high quality offspring or a higher number of poorer quality offspring since resources have to be shared between all of the nestlings in a brood. Because the consequences of this decision can be altered by environmental conditions, some avian species may produce more offspring than can normally be sustained, and eliminate the poorest quality offspring if resources are limited (Mock & Parker 1998; Royle & Hamer 1998). In this way, parents can produce the maximum number of recruits into the breeding population with the least affect on parental condition (Mock & Parker 1998). Whatever choices parents make with regards to how many offspring to produce, offspring will find themselves in competition for food resources with their siblings since chicks are selected to demand more than is in the interests of parents to give (Smith *et al.* 1988; Martin 1987).

8.2.1 Hierarchies within broods

Within avian taxonomic groups, competition between siblings is most pronounced in those species that exhibit asynchronous hatching since this will lead to a large variation in body size between individuals with the last hatched chicks being at a competitive disadvantage because of their small size compared to their older siblings (Bryant 1978; Hahn 1981; Gottlander 1987; Anderson *et al.* 1993; Oddie 2000). The size hierarchy that exists within broods of many species of birds leads to a similar hierarchy in competitive ability. The competitive hierarchy determines the distribution of food between nestlings with larger more competitive individuals gaining priority of access to food resources provisioned by the parents and therefore achieving a higher rate of growth, thus increasing the difference in size further (Greig-Smith 1985; Gottlander 1987; Nilsson & Svensson 1996; Royle *et al.* 1999; Nilsson & Gårdmark 2001). Larger nestlings can bias parental food allocation towards themselves by reaching the parents more easily when begging and occupying the preferred feeding positions in the nest which can involve pushing smaller competitors out of these positions (Gottlander 1987; Kacelnik *et al.* 1995; Kilner 1995). It is evident from a brood manipulation study on the marsh tit *Parus palustris* that a size hierarchy can be established very quickly within broods (*i.e.* 1-2 days) particularly in those broods with low provisioning rates resulting from poor quality parents or adverse environmental conditions (Nilsson & Gårdmark 2001).

It has been demonstrated in many species, including great tits (Perrins 1965; Tinbergen & Boerlijist 1990) and blue tits (Nur 1984b) that the body size of nestlings has important consequences for post-fledging survival (Hochanchka & Smith 1991). Because parental effort is mainly concentrated on fledged chicks rather than chicks that are still in the nest (fledged chicks are at a greater predation risk when begging for food), it is in the interests of the weaker competitors to fledge at the same time as their stronger siblings if they are to receive enough food to survive (Lemel 1989; Nilsson & Svensson 1993). It has been noted in some species that the poorer competitors within a brood compromise mass gain (and therefore body condition) in order to maximise wing length, which will allow them to fledge at the same time as the more competitive siblings (Nilsson & Svensson 1996; Nilsson & Gårdmark 2001). The smaller and weaker birds within brood competitive hierarchies may be those birds that achieve only low status in post-fledging dominance hierarchies formed by flocking species (Richner, Schneiter & Stirnimann 1989).

8.2.2 Immunocompetence in nestlings

Immunocompetence in birds has been a popular topic for research in recent years and it has been established that immune function can be dependent on various factors such as body condition (Saino, Calza & Møller 1997), nutrition (Lochmiller, Vestey & Boren 1993; Hoi-Leitner *et al.* 2001) and exposure to disease (Sheldon & Verhulst 1996; Fair, Hansen & Ricklefs 1999). Because chicks with lower competitive ability are fed less frequently, the development of their immune system may be impeded (Møller *et al.* 1998). Consequently, not only will they be disadvantaged because of their low nutritional status, but they may also be subject to higher incidence of disease or parasite loads. The Tasty Chick Hypothesis (Christe, Møller & de Lope 1998; Roulin *et al.* 2003) makes the assumption that the last hatched chicks within a brood will have a diminished ability to resist parasites because of their lower body condition. It has also been found that the first laid eggs in barn swallows *Hirundo rustica* contain more lysozyme (a component of the antibacterial immunity transferred from the maternal parent to their offspring), which is also reflected in nestlings at 5 days old thus furthering the competitive advantage of older chicks (Saino *et al.* 2002). Evidence to support this was recently demonstrated in broods of the barn owl *Tyto alba*, where the last hatched chicks were shown to have a lower humoral response than their older siblings (Roulin *et al.* 2003). However, a similar study by the same authors which was carried out on great tits, reported no difference in the cell mediated immune response of older and younger great tit nestlings possibly because of the lower degree of asynchronous hatching in this species.

8.2.3 Immunocompetence and brood size

It has been noted that the severity of the effects of a competitive hierarchy between nestlings can be affected by the size of the brood and hence level of competition (Saino, Calza & Møller 1997; Hõrak *et al.* 1999; Tella *et al.* 2000; Fargallo *et al.* 2002). It is often the case that larger brood sizes result in fledglings that have a lower mass at independence (because resources have to be shared amongst a greater number of individuals) and therefore lower survival (Saino, Calza & Møller 1997; Fargallo *et al.* 2002). This has been reported in nestling great tits from larger broods, which have a lower mass than those from smaller broods (Perrins 1965).

Most studies that have considered brood size and body condition have done so by enlarging or reducing broods and so increasing or decreasing the demand on parental provisioning (Saino, Calza & Møller 1997; Hõrak *et al.* 1999; Tella *et al.* 2000; Fargallo *et al.* 2002). It has been reported that barn swallow (Saino, Calza & Møller 1997) and great tit (Hõrak *et al.* 1999) nestlings from enlarged broods developed a lower immune response than nestlings from control or reduced broods. It is hypothesised that the maintenance of the immune system is costly and therefore when food is scarce, as is often the case with large broods, a compromise has to be reached between allocating resources to growth or immune function with the result that both are compromised to some extent (Saino, Calza & Møller 1997; Hõrak *et al.* 1999; Whitaker & Fair 2002). The lowering of growth rates and immunocompetence in large broods can reduce the probability of the nestlings surviving and this has been demonstrated with a positive correlation between immunocompetence and nestling survival in house martins *Delichon urbica* (Christe, Møller & de Lope 1998). Since a brood enlargement study on great tits demonstrated that an increase in the H/L ratio was apparent when brood size was increased, it is expected that great tit and blue tit nestlings from larger broods in this study will have a reduced immunocompetence compared to smaller broods (Hõrak, Ots & Murumägi 1998).

8.2.4 Timing of breeding and nestling immunocompetence

In many avian species, reproductive success decreases with hatching date in that those birds which breed earlier in the season produce most recruits into the breeding population (Verhulst & Tinbergen 1991; Brinkhof *et al.* 1993; Wiggins, Pärt & Gustafsson 1994; Verboven & Visser 1998). Individuals that breed later in the season usually produce fewer chicks due to their smaller clutch sizes and higher chick mortality (Verhulst & Tinbergen 1991). Studies have shown that the quality and quantity of food consumed with regards to dietary protein and amino acids can affect immunocompetence and therefore the impact of infections (Lochmiller, Vestey & Boren 1993). The increase in chick mortality with later breeding date has been confirmed to be related to both a decrease in the abundance of available food for chicks and the later breeding of lower quality parents *e.g.* younger birds tend to breed later in the season, producing nestlings with poor body condition (Verhulst & Tinbergen 1991; Brinkhof *et al.* 1993; Wiggins, Pärt & Gustafsson 1994; Verboven & Visser 1998).

The immune response has been found to decrease with hatching date in European magpies *Pica pica* and it was also found that nestlings from replacement clutches had lower immunocompetence, probably brought about by poor quality diet (Sorci, Soler & Møller 1997). Because nestlings develop their immune system whilst in the nest, those nestlings with low counts of lymphocytes or reticulocytes are at a disadvantage in terms of immunocompetence, because they will not be able to illicit a strong immune defence. As with post-fledging birds, it is not possible to distinguish between high counts of these blood parameters brought about by high immunocompetence or recent exposure to infection. The H/L ratios of nestlings have been demonstrated to be related to stress with high H/L ratios indicating high stress levels.

In this study I aim to determine whether the nestling competitive hierarchy within broods of great tits and blue tits causes a decrease in the health status of the smallest and less competitive nestlings. I also examine whether or not hatching date and brood size play a part in the health status of great tit and blue tit nestlings.

8.3 Methods

8.3.1 Nestling ringing and blood sampling

Nest boxes were monitored by the methods described in Chapter 2. When the nestlings of both species were 12 days old, they were ringed with BTO metal rings. Colour rings were not used at this stage since juvenile mortality is particularly high during the first winter and there were a limited number of colour ring combinations that were allocated to this project. Immediately following ringing, each nestling was weighed to the nearest 0.1g using a 50g pesola spring balance and tarsus length was measured with Vernier callipers to the nearest 0.01mm.

Nests were revisited when nestlings were 15 days old and a blood sample was taken for sexing and imunocompetence work. Approximately 10μl of blood was removed from the brachial vein by piercing the skin with a sterile needle and then drawing the blood into a heparinized capillary tube. This method is described in Chapter 2. Half of the blood taken from nestlings was used to make blood smears and the other half was used in DNA sex-typing (both methods described in Chapter 2). Health status was measured by counting the number of reticulocytes (immature red blood cells) in 10 000 erythrocytes (red blood cells), counting the number of lymphocytes in 10 000 erythrocytes and calculating the H/L (heterophil lymphocyte) ratio (See: Chapter 7).

