THE FUNCTIONS OF AGONISTIC INTERACTION, SOCIAL DOMINANCE AND DISPLAY IN A WINTER POPULATION OF THE GREAT TIT, *PARUS MAJOR* L.

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DECLARATION

I hereby declare that this thesis has been composed by myself and that the work described within it is my own except where duly acknowledged.

To my mother and father, without whose help I would never have started, and to Jennifer, without whom I might never have finished.

CONTENTS

ABSTRACT

The agonistic behaviour of great tits was studied between September and April in 1986/87, 1987/88 and 1988/89 in deciduous woodland and gardens at Ormiston Hall, Lothian, Scotland. 450 great tits *Parus major* were colour-ringed. 916 captures of great tits were made. On capture, measurements of body size were made and, in the second two winters, photographs were taken to record an index of the size of the black ventral stripe. Throughout the study, the outcome of dyadic interactions between great tits, and the display behaviour seen during such interactions were recorded in the vicinity of feeding stations within the study area. During the 1988/89 winter, small groups of great tits were maintained in captivity to test hypotheses about social organization and display function arising from the field study. Between February and May of each year, the identity of all great tits occupying breeding territories in the study area was ascertained, as was the distance of those territories to the three feeding stations. The proportion of colour-ringed birds in the territorial great tit population immediately outwith the study area was estimated in 1988 and 1989.

The population ecology of great tits in this study did not differ greatly from that of others in Britain and western Europe. Mild winter weather may have made mortality and dispersal less dependent on winter conditions, and flocking behaviour was poorly developed.

Male great tits were consistently dominant over females. Within the sexes, prior residence and prior territorial experience at a site are the primary correlates of social dominance, which is therefore site-related. Locally dominant and frequently present birds are more likely to establish local breeding territories than locally subordinate birds and rarer visitors, which leave the area at the end of the winter. Body size is a negligible correlate of dominance between male great tits, but there is a weak tendency for larger females to be dominant over smaller ones. Dominance hierarchies recorded at one site were very linear, but linearity declined with increasing number of individuals in the hierarchy. Dyadic relationships became increasingly peck-right with increasing frequency of interaction, implying the development of individual recognition. The differences between territoriality and other forms of site-related dominance are discussed.

Ventral stripe size is independent of body size and age and is positively correlated with dominance in all-female dyads. It is not correlated with dominance in all-male dyads. It is concluded that stripe size may signal social status in competition over trivial resources, or between mutually unfamiliar birds, Location, time of year and population structure may all influence whether social status signalling can be demonstrated in a great tit population.

Associations between postural display elements are described. Correlations between individual attributes and the incidence of different elements suggested two categories of information content of postural display elements. Wings-Out, Tail Fanned and Open Bill were hypothesized to be threat displays of aggressive intent. Head Up, Head Down, Horizontal Body and Turning Body were all hypothesized to convey information about prior residence and site attachment. These hypotheses were supported by observations of the incidence of postural display in groups of captive birds. Introductions of unfamiliar birds to established flocks suggested the existence of individual recognition. Relative ambiguity of dyadic dominance relationships and a low level of linearity in the dominance hierarchies of captive flocks may have been due to the prevention of consolidation of initial dominant-subordinate asymmetries through dispersal and site-related dominance.

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CHAPTER 1.

GENERAL INTRODUCTION.

1.1. BACKGROUND AND BASIC AIMS

One of the most fruitful areas of research into the evolution, function and mechanisms of intraspecific communicative behaviour has been the study of agonistic interactions between animals (e.g. Austad 1983; Caryl 1979, 1981; Dingle 1969; Enquist 1985; Enquist *et al* 1985; Hazlett 1980, 1982; Maynard Smith 1974, 1982a; Maynard Smith & Riechert 1984; Nelson 1984; Paton & Caryl 1986; Simpson 1968; Stokes 1962a; van Rhijn 1980; Turner & Huntingford 1986). The causes and consequences of conflicts of interest between conspecifics, and the mechanisms by which they are resolved are reviewed by Huntingford & Turner (1987). A glance at the 'Contents' pages of their book makes it clear that whatever the cause of a conflict of interest (e.g. a material resource or a potential mate), its resolution depends ultimately upon changes in the internal state of the competing animals. These changes will in turn depend upon the combined influence of internal and environmental stimuli, with the structural and behavioural stimulus properties of the opponent being pre-eminent amongst the latter.

The study of animal communication is concerned with the way in which animals use both structural and behavioural aspects of their phenotype to influence the behaviour of other animals. This is true whether the influence occurs through the transmission of accurate information between sender and receiver (e.g. Cullen 1966) or whether the receiver is behaviourally manipulated by the sender irrespective of the 'truthfulness' of any information transmitted (e.g. Krebs & Dawkins 1984). If we can achieve an understanding of the behavioural mechanisms by which conflicts of interest are resolved, within the framework of current evolutionary theory, then we may better understand, at a more general level, the evolution of communicative behaviour and the behaviour patterns of which it is composed.

Another main area of behavioural research stems from the consequences of conflicts of interest in the social interactions of animals. Competitive encounters between individuals are an important causal factor underlying social structure in animal populations, which has been studied from the simplest level of the concept of the 'dominant - subordinate' relationship (e.g. Bernstein 1981), through the 'dominance hierarchy' (e.g. Schein 1975) and the study of breeding systems (e.g. Dunbar 1988; Vehrencamp & Bradbury 1984) to the goal of developing a coherent theory of social evolution (Gauthreaux 1978; Lott 1984; Rubenstein & Wrangham 1986; Vehrencamp 1984). These studies have tended to concentrate on birds and mammals since long-term relationships based on individual recognition are prevalent in these cognitively advanced groups and their socioecology is therefore dependent on more than simply the changing distribution patterns of individuals (Rubenstein & Wrangham 1986; Simpson 1973; Wrangham 1983). The ethology of the great tit in competition over resources has been well described (Hinde 1952) and studied from the viewpoints of causation (Blurton Jones 1968) and function (Drent 1983). Its general biology and population dynamics are well known (Chapter 3 and references therein) from long-term studies, and social structure during the non-breeding season has received attention (Brian 1949; De Laet 1984; Drent 1983; Saitou 1978, 1979 a,b,c). Comparative information is also available from detailed studies and reviews of other species in the genus *Parus* (e.g. Glase 1973; Perrins 1979; Smith 1976). This background makes the great tit a potential model for the integration of the two main streams of behavioural research introduced above - communication and socioecology - through a study of its competitive social interactions.

This study attempts to add to a functional understanding of the behaviour by which animal contests are resolved, using the great tit as a model. This in turn requires an understanding of the proximate and ultimate goals of agonistic behaviour, and a knowledge of the attributes, both environmental and of the animals themselves, that are relevant to the course and outcome of contests.

1.2. THE GREAT TIT

Certain aspects of the life history of the great tit are introduced here to illustrate the suitability of the species for measuring a variety of physical and social attributes of individual birds which may influence their behaviour in competitive interactions.

A summary of the annual cycle of the great tit is given in Fig. 1.1.

as a composite derived from Drent (1983), Hinde (1952), Kluijver (1951), Perrins (1979) and Saitou (1978). The significance of year-to-year and geographical variation in this cycle (especially between the British race *P. m. newtoni* and the continental race *P. m. major*) is discussed in Chapter 3 and the importance of certain elements to this study is discussed here.

i) The establishment and maintenance of a territory by a breeding pair is crucial for successful reproduction. The data of Dhondt & Schillemans (1983) showed the much reduced productivity of birds that were compelled to breed without a territory in high density populations.

ii) Throughout the life cycle, great tits show some degree of flocking behaviour, although its intensity varies considerably on a diurnal and seasonal basis and with prevailing weather conditions (Drent 1983; Hinde 1952; Saitou 1979a). First-year birds flock almost immediately they become independent of their parents and flocking behaviour is usually maintained throughout the period of juvenile dispersal in the birds' first autumn and until their first breeding season begins in the following spring. Adult birds (i.e. after their first breeding season) tend to remain within their breeding territories during the immediate post-breeding period whilst moult is taking place, but show flocking behaviour throughout the autumn and winter (October to March in Britain). Saitou (1978) reported a quite rigid, predictable, hierarchical structure of 'basic' and 'compound' flocks in Japanese great tit populations during winter (see Chapter 4 for further discussion of this).