8.3.2 Estimation of competitive status of nestlings

The competitive status of nestlings was assumed to be reflected in their body mass since related literature has found this to be true (Bryant 1978; Hahn 1981; Gottlander 1987; Anderson *et al.* 1993; Oddie 2000), therefore, body mass was used as an index of competitive rank.

8.3.3 Statistical analysis

REMLs (using nest box as a random factor) were used to determine whether hatching date had an effect on the number of reticulocytes in 10 000 erythrocytes, the number of lymphocytes in 10 000 erythrocytes or the H/L ratios of great tits or blue tits. In the cases where hatching date had an effect, residuals were used from these analyses for all further analysis. Because the H/L ratios of blue tits were not normally distributed, they were $\log_{10}$ transformed for all subsequent analysis. REMLs were also used with nest box as a random factor to investigate the relationship between body mass and health status within the entire population.

Because nest box and sex could both potentially affect the health status of great tit and blue tit nestlings, nested ANOVAs were used to test for these effects with sex nested within nest box. To determine whether brood size was related to health status, an ANCOVA was used with brood size as the independent factor and nest box as a covariate.

In order to determine whether the competitive status of great tit or blue tit nestlings was related to the H/L ratio, or reticulocyte or lymphocyte counts, the blood parameters from the nestling with lowest competitive status for each brood were compared with the mean blood parameters of its siblings using a paired t-test. Pearson's correlations were used to test for a relationship between body mass and health status within the population.

8.4 Results

8.4.1 Comparison of nestling and post-fledging birds

Nestlings of both species had significantly greater counts of reticulocytes and lymphocytes than adult birds and had higher H/L ratios than adults (Table 8.1, 8.2).

	Age Class	Reticulocytes	Lymphocytes	H/L Ratio
Great tit	**nestling**	1288.33 ± 616.05	18.13 ± 8.93	0.78 ± 0.70
	post-fledging	337.50 ± 90.20	10.24 ± 6.86	0.36 ± 0.24
Blue tit	**nestling**	1579.69 ± 535.43	24.98 ± 12.39	0.98 ± 0.53
	post-fledging	364.75 ± 95.99	10.04 ± 5.99	0.60 ± 0.42

Table 8.1: A comparison of the mean ± s.d. for the blood parameters measured in nestling and post-fledging great tits (*n* values: nestling = 46, post-fledging = 42) and blue tits (*n* values: nestling = 130, post-fledging = 28).

	Reticulocytes		Lymphocytes		H/L Ratio	
	$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	$98.03_{1,86}$	<0.001	$21.33_{1,86}$	<0.001	$13.31_{1,86}$	<0.001
Blue tit	$142.49_{1,156}$	<0.001	$38.70_{1,156}$	<0.001	$12.82_{1,156}$	<0.001

Table 8.2: The effect of age class (nestling or post-fledging) on blood parameters measured in great tits (*n* values: nestling = 46, post-fledging = 42) and blue tits (*n* values: nestling = 130, post-fledging = 28).

8.4.2 Differences in early and late clutches

Nestling great tits that hatched earlier in the season had more reticulocytes than those that hatched later in the season (Table 8.3; Figure 8.1). There was no relationship between the H/L ratio or the number of lymphocytes and the date on which great tit nestlings hatched and there was no relationship between any of the measures of health status and hatching date in blue tit nestlings (Table 8.3).

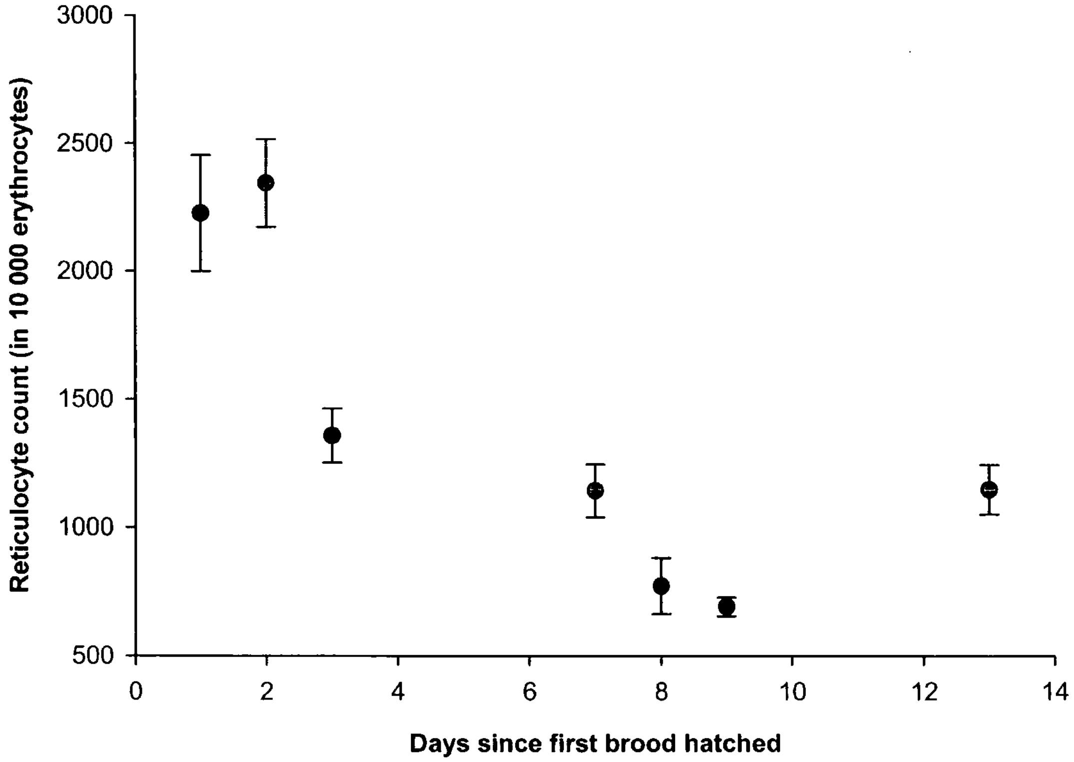

Figure 8.1: The relationship between hatching date and the reticulocyte counts in great tit nestlings.

	Reticulocytes		Lymphocytes		H/L ratio	
	Wald (χ^2)$_{d.f.}$	*P*	*Wald* (χ^2)$_{d.f.}$	*P*	*Wald* (χ^2)$_{d.f.}$	*P*
Great tit	$26.04_{7,48}$	<0.001	$1.88_{7,48}$	1.0	$4.36_{7,48}$	0.7
Blue tit	$4.01_{12,133}$	1.0	$4.53_{12,133}$	1.0	$4.78_{12,133}$	1.0

Table 8.3: REML results of the effect of hatching date on the health status of 15-day-old great tit (*n* = 46) and blue tit (*n* = 130) nestlings.

8.4.3. The effect of nest box and sex

The health status of great tit and blue tit nestlings did not differ between males and females. However the number of reticulocytes and the number of lymphocytes in 10 000 erythrocytes differed between nests for blue tits and H/L ratio differed between nests for both species (Table 8.4).

	Blood parameters	Nest Box		Sex	
		$F_{d.f.}$	*P*	$F_{d.f.}$	*P*
Great tit	**reticulocytes**	$0.08_{7,48}$	1.0	$0.69_{7,48}$	0.7
	lymphocytes	$1.54_{7,48}$	0.2	$0.72_{7,48}$	0.7
	H/L ratio	$5.15_{7,48}$	<0.001	$0.29_{7,48}$	1.0
Blue tit	**reticulocytes**	$5.85_{21,133}$	<0.001	$1.18_{21,133}$	0.3
	lymphocytes	$2.81_{21,133}$	<0.001	$0.73_{21,133}$	0.8
	H/L ratio	$1.96_{21,133}$	<0.05	$0.67_{21,133}$	0.9

Table 8.4: Results of nested ANOVAs on the effect of nest box and sex (within nest box) on the health status of great tit (*n* values: nest boxes = 8, males = 34, females = 21) and blue tit nestlings (*n* values: nest boxes = 22, males = 60, females = 68).

8.4.4. The relationship between body mass and health status at the population level

The body mass of nestling great tits was related to the number of lymphocytes in 10 000 erythrocytes (wald $\chi^2_{1,44} = 12.89$, $n = 45$, $P<0.001$; Figure 8.2) and to the H/L ratios (wald $\chi^2_{1,44} = 5.91$, $n = 45$, $P<0.05$; Figure 8.3) but not to the number of reticulocytes in 10 000 erythrocytes (wald $\chi^2_{1,44} = 0.15$, $n = 45$, $P = 0.7$). Lymphocyte counts increased with body mass and the H/L ratio decreased with body mass in great tits. The body mass of blue tit nestlings was related to their H/L ratios (wald $\chi^2_{1,129} = 16.04$, $n = 130$, $P<0.001$; Figure 8.4) but not to the numbers of reticulocytes (wald $\chi^2_{1,129} = 1.76$, $n = 130$, $P = 0.2$) or lymphocytes (wald $\chi^2_{1,129} = 3.46$, $n = 130$, $P = 0.1$) in 10 000 erythrocytes.

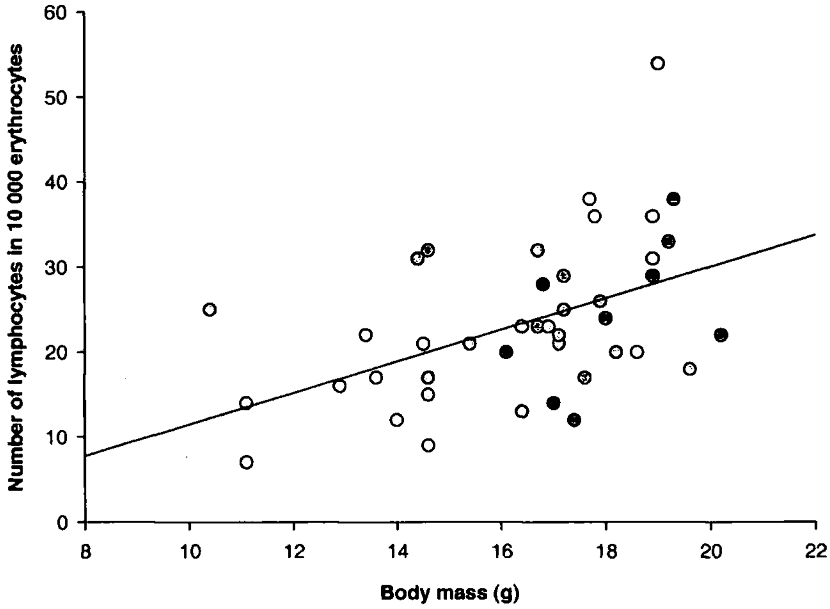

Figure 8.2: The relationship between the body mass of great tit nestlings and their lymphocyte counts. Different colours represent different broods.

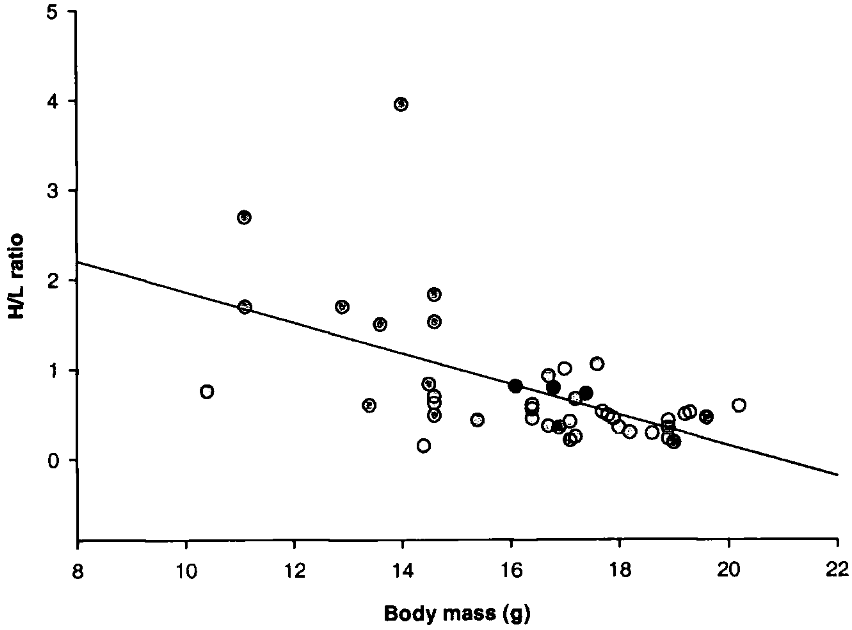

Figure 8.3: The relationship between the H/L ratio and the body mass of great tit nestlings. Different colours represent different broods.

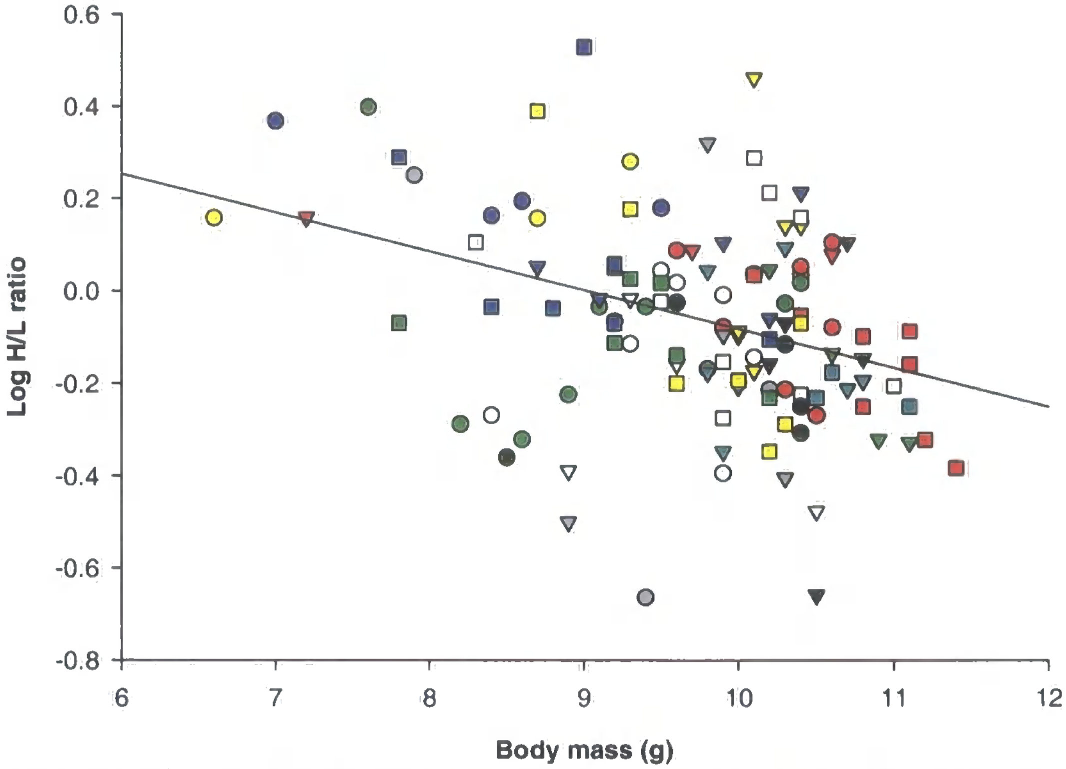

Figure 8.4: The relationship between the body mass of blue tit nestlings and their H/L ratios. Different colours and symbols represent different broods.

8.4.5. The effect of low competitive status on the health status of nestlings

The nestlings with the lowest competitive status within broods did not differ from their siblings with regards to immunocompetence and health status in great tits or blue tits (Table 8.5).

	Reticulocytes		Lymphocytes		H/L Ratio	
	$t_{d.f.}$	P	$t_{d.f.}$	P	$t_{d.f.}$	P
Great tit	0.20_{6}	0.9	0.77_{6}	0.5	-1.04_{6}	0.3
Blue tit	-1.31_{18}	0.2	0.45_{18}	0.7	-1.50_{18}	0.2

Table 8.5: Results of paired t-tests testing the effects of low competitive status on health status in nestlings (*n* values: great tits = 7, blue tits = 19).

8.4.6 The effect of brood size

Brood size affected the H/L ratio of nestling great tits but not blue tits (Table 8.6). The H/L ratios of great tit nestlings from broods of six to nine nestlings demonstrated little difference with brood size (mean ± s.d.: six: 0.56 ± 0.23; seven: 0.53 ± 0.27; nine: 0.47 ± 0.15) but a brood size of ten increased the H/L ratio (mean ± s.d.: 1.65 ± 0.98). The lymphocyte counts decreased with increasing brood size in great tits (Figure 8.5) and varied between broods in blue tits following a similar pattern. The reticulocyte count was affected by brood size in blue tits but not great tits in that as brood size increased, the numbers of reticulocytes decreased in blue tit nestlings (Figure 8.6).

	Reticulocytes		**Lymphocytes**		**H/L ratio**	
	$F_{d.f.}$	P	$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	$0.003_{3,45}$	1.0	$4.92_{3,45}$	<0.01	$12.51_{3,45}$	<0.001
Blue tit	$4.52_{6,129}$	<0.001	$3.20_{6,129}$	<0.01	$0.82_{6,129}$	0.5

Table 8.6: The effect of brood size on the health status of great tit (*n* = 46) and blue tit (*n* = 130) nestlings.

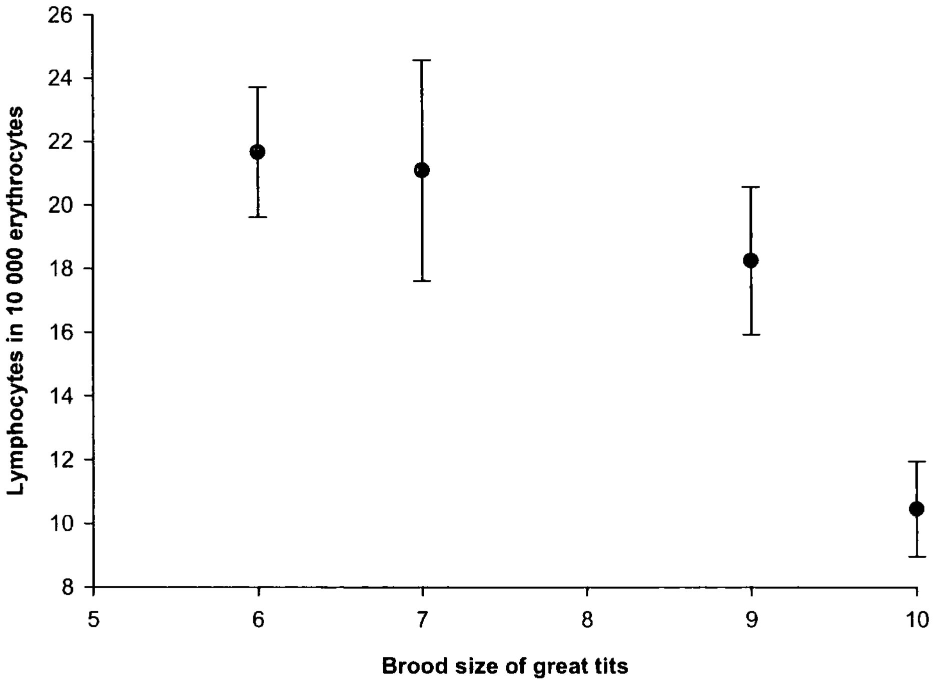

Figure 8.5: The decrease in the lymphocyte counts in great tit nestlings as brood size increases from 6-10 nestlings.