The implications of regular flocking behaviour and structured flocks in allowing repeated encounters between birds, and the possibility of the development of individual recognition, are considerable. Drent (1983) has shown that agonistic experience early in life has a significant effect on subsequent agonistic behaviour and, hence, the probability of territorial establishment, with the relationship being one of positive feedback (i.e. winning begets winning and defeat begets defeat). Great tits generally become more sedentary after their first breeding season (Hinde 1952; Kluijver 1951), especially in Britain, and the long-term effects of repeated encounters with the same neighbouring birds thereby become even more important. Drent also found that a combination of territorial status, length of prior residence and age (clearly, non- independent factors) accounted for much of the variation in social status, at least of males.

Two main points emerge. Firstly, *prior* experience might be expected to have a considerable effect on a great tit's *current* behaviour in social interactions. Secondly, the selection pressures on the outcome of specific agonistic encounters may extend far beyond the acquisition or loss of a proximal resource such as time at a food source. If current experience affects future success in the long term, then it may be appropriate to see each interaction as being influenced by more distant goals such as high social rank, long-term residence, territorial status and, ultimately, successful reproduction.

iii) Juvenile dispersal is a characteristic of all great tit populations and is thought to be a response to the need to avoid inbreeding (Greenwood *et al* 1978) and escape high population density and competition for food in the period following independence of the young (e.g. Dhondt 1979). British great tit populations are very sedentary in comparison with those in continental Europe (Chapter 3). Nevertheless, juvenile dispersal over distances of a few kilometres still occurs and movements, mostly of first-year birds, may take place at other times during the non-breeding season, either due to food shortage or to the search for suitable breeding habitat (Chapter 3). As a consequence, throughout the non-breeding season there is a turnover of birds in any given population with regular arrivals of birds whose social encounters will not be affected by mutual prior experience, in contrast to those between established birds. These new arrivals may be of particular interest since their emigration from another area may have been precipitated by a vicious circle of 'defeat begets defeat' (Drent 1983).

1.3. INTRODUCTION TO THE STUDY

After Tinbergen's (1952) seminal paper on the evolution of ritualized or 'derived' behaviour, the first ethological accounts of agonistic behaviour were concerned primarily with testing the causal hypothesis that the variety and variability of ritualized threat displays reflected the internal state of animals that were simultaneously stimulated to behave in conflicting ways, usually to attack or flee (e.g. Andrew 1956; Blurton

Jones 1968; Dunham 1966; Kruijt 1964; Marler 1956; McKinney 1961; Moynihan 1955; Stokes 1962a,b; Tinbergen 1959), and the idea still receives attention today (Maynard Smith & Riechert 1984; Veen 1987). This hypothesis was an extrapolation to immediate causation from Tinbergen's (1952) original evolutionary 'conflict hypothesis', reviewed by Baerends (1975), that ritualized, agonistic displays have evolved as signals from unritualized 'intention' movements occurring at times of motivational conflict, that were not specifically adapted to signal function (e.g. Daanje 1950; Morris 1956). This extrapolation depends on the validity of the assumption that current display patterns have not become emancipated from their original motivational causes over the course of evolution to serve an independent signal function (Baerends 1975; Blurton Jones 1968; Tinbergen 1952).

A second batch of studies (e.g. Amlaner & Stout 1978; Andersson 1976; Bossema & Burgler 1980; Hayward *et al* 1977; Nelson 1984; Stout & Brass 1969) has concentrated on a functional explanation of ritualized agonistic behaviour. This explanation is in terms of the theory that the evolution of agonistic display is based on selection pressures for the communication of semantic information about the future behaviour probabilities that result from motivational conflicts (e.g. Cullen 1966, 1972; Smith 1977) as a means of reducing the risk of overt aggression during contests. This has often been termed the 'traditional ethological view' (e.g. Caryl 1979).

More recently, emphasis on communication of information as a proximate function of agonistic display has been challenged by game theory analyses of animal contests (Maynard Smith 1972, 1974; Maynard Smith & Price 1973; Parker 1974). These analyses model the evolution of different agonistic 'strategies' on the basis of the overall payoff from the fitness costs and benefits of particular behavioural options, whilst recognizing the frequency- dependence of that payoff according to the options adopted by other members of the population. In the game theory approach it is treated as axiomatic that "the ultimate purpose is to win or defend a resource and not to communicate per se" (Enquist 1985). The approach therefore focuses on the ultimate function of agonistic behaviour (i.e. fitness gain) rather than providing an explanation at the proximate level of sensory interplay and motivational change (i.e. 'communication') in the competing animals. Nonetheless, some game theoretical models, notably Maynard Smith's (1974) 'War of Attrition' do make explicit predictions concerning the qualitative nature of communication which at first sight contradict those of the 'traditional ethological view'. This has resulted in much theoretical controversy and empirical research over the question of whether the transmission of semantic information is a proximate function of behaviour in agonistic encounters and, if so, exactly what is communicated (Caryl 1979, 1981, 1982a,b; Enquist 1985; Enquist *et al* 1985; Hinde 1981; Maynard Smith 1979, 1982a,b; Moynihan 1982; Nelson 1984; Paton 1986; Paton & Caryl 1986; van Rhijn 1980; van Rhijn & Vodegel 1980; Turner & Huntingford 1986).

The above is a brief overview of the course of the study of agonistic behaviour in animals since Tinbergen (1952) and its relationship to this study of great tits will be discussed in detail in the relevant chapters. However, in Section 1.2. it was suggested that individual social encounters between great tits might be far from independent in their causes and effects. Consequently, the behaviour of a great tit in any given interaction might be affected by its current social attributes which are, in turn, a product of experience in previous social encounters. This important point was recognized by Simpson (1973, p. 225) who summarized the argument thus:

i) "This chapter ... suggests a framework of interpretation" (of social displays) "which attends particularly to the sequential and temporal relationships among social actions."

ii) This approach leads us "to pay special attention to social interactions as processes occupying time which can lead to progressive and sometimes irreversible change in relationship."

Now add to this the possible effects of physical attributes such as sex, age and body size and weight (some of which are already known to influence contest outcome in great tits (De Laet 1984; Drent 1983; Garnett 1976; Jarvi & Bakken 1984; Perrins 1979; Saitou 1979b), on the course of an encounter. It is clear that a complex of physical and social variables may interact both within and between birds to provide the environmental stimuli that influence the behaviour of great tits in a competitive encounter and its eventual outcome. Howard's (1952) *Birds as Individuals* stands as testament to this complexity and contrasts markedly with the impression given by many of the ethological accounts of agonistic behaviour listed above.