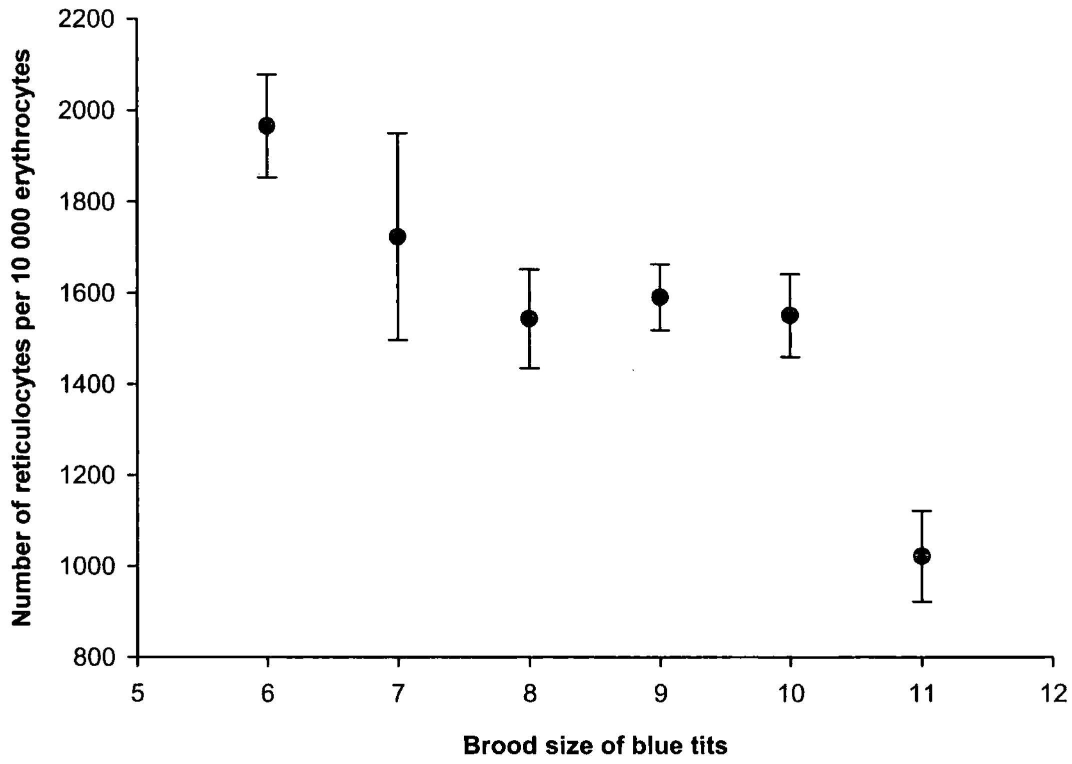

Figure 8.6: The relationship between brood size and reticulocyte counts in blue tit nestlings.

8.5 Discussion

8.5.1 The effects of hatching date

Nestling body condition and survival have been shown to decrease with later hatching date (Verhulst & Tinbergen 1991; Brinkhof *et al.* 1993; Wiggins, Pärt & Gustafsson 1994; Sorci, Soler & Møller 1997; Verboven & Visser 1998; Dubiec & Cichoń 2001). Most previous studies have used body mass or structural size as a measure of condition, although with the advent of molecular techniques in the field, recent studies have also considered the effect of breeding date on immunocompetence and the health status of nestlings (Sorci, Soler & Møller 1997; Dubiec & Cichoń 2001).

In this study, the density of reticulocytes decreased with hatching date in great tit nestlings, suggesting that nestlings born later in the season may be more susceptible to anaemia. The lack of a relationship between the H/L ratio or lymphocyte counts and hatching date in great tit nestlings, contrasts with other studies that have found immune function to decrease with hatching date using brood size manipulation experiments (Sorci, Soler & Møller 1997) or natural clutches (Dubiec & Cichoñ 2001). It has been hypothesised that the decrease in nestling body condition with later hatching date is due to the paucity of available food for chicks later in the season or the later breeding of low quality adults (Perrins 1965; Verhulst & Tinbergen 1991; Brinkhof *et al.* 1993; Wiggins, Pärt & Gustafsson 1994). Since the breeding of great tits is highly synchronised with caterpillar availability (Perrins 1965, 1979), it is likely that a shortage of chick food could account for later clutches having lower reticulocyte counts.

The results of this study with regards to blue tits seem to contradict previous reports and the results obtained for great tit nestlings in this study, since there was no relationship between nestling health status and date of hatching. It is possible that blue tits are less sensitive to caterpillar abundance than great tits. Also, since some previous studies on nestling health status manipulated the study birds to make them breed later, it is possible that the manipulation may have caused a difference in the health status if females had to lay two clutches or incubate for longer (Sorci, Soler & Møller 1997).

8.5.2 Differences between broods

The results from this study establish that great tit broods from different nest boxes differed in their H/L ratios and blue tit broods differed in all three of the blood parameters that were used to measure health status. This was probably an effect of parental quality, which can affect the health status of nestlings in three ways: if health status is heritable, high quality parent birds will pass on their high quality genes to the nestlings (Brinkhof *et al.* 1999); high quality females may be able to provide their eggs with more immunoglobulins or yolk therefore giving their nestlings a better start than those with poor quality parents (Saino *et al.* 2002); high quality adults will secure high quality territories and therefore will have access to better food resources for their nestlings (Perrins 1965). Differences between broods could also have been due to properties of the nest boxes themselves. However, cell-mediated immunity was considered to be heritable in great tits from cross fostering experiments, which showed that a common origin was more likely to explain the variation in cell-mediated immunity than a common rearing environment (Brinkhof *et al.* 1999).

Nestlings from larger broods generally had poorer health status, as indicated by higher H/L ratios and lower lymphocyte or reticulocyte counts. From the results of this study, it seems that increasing brood size affects the health status of great tits and blue tits in different ways since the H/L ratios were only affected in nestling great tits and the number of reticulocytes was only affected in blue tits, though lymphocyte numbers were affected by brood size in both species. Previous studies have also demonstrated a negative relationship between brood size and nestling quality using either mass or immunocompetence as measures of quality (Nur 1984b; Smith, Källander & Nilsson 1989; Korpimaki & Rita 1996; Saino, Calza & Møller 1997; Hõrak *et al.* 1999; Nilsson & Gårdmark 2001). Survival rate was also shown to be lower in enlarged and control broods of kestrels compared to reduced broods (Fargallo *et al.* 2002). The main reason as to why brood size should affect the quality of offspring is that food provisioning by parent birds is not necessarily proportional, so that nestlings from larger broods receive less food per capita than those from smaller broods (Smith *et al.* 1988; Saino, Calza & Møller 1997; for review see: Martin 1987). Since immunocompetence is costly (Fair, Hansen & Ricklefs 1999; Lochmiller & Deerenberg 2000; Whitaker & Fair 2002), the development of the immune system in nestlings may have to be compromised in order to maximise growth when food is in short supply, since smaller nestlings may need to reduce the size difference between themselves and their larger siblings so that they can fledge at the same time (Lemel 1989; Nilsson & Svensson 1993).

8.5.3 The significance of competitive status

It is now widely accepted that nestlings with the smallest mass have the lowest chances of survival (Perrins 1965; Bryant 1978; for review see: Martin 1987). At the population level, the H/L ratios of great tits and blue tits were negatively correlated with body mass, suggesting that the lightest birds were under the greatest stress. This is supported by the fact that body mass in great tit nestlings was also positively correlated with the number of lymphocytes per 10 000 erythrocytes. Previous studies have also found that immune response was positively correlated with body condition (Brinkhof *et al.* 1999; Tella *et al.* 2001).

Within nests where siblings were competing with each other, the smallest competitors did not differ in their health status from the rest of their siblings. Competition occurs to some extent within all broods and related literature demonstrates that larger nestlings bias food resources towards themselves by being in the optimum position during feeding by the parents (Gottlander 1987; Kacelnik *et al.* 1995; Kilner 1995). In this study however, the lowest ranking nestlings did not show evidence of impaired immune function, and so it is likely that the intensity of competition in the majority of great tit and blue tit nests was not sufficiently intense to cause a decline in the health status of the smallest nestlings.

The results from this study are consistent with those of Roulin *et al.* (2003) who found no relationship between the competitive status of great tit nestlings within broods and tick distribution. It was in fact found that ticks were distributed randomly within broods of great tits (Christe, Møller & de Lope 1998; Roulin *et al.* 2003).

8.5.4 Conclusions

The health status of great tit and blue tit nestlings was affected by their rearing environment, probably brought about by the quality of their parents or environmental conditions. Hatching date had consequences for the health status of nestling great tits, probably because they rely heavily on the abundance of caterpillars for food (Perrins 1979). Because blue tits may not time their breeding as strongly with caterpillar abundance, this may explain why similar results were not obtained for this species. Since increasing brood size reduces the amount of food per capita to the nestlings irrespective of prey species (Smith *et al.* 1988; Saino, Calza & Møller 1997; for review see: Martin 1987), it is consistent that the health status of nestling great tits and blue tits decreased with increasing brood size.

It is probable that the small level of asynchronous hatching compared to species from past studies and thus small differences in body size of great tit and blue tit nestlings within broods accounted for the lack of relationship between competitive status and health status. Perhaps if conditions had been more harsh or the birds had been forced to breed later in the season (which sometimes forces females to incubate before the entire clutch is laid), more broods would have shown this relationship as there would have been more competition for food and possibly a greater within-brood size difference.

Chapter 9

General discussion

This study clearly demonstrates that there are significant costs and benefits associated with dominance rank and that these are only reflected in some of the variables considered in this thesis. Previous studies that have considered the effects of dominance status have found that generally, subdominants suffer disadvantages associated with their dominance status compared to dominant individuals (Kaufmann 1983; Ens & Goss-Custard 1984; Arcese & Smith 1985; Hegner 1985; Frank 1986). Disadvantages associated with low dominance status in Parids include being forced to forage in less profitable areas of trees, being forced to forage in areas with high predation risk, having to take greater risks in the presence of predators, having low quality territories in the breeding season and, as a result of these factors, having lower survival probability (Ekman & Askenmo 1984; Arcese & Smith 1985; Hegner 1985; Ekman 1986, 1987; Gosler 1987; Hogstad 1988). Dominant birds, on the other hand, have priority of access to the most profitable and safest food resources and roosting sites and can secure the territories with the highest profitability. As a consequence, dominant birds have been shown to have higher survival rates (Arcese & Smith 1985).

The costs associated with high dominance status have been highlighted from studies that have demonstrated that dominant individuals have a higher metabolic rate during the day, which is likely to be due to the stress of interacting with conspecifics (Røskaft *et al.* 1986; Hogstad 1987, 1989; Bryant & Newton 1994; Buchanan *et al.* 2001). It has been previously reported that dominant individuals are involved in a greater number of agonistic interactions compared to subdominants in order for them to keep their dominance status secured (Järvi & Bakken 1984), though this was not the case for the three species in this study when interacting in the vicinity of the feeders. Despite several studies finding a metabolic cost to dominance, related studies have contradicted this and found that dominance rank has no effect on the metabolic rate of dark-eyed juncos *Junco hyemalis* and that subdominants have higher metabolic rates than dominants as in the siskin *Serinus serinus*, explained by the stress imposed by the lifestyle of subdominants in terms of gaining access to resources (Senar *et al.* 2000).

The results presented in this thesis differ from those of some previous work and demonstrate the importance of studies being carried out on a range of different species before general conclusions can be drawn. Despite the close phylogenetic relationship between the three species in this study, individuals from each species were affected to differing extents by their dominance status and its associated costs and benefits.

9.1 The structure of the dominance hierarchies

In the majority of cases, the structure of the dominance hierarchy of great tits, blue tits and coal tits, agreed with that presented in the related literature in that males were generally dominant to females. However, contrary to previous studies, it was not demonstrated in great tits, blue tits or coal tits, that within the sexes, adults were dominant over juveniles. The dominance of adult birds over juveniles has been an integral part of many studies, particularly of willow tits where this has often been found (Hogstad 1987, 1992; Lahti *et al.* 1996; Brontons *et al.* 2000). It is possible that the mild conditions experienced during this study allowed inexperienced juvenile individuals with high competitive ability to dominate adults, since the stress imposed on these juveniles may have been lower than that of those birds in studies carried out under poor environmental conditions.

Though the higher metabolic rate of dominant birds has been attributed to their higher activity levels and aggressiveness (Røskaft *et al.* 1986), this study did not find a relationship between dominance status and frequency of agonistic interactions. Therefore, any benefits of dominance in great tits, blue tits or coal tits in this study were not offset by being involved in a greater number of aggressive interactions. However, since the intensity of aggressive interactions was not measured, it is possible that the interactions of dominant birds may have lasted for longer and may have involved a greater probability of physical strength being used if neither bird was willing to accept defeat.

The non-random manner of great tit and coal tit dominance interactions has not been reported in the past. As discussed in Chapter 3, the interactions of great tits and coal tits are likely to result from each bird attempting to displace the bird above it in the hierarchy and defend its own place from the bird below. Interactions with birds of lower dominance status are likely to result from birds with high dominance status displacing lower ranking birds from the food resource because they want to utilise the food resource themselves. Similar patterns of non-random interactions within dominance hierarchies have previously been reported in red deer (Darling 1937; Freeman, Freeman & Romney 1992) and grey wolves (Hay, unpub. data).

9.2 The costs of being subdominant

Reduced foraging efficiency is a common cost of being subdominant in birds that feed in flocks because of the higher vigilance levels that subdominant birds have to attain when in the company of dominants (Goss-Custard, dit Durrell & Ens 1982; Pöysä 1988). It has been found that subdominant individuals are often forced to feed in the areas of trees with the highest predation risk (the outer branches and lower branches) because dominant conspecifics will not allow them access to the safer foraging areas (Ekman & Askenmo 1984; Hogstad 1988; Brotons *et al.* 2000). Under those circumstances (when feeding in the high risk areas of trees), subdominants have been shown to increase their vigilance levels to account for the increase in predation risk (Ekman 1987). For the coal tits in this study, the cost of being subdominant was reflected in their vigilance rates whilst feeding, which might also have affected their seed handling times though seed handling times were not measured for this species. The difference in the vigilance of dominant and subdominant coal tits in this study cannot be attributed to subdominants feeding in higher risk areas since all observations were made whilst the birds were feeding on the same feeder. It is more likely therefore, that the difference in vigilance between dominant and subdominant coal tits was a result of subdominant birds increasing their vigilance in order to monitor dominant conspecifics that may try to displace them (Waite 1987a, 1987b; Pravosudov & Grubb 1999).

In this study, feeding great tits realised a cost of subdominance during seed handling when other flock members were present. Though Chapter 4 had found no difference in the seed handling times of dominant and subdominant great tits, it was demonstrated that when at least one other titmouse was within one metre of a feeding great tit, subdominants experienced a greater increase in seed handling time than dominants. Though all great tits increased their seed handling times to some extent in the presence of another titmouse, the increase was significantly greater in lower ranking birds, possibly because they were increasing their vigilance levels to a greater extent in order to monitor the more dominant titmice in the vicinity. A previous study similarly found that subdominant blackbirds increased their seed handling times to a greater extent than dominants when other birds were present and that subdominant birds had higher levels of vigilance than dominant birds when they were feeding together (Smith, Ruxton & Cresswell 2001). The negative effect that low dominance status has on the foraging efficiency of great tits and coal tits is possibly a short term cost since effects of lower feeding efficiencies were not reflected in the body condition of subdominant birds when feather growth rates or feather quality were measured (See: Chapter 6) and when health status or immunocompetence were assessed (See: Chapter 7).

Though actual dominance hierarchies derived from interactions won and lost were not measured for nestlings, it has been suggested that nestling mass reflects their place in the competitive hierarchy that occurs when competing for food provisioned by the parent birds (Greig-Smith 1985; Gottlander 1987; Nilsson & Svensson 1996; Royle *et al.* 1999; Nilsson & Gårdmark 2001). It has also been shown that less competitive nestlings achieve lower dominance rankings post-fledging (Richner, Schneiter & Stirnimann 1989) and this highlights the importance of having a high competitive status from early in life, which may go on to determine future survival. However, the immunocompetence of the smallest nestlings and hence the poorest competitors was not significantly different from that of their higher ranking siblings in this study, suggesting that competition within great tit and blue tit broods was not sufficient as to impair the development of the immune system.

9.3 Costs of dominance

The costs of having high dominance status have been highlighted from a range of species in the past in the form of a higher metabolic rate (Røskaft *et al.* 1986; Hogstad 1987; Bryant & Newton 1994) and higher levels of fluctuating asymmetry in the primary feathers of dominant starlings compared to subdominant starlings (Swaddle & Witter 1994; Witter & Swaddle 1994). Though this study raised the issue that dominant birds were not involved in a greater number of aggressive interactions than were the subdominant flock members that had been suggested in the past (Järvi & Bakken 1984), a cost of dominance was found when considering the growth of feathers induced during the winter period in coal tits (See: Chapter 6).

The results from this study differ from those of previous studies which have considered the effect of dominance status on feather growth rate using ptilochronology, since it has been reported that dominant birds can grow an induced feather in winter at a faster rate and of a higher quality than subdominant birds (Grubb 1989; Hogstad 1992, 2003; Carrascal *et al.* 1998). Though there was no difference in the feather growth rates or indices of quality between dominant and subdominant great tits or blue tits in this study, dominant coal tits grew their induced central tail feathers at a slower rate and produced feathers that were of poorer quality (with regards to length and density) than those produced by subdominant birds. It has been reported however, that dominant starlings grew primary feathers during moult with a higher degree of fluctuating asymmetry (which was shown to be related to stress) than subdominant birds (Swaddle & Witter 1994; Witter & Swaddle 1994). The authors attributed this either to the birds being housed in separate cages so that the dominant birds paid the cost of being dominant but did not gain the benefits of high dominance status from winning resources from aggressive interactions or when birds were housed together, competition was too low for the dominant birds to benefit from their social status. The dominant coal tits in this study had opportunities to gain benefits from their high dominance status since they were free-living and were shown to have lower vigilance levels than subdominants when feeding thus allowing for more foraging time (See: Chapter 4). However it seems that the costs paid by subdominants were a temporary cost since their increase in vigilance levels was not reflected in long-term body condition with regards to feather growth rate and quality. Dominants on the other hand, gained the short-term benefits of access to food but demonstrated a cost that affected them in the long term until their feathers could be replaced during the following moult six months later.