Perhaps because of their emphasis on conflicts and fluctuations in *internal* state, many of the early studies on the causation and function of ritualized display (e.g. Blurton Jones 1968; Dunham 1966; Stokes 1962a,b) do not discuss the possibility that physical and social attributes of competing animals might underlie these motivational states and that signalling *them* might be the proximate function of the displays, rather than the signalling of internal state itself. The advent of the game theoretical approach has stressed the importance of differentiating the exchange of information about physical attributes or 'resource-holding power' (RHP) (Parker 1974) and other asymmetries that may be relevant in determining contest outcome (Maynard Smith & Parker 1976), from the communication of motivational information or 'intentions' (Maynard Smith 1979, 1982a,b). This theoretical division is based on the argument that RHP is a measure of an animal's actual ability to hold a resource and is not susceptible to 'bluffing' (i.e. signalling at a higher level than is actually possessed) since such bluffing would incur a fitness cost. In contrast, current motivational state and intentions can be bluffed at any level without any inherent additional cost. In other words, "If an animal could win contests by signalling 'I am larger than you', then it would pay to do so. But it may be impossible to signal that it is larger unless it actually *is* larger, and it cannot actually *be* larger without paying a cost. Hence the settling of contests by signalling RHP can be evolutionarily stable, but not by signalling intentions." (Maynard Smith 1982b, p5). The issue of susceptibility to bluffing led Maynard Smith (1974, 1979, 1982a,b) and Caryl (1979) to predict that ritualized display would not, in general, have evolved to transmit motivational information but might signal costly attributes such as RHP and allow resolution of contests by mutual assessment of any asymmetry in the attribute concerned (e.g. Enquist & Leimar 1983; Hammerstein 1981; Maynard Smith & Parker 1976; Parker 1974; Parker &

Rubenstein 1981).

The game theory approach to agonistic behaviour has shown the importance of individual differences between animals in explaining the behavioural mechanisms of contests, and there is now much empirical evidence in support of the use of asymmetries as cues in the resolution of contests (e.g. Clutton Brock & Albon 1979; Davies & Halliday 1978; Ewald 1985; Yasukawa & Bick 1983, and a review in Huntingford & Turner 1987, p.282). Similarly, more recent work on the question of communication of 'intentions' has taken account of these individual differences (e.g. Amlaner & Stout 1978; Andersson 1976; Black & Owen 1989; Bossema & Burgler 1980; Nelson 1984; Popp 1988; Shawcross & Slater 1984; Veen 1987). As a consequence, Maynard Smith's stress on the dichotomy between signalling of bluff-resistant asymmetries and bluffable internal state has gradually been broken down. There is now considerable theoretical and empirical evidence to suggest that there are circumstances in which signalling of motivational state and immediate intentions might be adaptive (e.g. Barlow *et al* 1986; Bronstein 1985a,b; Hazlett 1987; Hazlett & Bossert 1965; Riechert 1978; Turner & Huntingford 1986; van Rhijn 1980; van Rhijn & Vodegel 1980). The most recent work on this subject emphasizes an economic analysis of the chances of evolutionary stability of intention signalling, based on the cost of bluffing versus the value of the contested resource (e.g. Bond 1989; Enquist 1985; Enquist *et al* 1985; Harper *et al* in press; Maynard Smith & Harper 1988; Popp 1987a). Moynihan (1970) and Andersson (1980) have proposed that these simultaneous selection pressures for signalling of intentions and for its immediate exploitation by bluffing may give rise to a continuous evolutionary cycle of replacement of old, deceit-ridden displays by effective new ones, thus leading to the observed diversity in the agonistic display repertoires of many vertebrates. To bring the wheel full circle, Maynard Smith & Riechert (1984) have developed a game theory model of the agonistic behaviour of the spider *Agelenopsis aperta* that is based on Tinbergen's original two-tendency conflict hypothesis of agonistic motivation (Chapter 6.1.). The model successfully reproduces the qualitative nature of contests, including the importance of asymmetries such as weight, web ownership and site quality which are known to be used as cues in real contests.

Thus there is evidence for both the signalling of physical and social asymmetries and internal state, and for the interaction of these types of signalling during the course of a contest (Archer 1988; Maynard Smith & Riechert 1984; Turner & Huntingford 1986). In addition, different signals may be represented by different displays or variation within a display (Enquist 1985), or by different frequencies of performance of a display within a behaviour sequence (e.g. Schleidt 1973). With such complexity, a single study cannot hope to unravel all these possibilities. In any case, there is no *a priori* reason to suppose that behavioural mechanisms of contest behaviour that operate in one population will do so in another (see Chapter 5).

Blurton Jones' (1968) study of agonistic behaviour in great tits, a test of Tinbergen's (1952) conflict hypothesis, has never been repeated as a functional analysis, and both his study and that of Stokes (1962b) stand out as examples which did not take account of individuality. This study therefore has the following aims.

i) To determine the importance of physical, social and experiential attributes of the individuals constituting a population of great tits, as predictors of the outcome of competitive encounters.

ii) To record the postural displays and behaviour sequences used and the resulting outcome of dyadic encounters between known individuals.

iii) To combine these data to determine the relative importance of asymmetry assessment and signalling of internal state as proximate functions of agonistic communication by display, and to relate different elements within the agonistic display repertoire of the great tit to these possible functions, using both wild and captive populations.

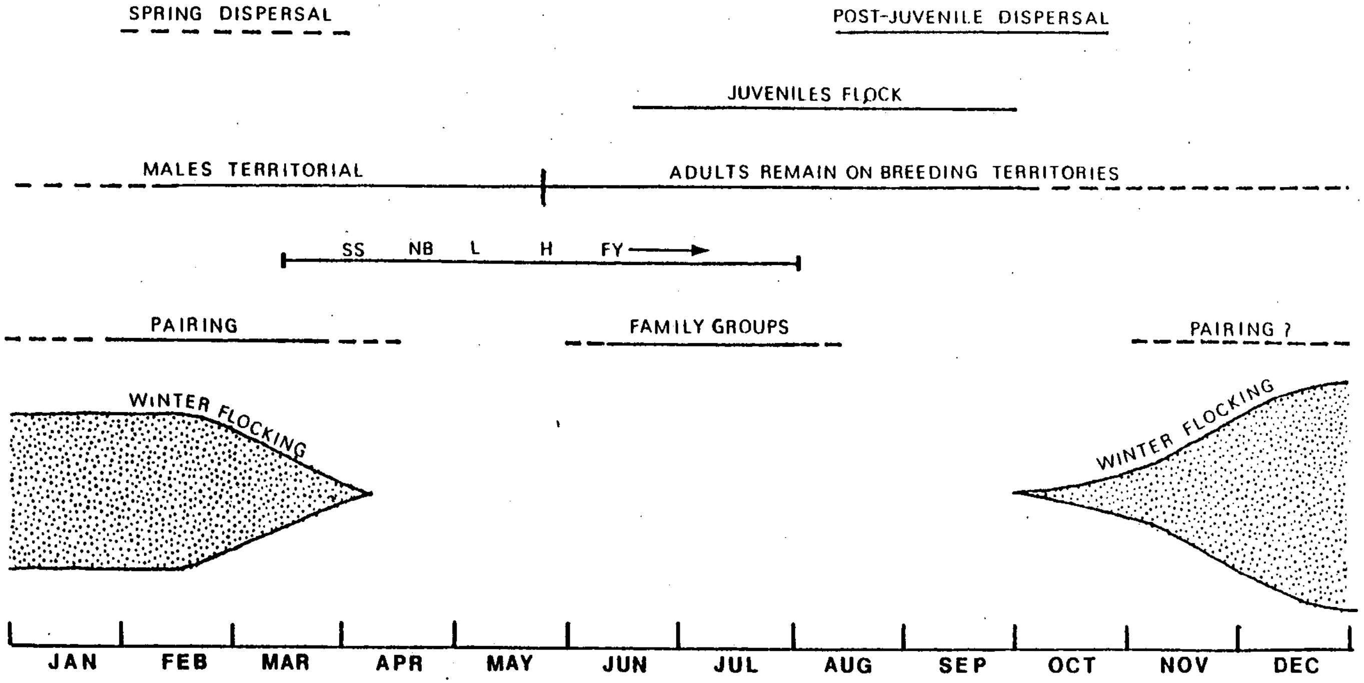


Fig. 1.1. Key aspects of the annual cycle of the great tit. SS = nest site selection, NB = nest building, L = laying, H = hatching, FY = fledged young.