9.4 The importance of age and sex

It is clear from the results of this study that dominance status does not impact all aspects of Parid health and condition. For example, the seed handling times and vigilance of great tits and blue tits were independent of dominance status, as were feather growth rate in great tits and the health status and immunocompetence of adult great tits and blue tits

Two factors that are often deemed to be important in explaining differences in body condition or foraging efficiency between individuals are age and sex (Stevens 1985; Goss-Custard & dit Durrell 1987; Grubb & Woodrey 1990; Grubb, Waite & Wiseman 1991; Brontons *et al.* 2000; Fargallo *et al.* 2002). Evidence from this study showed that sex was important in determining the seed handling times of blue tits, whereas dominance status was reported to have no effect on seed handling times. The difference in the seed handling times of male and female blue tits was attributed to the differences in bill size between the sexes (Appendix 5). Since the dominance rank of blue tits did not affect any of the variables measured in this study, possibly because blue tits tended to forage alone on the majority of occasions (so would not benefit a great deal from winning interactions), other factors not considered during this study may be important in determining individual fitness such as food finding ability or efficient thermoregulation. Though sex was related to seed handling times, it was not related to the health status of blue tits and so may not affect long-term fitness.

In adult great tits, sex and age were important in determining the probability of an individual harbouring Coccidian parasites. Adult females had the highest incidence of Coccidians followed by juvenile females which was contrary to the results of previous studies which have found that females are more immunocompetent than males, often explained by the immunosuppressive effects of testosterone (Zuk & McKean 1996; Klein, Gamble & Nelson 1999; Klein 2000). However, many studies have found that testosterone has no immunosuppressive effects or may even enhance immunocompetence (Weatherhead *et al.* 1993; Saino *et al.* 1995; Klein, Gamble & Nelson 1999; Hasselquist *et al.* 1999). The results of this study may result from the differing effects of the sex hormones or from the different foraging behaviours of male and female great tits, *i.e.* females may forage in areas where they are more likely to pick up Coccidian parasites (Gosler 1987).

The age of great tits in relation to body condition was an important determinant of the density of the feathers produced when they were induced during both winters. Juvenile great tits were not capable of producing such high quality feathers as adults which may reflect their poorer ability to forage during their first winter but which is not related to seed handling times (Greig, Coulson & Monaghan 1983; Goss-Custard & dit Durrell 1987; Caldow *et al.* 1999). Age has been demonstrated to affect survival in many studies, with juveniles having lower survival rates than adults as a result of their reduced ability to forage effectively (Hogstad 1989; Gosler 1993; Carrascal *et al.* 1998).

9.5 Temporal variation in the variables measured

There was a great deal of temporal variation in the variables measured in this study, which was taken into consideration when analysing the data. Among dominance interactions, the frequency of aggressive interactions in all three species increased as the winter progressed and in great tits and coal tits, the frequency of aggressive interactions increased with time of day. The increase in the frequency of aggressive interactions from early to late winter probably reflects the increase in competition levels as natural food resources diminish over the winter and so competition for those resources increases as well as the onset of spring and the increase in territoriality (Gosler 1993; Pulido & Diaz 2000). The increase in the frequency of aggressive interactions with increasing time of day may reflect the increased stress and competition that the birds are undergoing towards the end of the day to gain enough energy to survive the night.

Seed handling times and vigilance levels were affected by temporal changes in all three species (other than the vigilance of great tits which demonstrated no variation with date or time), though because of the lack of related literature, it is difficult to interpret why this may occur. The variation in seed handling times in great tits as winter progressed was not a result of bill wear and may be due to some other factor which fluctuates with date *i.e.* weather may affect seed handling times. The decrease in the vigilance of blue tits and coal tits with time of day may have been the result of birds taking more risks (by being less vigilant) as the day progressed in order to gain enough reserves for the coming night.

The date on which the original tail feathers were removed from great tits affected their feather growth rate during one winter. This relationship was probably a result of a change in the environmental conditions over the two-week period when the feathers were removed or the period afterwards when the feathers were re-growing. These results highlight the importance of having a short sampling time and shows why the original feathers cannot be used for studies of ptilochronology since they are grown over a longer time period during the annual moult.

Though temporal variation did not generally affect the health status of adult great tits, blue tits (lymphocyte counts increased with date but was mostly due to one sample) or coal tits, the temporal variation in hatching date affected the health status of great tit nestlings in that the number of reticulocytes in 10 000 erythrocytes decreased with date. The relationship between breeding date and nestling health status has been highlighted in the past (Verhulst & Tinbergen 1991; Brinkhof *et al.* 1993; Verboven & Visser 1998) and in the case of great tits which time their breeding with the abundance of caterpillars, a decrease in nestling food supply is most likely to be the cause (Perrins 1979). It has also been reported that the lower quality adults breed later in the season thus producing lower quality chicks later in the season because the parents are inferior at provisioning.

9.6 General conclusions

Though dominance hierarchies in *Parus* species have been intensively studied in terms of the costs and benefits of flocking, particularly with regards to subdominant birds, this study demonstrates that age and sex, in many cases, may be more important in determining the body condition and survival of *Parus* species. One of the main points of this study is that many of the factors measured were not affected by dominance status and therefore where these factors are concerned, dominance status has no costs or benefits. What is clear from these results is that different species, even the closely related species in this study, seem to benefit from their dominance status in different ways. For example, the dominance status of blue tits does not have an affect on their foraging efficiency or their body condition, possibly as a result of this populations loose structure where birds feed alone for most of the time (pers. obs). However, the foraging efficiency of great tits and coal tits is affected by their dominance status and the body condition (measured by feather growth rate and quality) of coal tits is also affected by dominance status but in the opposite way to that which was expected.

Subdominants experienced greater increases in seed handling times due to interference competition than their dominant conspecifics, though there were no differences in the feather growth rates or health status of adult great tits suggesting that the costs to subdominance may be short term. However, during harsh weather conditions, susceptibility to interference may be crucial in determining the survival of individuals and dominance status may determine whether an individual can obtain enough food to survive. The competitive status of great tit nestlings does not disadvantage the nestlings with the lowest competitive ability with regards to the development of the immune system but other indices of condition were not investigated in nestlings therefore it is not known how the hierarchy may affect the survival of nestlings.

Contrary to past studies, the results obtained from coal tits in this study suggest that dominant coal tits may actually incur more serious costs than subdominants since the costs of high dominance status seem to be long-term and those of low dominance status seem to be short-term costs. The higher vigilance of subdominant coal tits may be reflected in longer seed handling times but as these were not measured in coal tits, this cannot be assumed. The higher vigilance of subdominant birds was not sufficient to cause a decrease in body condition like that seen in dominant birds. Therefore, the results of this study suggest that dominant coal tits incur a higher cost than subdominants, possibly due to their unstable social system reflected in the high numbers of unringed birds visiting the bird feeders (pers. obs).

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	Season	Date		Time	
		$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	**2000 - 2001**	$120.39_{24,190}$	<0.001	$204.69_{97,190}$	<0.001
	2001 - 2002	$43.86_{21,151}$	<0.01	$71.36_{105,151}$	1.0
Blue tit	**2000 - 2001**	$36.01_{25,168}$	0.1	$111.63_{79,168}$	<0.01
	2001 - 2002	$294.89_{22,125}$	<0.001	$212.98_{76,125}$	<0.001
Coal tit	**2000 - 2001**	$78.64_{23,87}$	<0.001	$81.64_{46,87}$	<0.001
	2001 - 2002	$526.42_{16,114}$	<0.001	$137.50_{75,114}$	<0.001

Appendix 1: REML results of the effect of date and time of day on the body mass of great tits, blue tits and coal tits during the field seasons of 2000-2001 (*n* values: great tits = 87, blue tits = 101, coal tits = 32) and 2001-2002 (*n* values: great tits = 81, blue tits = 80, coal tits = 33).

	2000-2001		2001-2002	
	$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	$106.33_{21,131}$	<0.001	$62.82_{21,121}$	<0.001
Blue tit	$46.51_{25,118}$	<0.01	$37.20_{25,110}$	0.1
Coal tit	$55.88_{19,61}$	<0.001	$43.34_{16,101}$	<0.001

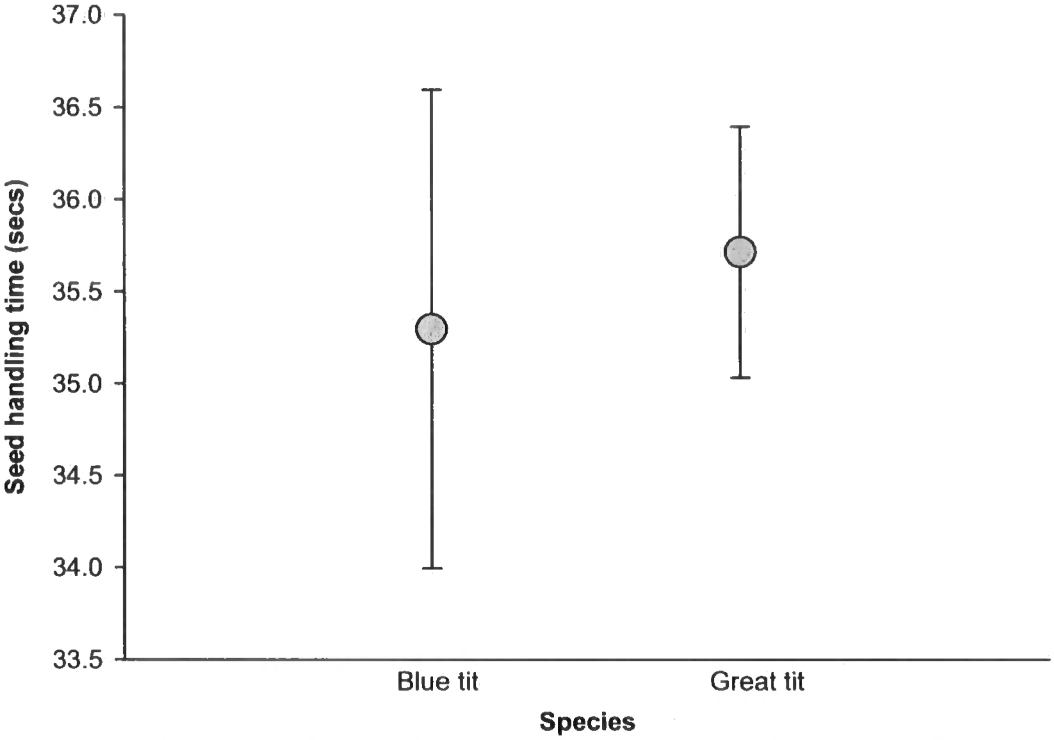
Appendix 2a: REML results of the effect of date on the head plus bill lengths of great tits, blue tits and coal tits during the winters of 2000-2001 (*n* values: great tits = 78, blue tits = 94, coal tits = 32) and 2001-2002 (*n* values: great tits = 78, blue tits = 78, coal tits = 37).

	$F_{d.f.}$	P
Great tit	$50.71_{19,105}$	<0.001
Blue tit	$51.18_{23,106}$	<0.001
Coal tit	$50.65_{14,72}$	<0.001

Appendix 2b: REML results of the effect of date on the bill lengths of great tits (*n* = 74), blue tits (*n* = 73) and coal tits (*n* = 37) during the 2001-2002 field season.

	Sex	2000-2001		2001-2002	
		$F_{d.f.}$	P	$F_{d.f.}$	P
Great tit	male	$1.26_{1,92}$	0.4	$0.61_{1,115}$	0.1
	female	$0.27_{1,92}$	<0.001	$0.38_{1,111}$	<0.01
Blue tit	male	$0.56_{1,122}$	0.1	$0.86_{1,102}$	0.6
	female	$0.64_{1,149}$	0.1	$0.65_{1,100}$	0.2
Coal tit	male	$0.52_{1,49}$	0.1	$0.84_{1,49}$	0.7
	female	$0.53_{1,39}$	0.3	$0.71_{1,48}$	0.5

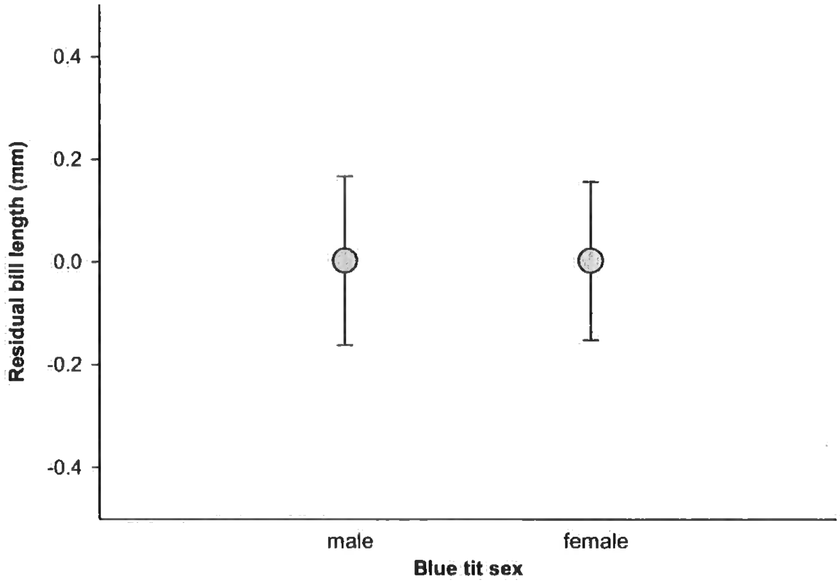
Appendix 3: Results of F-test comparing variance in body size of each sex with the variance in body size within the whole population. Female great tits demonstrated little variance in body size compared with the population (*n* values: 2000-2001: great tit males = 31, great tit females = 31, blue tit males = 32, blue tit females = 59, coal tit males = 20, coal tit females = 10; 2001-2002: great tit males = 40, great tit females = 37, blue tit males = 35, blue tit females = 33, coal tit males = 18, coal tit females = 17).



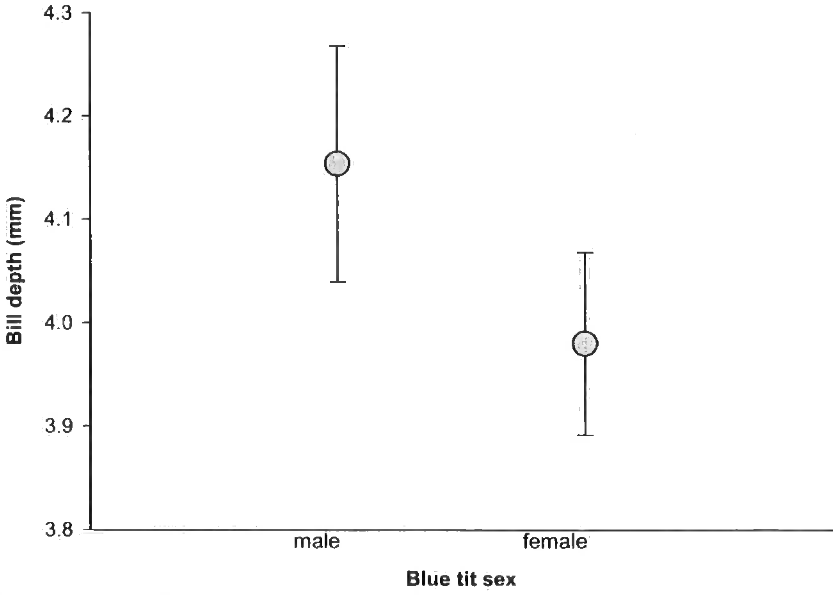
Appendix 4: Mean (with 95% confidence intervals) seed handling times did not differ between blue tits (*n* = 34) and great tits (*n* = 55) despite the differences in body size between the two species ($F_{1,1859}$ = 0.46, *P* = 0.5).

	r	n	P
Great tit	-0.02	29	0.9
Blue tit	-0.23	22	0.3

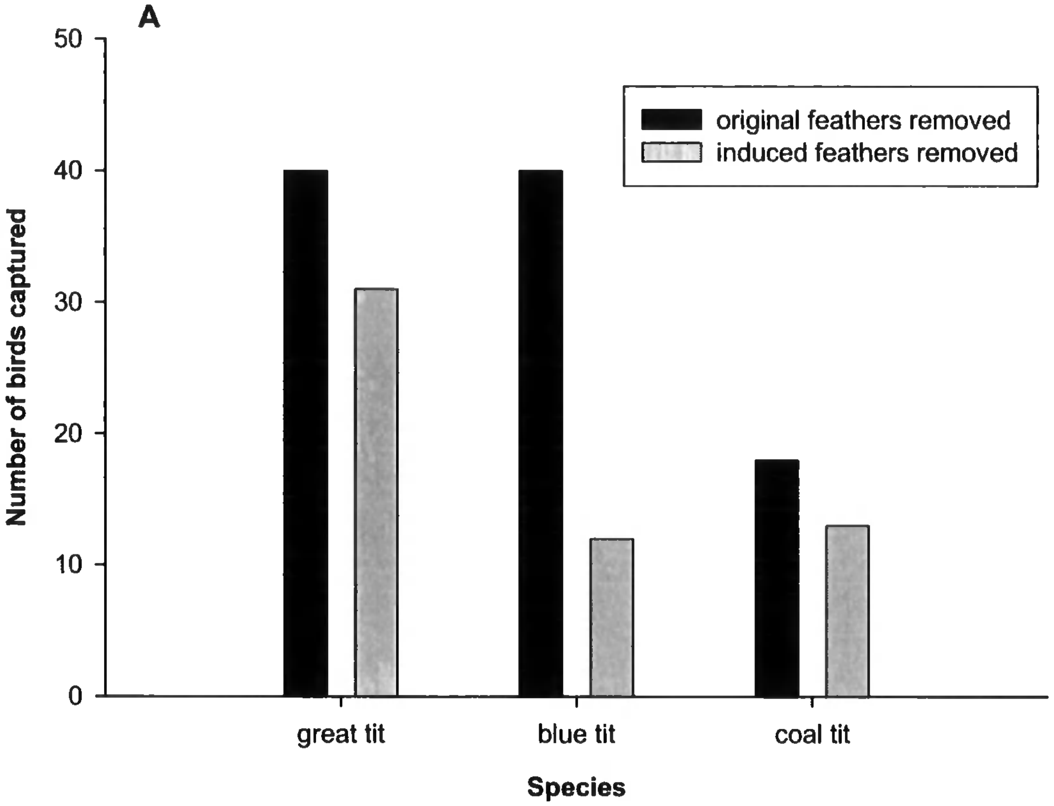
Appendix 5a: Results of Pearson's correlations showing the lack of relationship between bill length seed handling time in great tits and blue tits.