CHAPTER 2.

STUDY SITE AND GENERAL METHODS.

2.1. THE STUDY AREA

The study was carried out in 30 hectares of mixed woodland, hedgerows and gardens around Ormiston Hall, East Lothian, Scotland, at 120m above sea level (55^{o} 54'N 2^{o} 57'W). Formerly a managed estate, the woodland is now dominated by young sycamore *Acer pseudoplatanus* with a paucity of those species favoured as food sources by great tits such as hazel *Corylus avellana*, oak *Quercus spp.*, beech *Fagus sylvatica* and birch *Betula pendula* (Gibb 1954). Active management has recently been re-started in the wood (A. Manning & U. Loening pers. comm.) and several clearings, planted with ash *Fraxinus excelsior*, oak and beech, were created during the course of the study. The understorey is well developed in places with elder *Sambucus nigra*, hawthorn *Crataegus monogyna*, yew *Taxus baccata* and rhododendron *Rhododendron ponticum* as the predominant species. The first two are much used by tits searching for insect prey and fruiting yews are heavily seed-predated by great tits during the autumn.

Fifty nestboxes were erected in the area during the 1985/6 and 1986/7 winters to compensate for a lack of natural nest and roost holes, and between one and three artificial feeding stations were established within the study area between October and April of each year of the study. These are more fully described in Chapter 2.3. In addition, at least three other artificial food sources were available to the birds during the study due to the provision of food by local residents.

Mapping of the positions and identities of territorial great tits was carried out within a 3km radius of the study site during spring 1988 and 1989. This work is more fully described in Chapter 3.3.3. The area is a mosaic of arable land, grazing, and mixed woodland in the catchments of Tyne Water and Humbie Water and encompasses the villages of Ormiston and Pencaitland.

2.2. CAPTURE, RINGING AND MEASUREMENT OF BIRDS

Between October 1985 and June 1989, great tits were captured by mist-netting at several sites around the study area when weather conditions were suitable. During inclement weather, a few birds were caught in chardonneret traps (Davis 1981) baited with peanuts. Each bird was sexed according to the length of the ventral black stripe (Fig. 2.1.) and aged as first-year or 'adult' according to the presence or absence of juvenile primary coverts retained after the post-juvenile moult (Svensson 1984) which occurs in the period July-September after hatching (Perrins 1963, Ginn & Melville 1983). After the first post-nuptial moult at the end of a bird's first year, there are no reliable age-related plumage differences and the precise age of these 'adults' cannot be determined.

After ageing and sexing, each bird was fitted with a uniquely numbered metal ring supplied by the British Trust for Ornithology (B.T.O.) and three coloured plastic split-rings. One colour ring, placed above the metal ring, specified the bird's sex and age at time of ringing. The two colour rings on the other leg made the overall combination unique and allowed identification of the individual in the field. For details of colour rings and combinations used, see Appendix 1. All rings were fitted to the tarsometatarsus. The date and time of ringing were recorded to an accuracy of 1 minute and corrected to G.M.T.

After ringing, and at each subsequent capture, the maximum wing length (Svensson 1984) was measured to an accuracy of 1mm using a stopped 50mm wing rule and tarsus length was measured using the method of Svensson (1984) to an accuracy of 0.1mm using CAMLAB vernier calipers. Before release, the weight of each bird was recorded to an accuracy of 0.1g using a 50g Pesola spring balance and 2g polythene weighing cone.

2.3. FEEDING STATIONS

Between October 1986 and April 1987, one feeding station was established in a 25m x 25m walled garden near the centre of the study area (Fig. 2.2.) and was stocked continuously with lard and peanuts provided at a 42cm x 35cm table, 2m from the ground or in hanging feeders suspended from this table. Hereafter, this site is referred to as the 'Garden'.

Between October 1987 and April 1988 and September 1988 and

April 1989, two additional feeding stations were established, one near the Great Yew and one in Church Wood (Fig. 2.2.). These sites are hereafter referred to as the 'Yew' and the 'Wood' respectively. All three sites were continuously stocked with peanuts dispensed from each of two hanging feeders suspended 1m above the ground. The precise arrangement of food provision varied during the 1987/88 and 1988/89 seasons according to the requirements of three undergraduate Honours projects carried out on the same population during these two winters. More detailed descriptions of feeder arrangements are given where appropriate.

2.4. COLLECTION OF BEHAVIOURAL DATA

At the Garden, observations were made from a permanent hide located between 5 and 13m from the feeders. At the Yew and the Wood, observations were made from a portable canvas hide erected at the start of each field session. At none of the sites did the presence of an observer or hide appear to affect the behaviour of the birds visiting the feeding station. Observations were made using either Swift Audubon 8.5x44 or Carl Zeiss Jenoptem 8x40 binoculars and all data were recorded on to audio cassettes for later transcription. During the 1986/87 season, additional data were collected by videotaping activity at the Garden feeders using a JVC GX-N8E colour video camera, Panasonic NV180 video recorder and JVC E-180PRO three-hour video cassettes.

At the start of each observation session, date and G.M.T. were recorded and all data were divided into successive five minute periods. During each period, the identity of every great tit visiting the feeding station was noted as were details of any intra- or inter- specific interactions involving a great tit. Two birds were deemed to have interacted if they were present at the feeder simultaneously. Interactions involving three or more birds simultaneously were not used in subsequent analyses.

Intraspecific interactions were subdivided according to whether or not they occurred at a food source and, in the case of feeder interactions, whether the bird already at the feeder (the 'owner') or the incoming bird (the 'intruder'), proved to be dominant. One bird was assigned as the 'dominant' and the other as the 'subordinate' in a given interaction if:

a) one bird actively displaced the other by means of a simple supplant in which the supplanter caused, through its arrival or approach, the departure of the supplantee, but without any overt postural display or aggression. Alternatively, displacement involved postural display and/or direct attack.

b) one bird appeared to the observer to avoid another at the feeder or wait for the other to finish feeding and leave before feeding itself. For a fuller discussion of the methodology and problems of assigning dominance and subordinance to animals involved in social interactions, see Chapter 4.

Any postural display used by a great tit during an interaction was recorded using a classification modified from Blurton Jones (1968) (Chapter 6.1). Where data were recorded on videotape, only the identity of birds visiting the focal food source were recorded in the field in order to ensure that all birds recorded on videotape were unambiguously identified. All behavioural data were transcribed from the videotape in the laboratory. The ability to view behavioural sequences repeatedly and in slow motion allowed an expanded behavioural classification to be used in the analysis of videotape data (Chapter 6.1).

Throughout April-May 1987, February-May 1988 and February-May 1989, regular morning surveys of the study area were carried out. The identity, position and behaviour of each great tit seen were plotted on to an Ordnance Survey map of the study area in order to establish the identity of all non-territorial birds and territorial pairs remaining in the study area during the breeding season, and to provide an estimate of the location of the breeding territories. The behaviour of each bird recorded was classified as follows.

S: singing, V: other vocalization, D: display, F: feeding, C: courtship.

The order of visit to different parts of the study area during one morning was randomized and not all surveys covered the entire area.

However, all parts of the study area were visited at least ten times during the course of one season.

For each male recorded in territorial activity (S,V, D or C), the distance of its territory to each of the observation sites was estimated as the mean of the distances of all sightings of the bird when engaged in territorial activity. When a male was known to be paired with a particular female, the same territory distance value was also assigned to that female. Distances were calculated simply by scaling up the distances on the base map plots and rounding to 0.5m. A sample base map at the end of a season's territory mapping is shown in Fig. 2.3. This map shows six clusters of sightings representing the breeding territories of five males. A and D are examples of territories occupied by the same males in all three years of the study, each bird having become established as a locally dominant first-year bird during the 1986/87 winter. B1 was occupied by male 9493 throughout spring 1988 until early May when his mate disappeared and is presumed to have died. Thereafter, he moved to a vacant area (B2) and defended a small territory, though did not succeed in re-pairing or breeding. On the vacation of B1 by 9493, male 9494 moved from the stream valley around the pond to re-occupy the area. C is an example of a territory established by a locally dominant first-year bird in 1988. Other pairs occupied intervening areas to give a total population of 21 pairs within the mapped area during the 1988 breeding season.

2.5. RINGING OF PULLI

All tit pulli raised in nestboxes within the study area were ringed during June of each year, as soon as they were large enough that there was no risk of the ring slipping down over the foot. Most of the nestboxes were occupied by blue tits and the pulli of this species were fitted only with a B.T.O. metal ring. Those of great tits were fitted with a B.T.O. ring on the right leg and a single colour ring on the left leg which specified the nestbox of origin. Any of these birds recaptured after their post-juvenile moult, at which time they could be easily aged and sexed, were then fitted with a full colour ring combination.

2.6. METEROLOGICAL DATA

Detailed meteorological data (mean, minimum and maximum temperatures, rainfall, snow cover, wind speed and direction, cloud cover and sunshine hours) were provided by the Meterological Office, Edinburgh, from the Pathhead weather station (4km south-west of the study area and at a similar altitude) throughout the study. A summary of these data for the period of the study is given in Appendix 2 and is discussed in Chapter 3.

2.7. DATA ANALYSIS

Except where otherwise stated, all statistical tests used follow Siegel & Castellan (1988) and Sokal & Rohlf (1981). All analyses were carried out using the SPSS-X (SPSS-X Inc. 1988) and MINITAB (Ryan *et al* 1985) statistical packages. A list of abbreviations used in connection with statistical tests is given in Appendix 3.

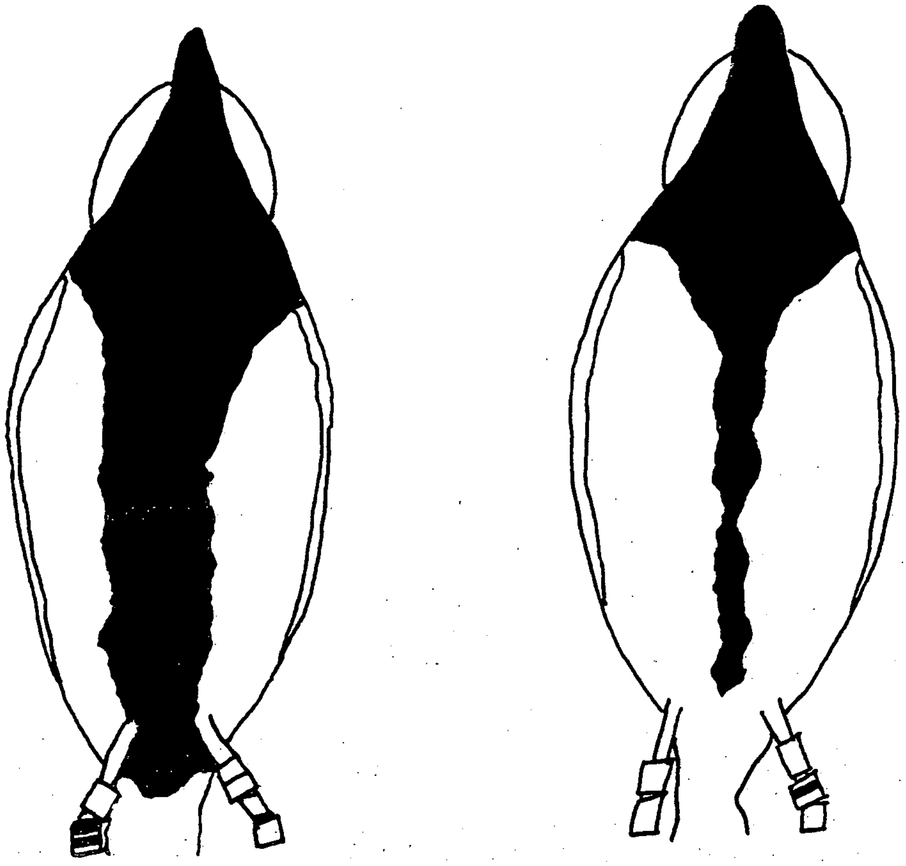


Fig. 2.1. Ventral views of male and female great tits, showing the extension of the ventral stripe between the legs in the male.

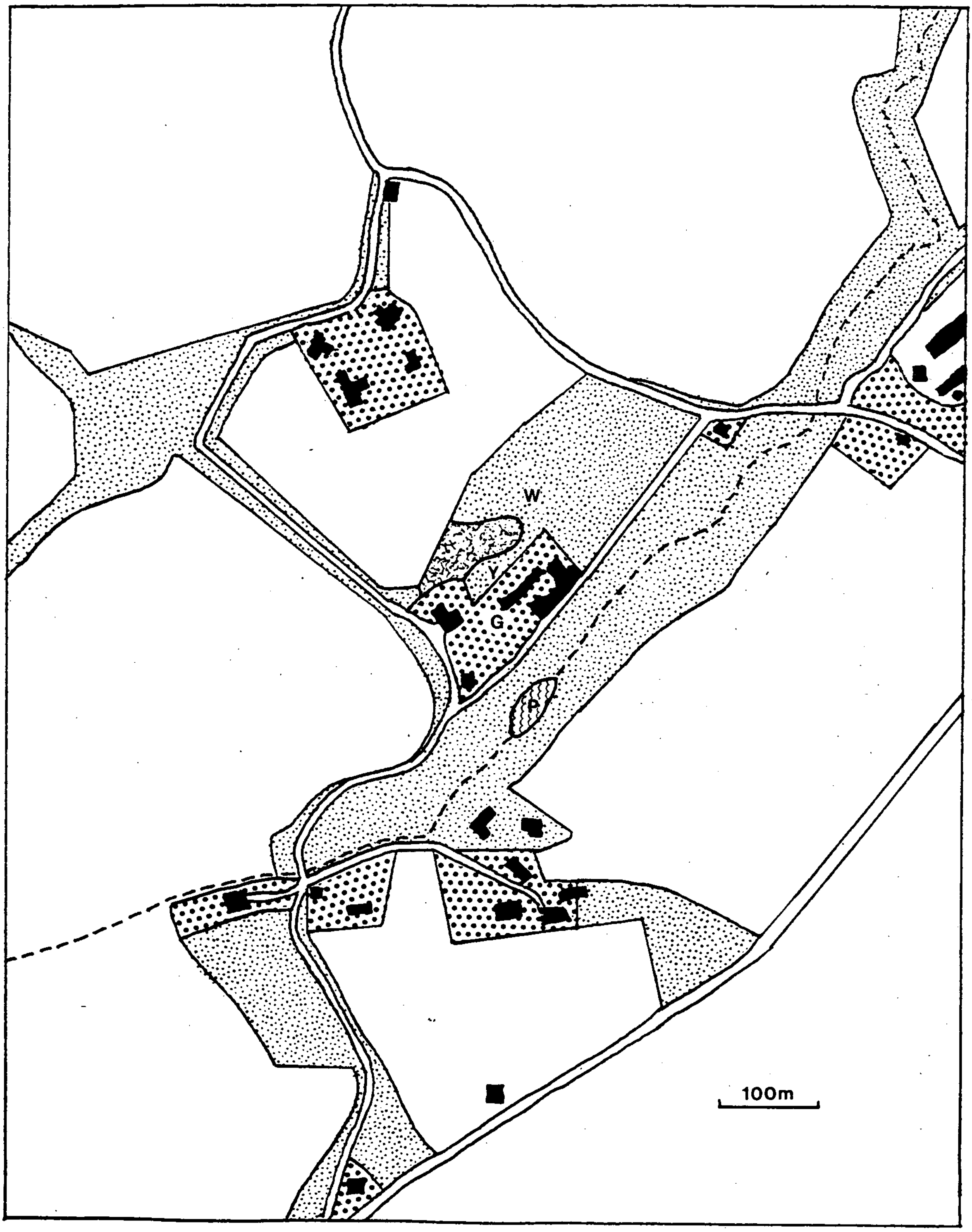


Fig. 2.2. Map of the study area. G = Garden. Y = Yew. W = Wood. p = pond. Coarse stippling = gardens. Fine stippling = woodland. Mosaic shading = scrub. Solid shading = inhabited buildings. Dashed line marks the course of a stream.