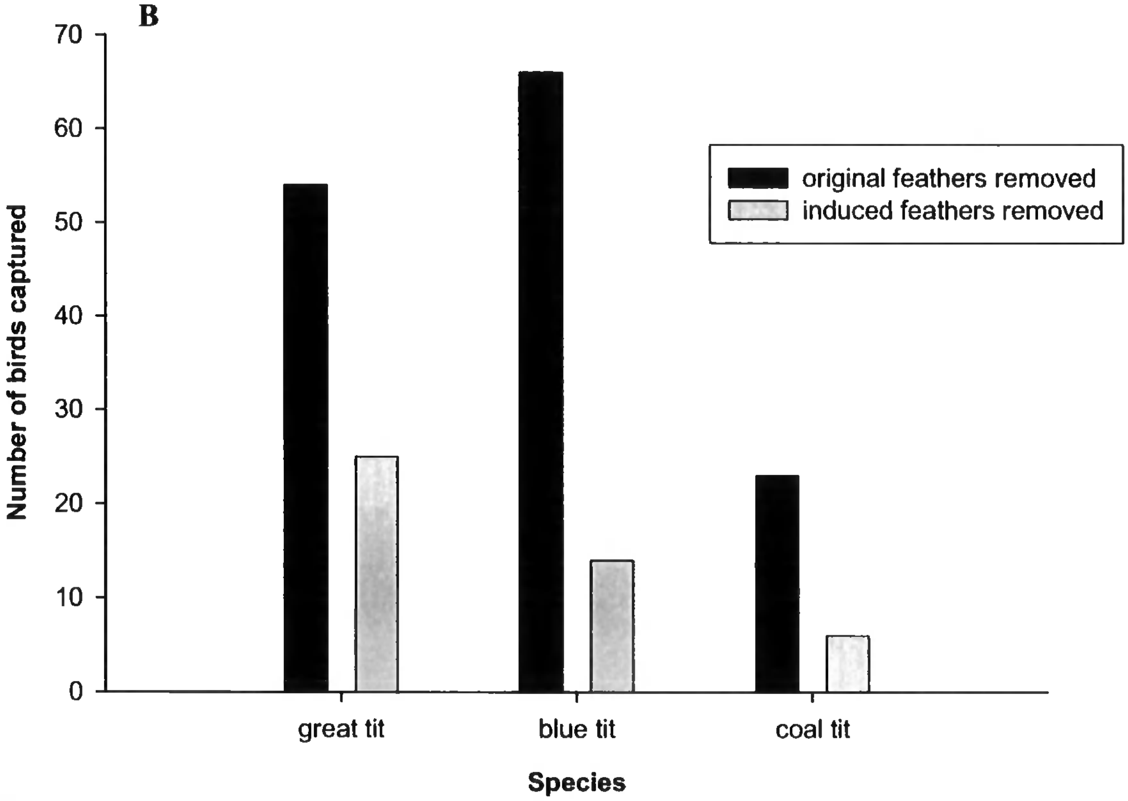


Appendix 5b: Mean (with 95% confidence intervals) bill length did not differ between male (n = 38) and female (n = 35) blue tits (GLM, $F_{1,72}$ = 0.00, P = 1.0).

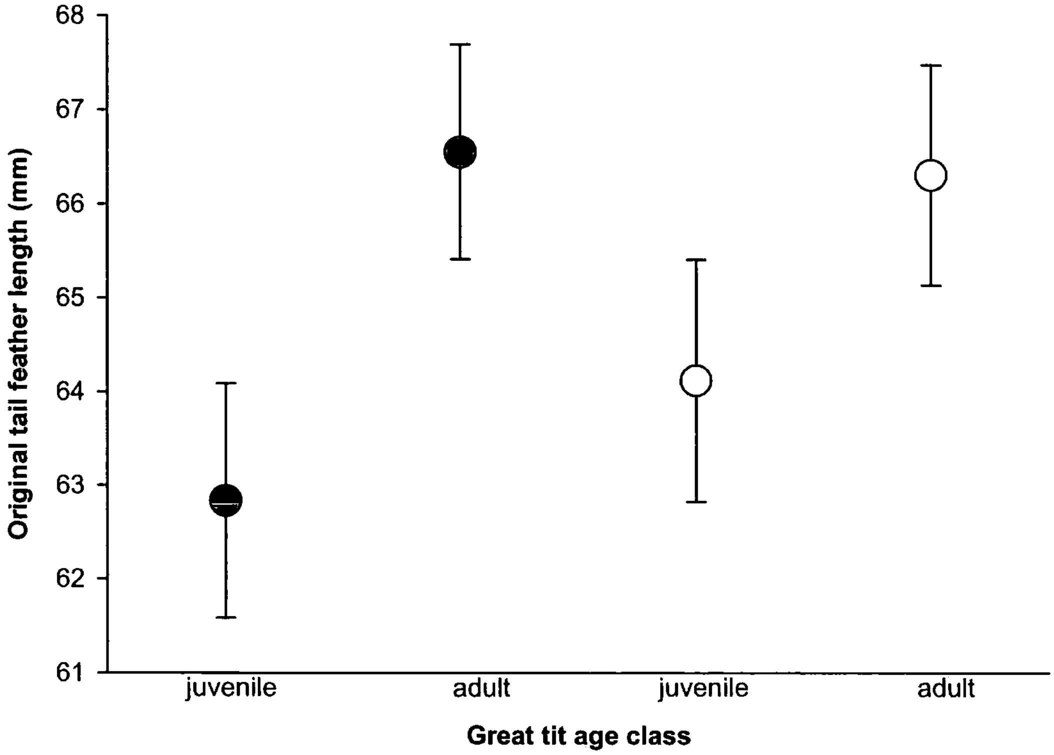


Appendix 5c: Mean (with 95% confidence intervals) bill depth differed between male (n = 13) and female (n = 15) blue tits (GLM, $F_{1,27}$ = 5.72, P<0.05).

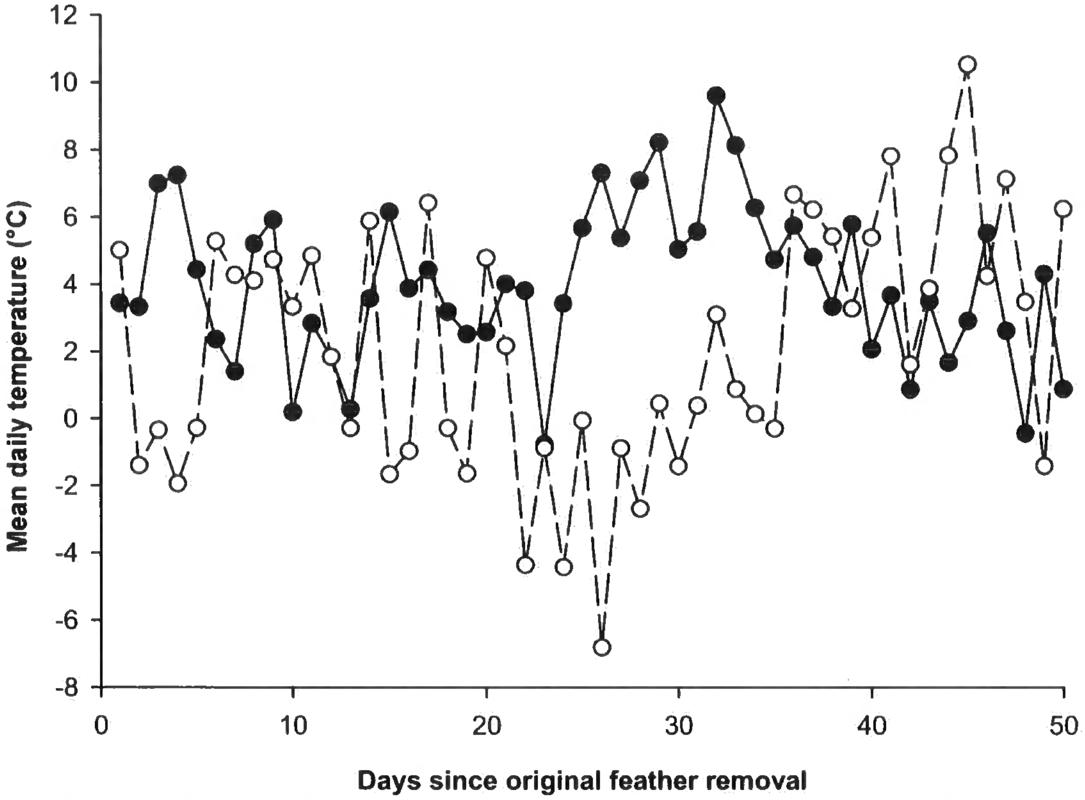




Appendix 6: The number of birds captured for original tail feather removal and then subsequently captured for removal of the induced feathers in the 2000-2001 (A) winter and the 2001-2002 (B) winter.



Appendix 7: The mean lengths (with 95% confidence intervals) of the original tail feathers removed from great tits of different age classes during 2000-2001 (•) and 2001-2002 (o) (*n* values: 2000-2001: adult = 11, juvenile = 27; 2001-2002: adult = 29, juvenile = 24).



Appendix 8: Mean daily temperature during the 50 days following the removal of the original feathers during the 2000-2001 field season (•) and the 2001-2002 (○) field season (all temperature data was provided by Prof. T. Burt, Department of Geography, University of Durham).