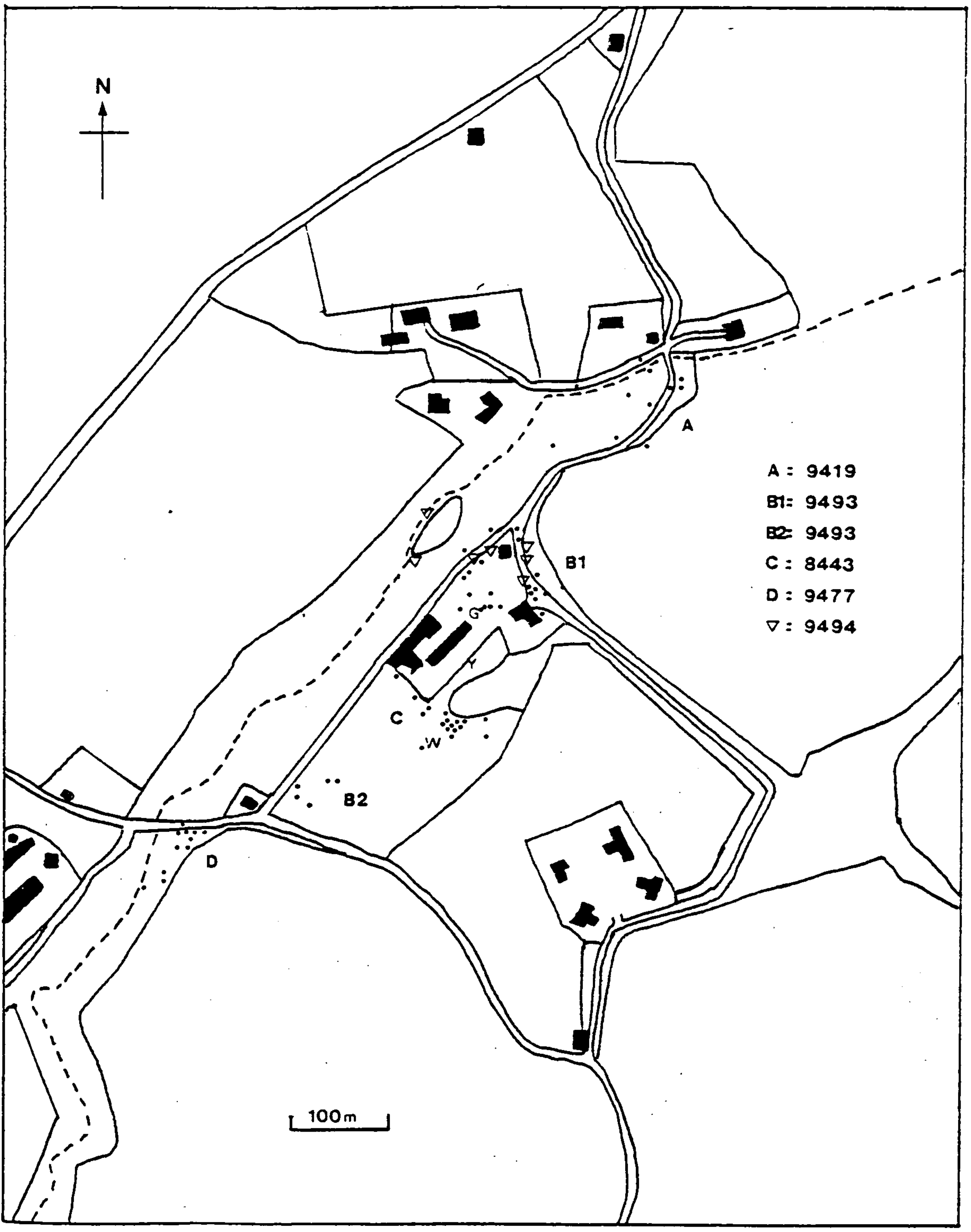


Fig. 2.3. Sample territory map after the 1988 breeding season showing breeding territories A, B1, B2, C and D as defined by sightings of the occupying males (ring numbers given). Other males (not shown) established territories in intervening areas. See text for further discussion.

CHAPTER 3.

THE STUDY POPULATION: A COMPARISON WITH OTHER GREAT TIT POPULATIONS.

3.1. INTRODUCTION

The population ecology and breeding biology of the great tit have been thoroughly studied (Clobert *et al* 1988; Dhondt 1970, 1971; Drent 1983; Gibb 1950; Hinde 1952; Kluijver 1951; O' Connor 1980; Ulfstrand 1962; van Balen 1980). A review of much of the earlier work and of the general biology of the great tit is given by Perrins (1979). This study has not attempted a detailed examination of great tit ecology in another population. However, observational, ringing and biometric data all allow comparison with these previous studies. The aim of this chapter is to use these data to make comparisons of a few simple parameters of population structure in this study with those obtained elsewhere. At the very least, this is necessary before any results from this study can be generalized to the species as a whole. In addition, any significant differences between the ecology of this population and that of other intensively studied populations in England, continental Europe and Japan may be important in understanding the patterns of social structure and communicative behaviour that are the main subject of this study.

3.2. THE BREEDING POPULATION

The number of breeding pairs of great tits within the 30ha study area, as estimated by territory mapping, increased from 16 pairs in 1987 (0.53 per ha) to 21 pairs in 1988 (0.70 per ha) and 24 pairs in 1989 (0.80 per ha). This density is fairly typical of mixed woodland and gardens (Kluijver 1951; Perrins 1979), where the density of breeding pairs is not artificially increased by the provision of very high densities of nestboxes (e.g. Dhondt & Schillemans 1983). Non-territorial 'floaters' were very rarely observed during the breeding season. This apparent absence of a non-breeding surplus during the breeding season has also been reported by Krebs (1971) in great tits and Desrochers *et al* (1988) in black-capped chickadees *P. atricapillus*, but such a surplus may exist in years of high population density when birds forced out of an area during spring territory establishment are unable to find vacant breeding habitat (e.g. Krebs 1977; Smith 1984).

Although the apparent increase in the breeding population during the study may partially reflect increasing observer competence, the mildness of the 1987/88 and 1988/89 winters in comparison with the previous two (Appendix 2), coupled with the increased provision of artificial food may mean that the increase is real.

Most of the 50 available nestboxes were occupied by blue tits. However, a few pairs of great tits did breed in these boxes. The annual totals are: 1987 - 0; 1988 - 5; 1989 - 6.

3.3. RESULTS

3.3.1. Distribution of captures

Between November 1985 and April 1989, 450 fully grown great tits were captured using mist-nets or chardonneret traps and colour-ringed. Virtually all catching was carried out at feeding stations or on the regularly used flight paths between them. The distribution of these catches by year is given in Table 3.1. Because catching effort varied considerably over the course of the study, corrections for this are also shown. For the sake of convenience, the use of a chardonneret trap has been equated with the use of one 6m mist-net.

Rate of capture of unringed great tits declines throughout the study despite a steady increase in total numbers caught, and the proportion of newly captured adults declines from over 30% in the first two seasons to 10-20% in the second two. The sex ratio of newly captured birds fluctuates around 50%.

A total of 466 recaptures of these birds was made during the study and the distribution by month of the overall total of 916 captures is given in Table 3.2. Overall capture rate peaks in December for all age-sex classes with an apparent subsidiary peak in February, although the capture rate for adult females remains constant between November and February. The sex ratio of the overall capture total remains female biased throughout the season. The proportion of adults in catch totals increases during the autumn but remains at 30-40% from December to April. The distribution by age-sex class of each year's total number of captured individuals is given in Table 3.3. The sex ratio of captured birds tended to be slightly female biased and the proportion of adults in the captured population fluctuates between 27 and 39%. Within age-sex classes, the sex ratio was always female biased in first-year birds but in adults was male biased until the final season, reflecting a steady decline in the proportion of adult males in the population of captured birds.

Females were caught earlier in the day than males (t = 2.26, df = 915, p = 0.024) and first-year birds were caught earlier than adults in both sexes (males, t = 2.61, df = 405, p = 0.0096; females, t = 3.71, df = 508, p = 0.0003).

3.3.1.1. Discussion

The decline in rate of capture of unringed great tits as the study proceeded reflects both the year to year survival of many members of a relatively stable and sedentary (Perrins 1979; O'Connor 1980) population and the mildness of the third and fourth seasons (Appendix 2). The increase from year to year in the absolute numbers of unringed birds caught is due to a considerable increase in ringing effort (333 net-metre-hours in 1985/86, 1120 in 1986/87, 2369 in 1987/88 and 9243 in 1988/89).

The pattern of capture rate suggests December and February as the two months when great tits experience the greatest shortages of natural food and thus show the greatest tendency to visit feeding stations. In December, this probably reflects the need to find sufficient food in a short daylight period to survive a long night. Great tits are known to devote the greatest proportion of their daily time budget to feeding in December (Gibb 1954a) and to rise earlier and roost later in relation to sunrise and sunset at this time (Dunnett & Hinde 1953; Kluijver 1950). In February, daylength is increasing but the previous season's food stocks have been depleted (Gibb 1954a) and many remaining seeds may be rendered inedible by germination (Perrins 1979). As temperatures rise in March, increasing invertebrate activity gradually alleviates this shortage.

Kluijver (1951) reports a consistent male bias in the sex ratio of great tits visiting artificial feeding sites during winter. In this study, this phenomenon, as estimated by capture totals at feeding stations, is reversed despite the fact that female mortality rates are known to be higher than those of males throughout the life cycle of several tit species (Bulmer & Perrins 1973; Dhondt 1970; Kluijver 1951; Perrins 1979; Southern & Morley 1950). This probably reflects the relative mildness of the winters of this study. In this situation, males may be able to obtain a greater proportion of their food from natural sources and apportion a greater part of their daily time budget to singing and territory establishment (Perrins 1979).

The increasing number of adults in catch totals as autumn progresses corresponds with the findings of Kluijver (1951), Hinde (1952) and Saitou (1979a) who all report that adults remain in a restricted winter range, roughly corresponding to their former breeding territory, whilst first-year birds flock together over a wider range encompassing several breeding territories. A gradual increase in the proportion of adults visiting feeding stations is to be expected both as dwindling food supplies force adult birds to extend their daily ranges, and as differential mortality increases the proportion of adults in the population as a whole (Bulmer & Perrins 1973; Kluijver 1951). The age-related reversal of sex ratio in birds visiting feeding stations that occurs in three of the four seasons is probably also a reflection of the lower life expectancy of females throughout the life cycle (Bulmer & Perrins 1973), although Clobert *et al* (1988) found that mortality rates of female great tits fluctuated considerably and were not consistently higher than those of males.

The earlier capture of first-year birds in relation to adults on a given day may be a consequence of both the relative inefficiency of young birds in finding and exploiting natural food sources (e.g. Gochfeld & Burger 1984) and the age-related differences in flocking behaviour and range size, already discussed.

3.3.2. Mortality and Site Fidelity

The return in subsequent seasons of birds ringed during a given season is shown in Table 3.4. using estimates from recapture and observational data respectively. Daily observation clearly provides a more accurate estimate of the numbers of birds remaining from previous seasons than does recapture. Some errors in reading of colour rings must have occurred during observational data collection and a few records of birds reappearing for a single day after long absences seem suspicious. However, the identity of a few retrapped birds confirms that this kind of record does occur. There is thus no objective basis for rejecting certain 'suspicious' records and any such errors in colour ring reading that did occur are assumed to be negligible. The data set derived from field observations is thus used in the following analyses. These data are plotted in Fig. 3.1. and for all age-sex classes show a decline in the rate of disappearance between birds' first and second, and second and third seasons at the site, although none of these differences is statistically significant (chi-square tests).

Date of ringing is not related to the probability of a bird reappearing in a following season (Table 3.5.) and reappearing birds are not significantly different in size to those which disappear (Table 3.6.).

The proportion of birds present in one season that are known to be alive in the next season is shown in Table 3.7. Adults of both sexes show an inter- season disappearance rate of 45-50% over the whole study whereas the proportion of disappearing first-year males is significantly lower than that of first-year females (males = 44.7%, females = 60.3%: $X^2 = 5.45$, df = 1, $p<0.05$).

3.3.2.1. Discussion

Most of the birds in this study were ringed between September and April and disappearance before the next season could reflect death or dispersal at any time except during the immediate post-fledging period. Since much of first-year mortality is concentrated in this period (see later), the disappearance rates recorded in this study (Table 3.7.) for first-year birds are not directly comparable with mortality estimates from previous studies (e.g. Kluijver 1951; Lack 1964, 1966; Bulmer & Perrins 1973, Clobert *et al* 1988), and might be expected to be more similar to those of adults. The effects of both intraspecific (Dhondt 1971; Tinbergen *et al* 1985; van Balen 1980) and interspecific (Dhondt

1977; Dhondt & Eyckerman 1980; Minot 1981; Minot & Perrins 1986) density dependence in the survival rates of great tits are undoubted, but their consideration in a short term study such as this is unlikely produce interpretable results. Similarly, serial bivariate analyses of the effects of different possible causal factors on survival rates (e.g. Bulmer & Perrins 1973) will lead to weakened conclusions because the effects of interactions between sources of variation are ignored (Clobert *et al* 1988). Multivariate analysis techniques such as analysis of variance would take into account these interactional effects but are probably disproportionately sophisticated approaches to making simple interpretations of demographic processes and their causes, based on a crude observational record of the composition of the population in each year. With these provisos, the intensive observation of this great tit population should have made the estimates of year-to-year survival and disappearance fairly reliable and open to comparison with those of other studies.

The trend towards decreasing rate of disappearance with increasing prior residence (Fig. 3.1.) corresponds with data from previous work. Kluijver (1951) reported that long distance dispersal was much commoner in first-year birds than in adults in a Dutch population and although the British population is, in general, much more sedentary (Perrins 1979), dispersal is still more typical of first- year birds (Hinde 1952; Perrins 1979). The other component of disappearance is mortality. This is also known to be higher in the first year of life than in adults (e.g. 87% in first-year, 49% in adults - Kluijver 1951; 78% of fledged young, 50% of adults - Bulmer & Perrins 1973), although much of first-year mortality is probably concentrated in the first weeks (Gibb 1954b; Lack 1964; Perrins 1963, 1965; van Balen 1973; Webber 1975) or months (Dhondt 1979) after fledging, perhaps due to inexperience or food shortage (Cowie & Hinsley 1988).

The absence of a correlation between date of ringing and probability of reappearance in a subsequent season suggests that the mild winter weather was not a key cause of great tit mortality during this study. Both Kluijver (1951) and Lack (1966) reported that adult mortality was largely independent of winter weather, although first-year birds may be susceptible to very cold weather, as occurred in 1962/63

(Lack 1964, 1966).

Lehikoinen (1986) found that survival was related to size of great tits only in severe winters and that this relationship was only significant in adult males - the most sedentary age-sex class. Other birds escaped size-related mortality behaviourally by visiting urban areas and artificial food supplies (Hilden & Koskimies 1969; Jansson *et al* 1981; Orell 1989). Since Lehikoinen's data were collected in an area with an average daily mid-winter mean temperature of -6° C, the absence of a relationship between size and probability of disappearance in a British study in which minimum mean temperatures in January-February are much higher is hardly surprising.

The disappearance rate of adults of 45-50% between seasons and the fact that first-year females seem to suffer a higher mortality than first-year males are both characteristic of other studies (e.g. Bulmer & Perrins 1973; Kluijver 1951) although the latter may not be a consistent difference (Clobert *et al* 1988). Females are smaller and socially subordinate to males (see later) and may suffer in intraspecific competition for food (e.g. van Balen 1967), and breeding season predation of females on the nest is known to be significant (Dunn 1977; Kluijver 1951; Lack 1966; Perrins 1965, 1979). It is also possible that greater dispersal distances of females (Dhondt 1979; Dhondt & Huble 1968; Harvey *et al* 1979) may contribute to a higher disappearance rate in females, although Kluijver (1951) considers this unlikely.

3.3.3. Dispersal

3.3.3.1. Methods

During February-April 1988, as many as possible of the woodlands and hedgerows within a 3km radius of the ringing site were searched on either one or two occasions in order to estimate the degree of dispersal of great tits from the main study area during the breeding season. Each great tit found was recorded as 'colour-ringed' or 'unringed'. The precise identity of colour- ringed birds was noted where possible and the sex of unringed birds was also recorded. The location of each bird was then plotted on to a 1:50 000 base map of the area. This exercise was repeated during February-April 1989, but was restricted to a 2km radius of the ringing site.

3.3.3.2. Results

The distribution of colour-ringed and unringed birds at different distances from the ringing site is shown in Fig. 3.2. In both years, the proportion of colour-ringed birds falls very rapidly with distance from the site of ringing, with, in 1988, no colour-ringed birds being found outwith a 2km radius.

In addition to these data, I received two reports of colour-ringed great tits seen outside the study area, two were recovered dead and reported to me by the B.T.O., one was controlled by another ringer, and one was controlled at the study site, having been ringed elsewhere. This information is summarized in Table 3.8.

3.3.3.3. Discussion

Apart from the main period of juvenile dispersal in the early autumn, great tits may undertake dispersive movements at any time during the winter because of food shortage (Gibb 1950), with many birds appearing at suburban bird tables (Hinde 1952; Perrins 1979; Orell 1989). In continental Europe, these movements are more regular and orientated in the more northern and eastern populations where winters are very severe (Kluijver 1951; Perrins 1979). These birds tend to move in a southerly or south-westerly direction in autumn, returning north and east in the spring. In more westerly populations, these movements are more irregular and irruptive in character but still maintain a generally southerly and westerly orientation (Cramp *et al* 1960; Harrison 1948; Kluijver 1951; Romer 1949) and are markedly associated with the availability of food, especially beechmast (Perrins 1966) in autumn (Perrins 1979; Svardson 1967; Ulfstrand 1962). In the relatively mild winter conditions in Britain, movements relating to food shortage tend to be much shorter, more irregular and less orientated (Hinde 1952) but nonetheless result in a some pre-nesting movement of birds returning to favourable breeding habitat during February and March (Hinde 1952, Perrins 1979); behaviour which led Maynard (1936) to consider great tits as "non-resident" at this time of year. Rapid, long-distance dispersal of the juvenile population in late summer and autumn, after the break-up of family groups, followed by a small spring movement of birds before the breeding season is also recorded as typical in the black-capped chickadee (Weise & Meyer 1979).

It is the combination of mortality, juvenile dispersal, movement in relation to food shortage and pre-breeding movement to suitable habitat that is largely responsible for the observed breeding season distribution of colour- ringed birds around the study area. The main conclusion to be drawn from these data is that the local great tit population is very sedentary. Despite all these potential sources of dispersion of colour-ringed birds, almost none appear to settle outwith a 2km radius of the ringing site. To the extent that juvenile dispersal is a key causal factor, this result corresponds closely with those of other studies in Britain (Goodbody 1952) and Sweden (Dhondt 1979) and suggests that food-related winter movement and pre-breeding season movement are not further extending the radius of dispersal of birds caught at the study site. This suggestion is supported by reference to Appendix 2 which shows that, compared with 1986 and 1987, the 1988 and 1989 breeding seasons followed very mild winters.

That a few great tits ringed at the study site do undertake longer distance movements is indicated by Table 3.8. and, in particular, by the observation of a colour-ringed bird in Peebles, 32km to the south-west and the control at the study site of a bird ringed 35km to the south-west, thirteen days earlier. The latter record is especially interesting, taking place at the time of year that pre-breeding dispersal is hypothesized to occur, but also corresponding in timing, speed and direction of movement with the return of a continental bird to its breeding grounds (Cramp *et al* 1960).

3.3.4. Biometrics

Mean values for the biometrics of aged and sexed great tits are presented in Table 3.9. The body weight analysis is based on non-independent data points since many birds are recaptured. This weakness has been accepted because weight varies rapidly on a daily basis and reductions in the data set caused by using a "first capture only" or "birds captured once" subset or by reducing a series of capture weights of one bird to a single mean would all result in a considerable loss of information in the analysis. Males are significantly larger than females in wing length, tarsus length and weight, but the two age classes differ significantly only in wing length with adults being longer winged than first-year birds in both sexes. The within-season repeatability of the three biometrics is shown in Table 3.10. Measurement error is only one reason for the imperfection of these correlations. Wing length may decrease during the season due to abrasion of the remiges and weight is known to be variable Table 3.11. shows the relationship between overall change and inter-capture interval for successive pairs of captures within one season. All correlation coefficients are statistically significant but only that for tarsus length could be interpreted as being anything more than negligible (Martin & Bateson 1986). This correlation actually reflects an apparent decline in the tarsus length of some birds during the winter.

Previous research on the body size of great tits (Haftorn 1976; Owen 1954; van Balen 1967) and of passerines in general (Baldwin & Kendeigh 1938) has found that body weight is linearly related to other measures (e.g. wing length) and to environmental variables such as time of day and current and preceding weather conditions. The same work has also demonstrated a regular seasonal weight cycle. Table 3.12. presents a multiple factor linear regression analysis of the effects of wing and tarsus length, time of day and four measures of temperature, as predictors of body weight in each age-sex class. In all four cases, both biometrics show a significant positive relationship with body weight and in all classes except adult males, weight increases significantly as the day progresses. There is no effect of prevailing or preceding temperature on body weight in any age-sex class.

The effect of time of capture on weight is examined by single factor linear regression in Table 3.13. In all four seasons (Sep - Apr), females show an increase in weight over the course of the day but in males this relationship only exists during the first two seasons. In both sexes, the relationship persists when all years' data are pooled. The latter data are presented in Table 3.14., classified by month. Significant diurnal increases in weight are only characteristic of the late autumn (October–December) and late winter (February). When these regression equations are used to estimate the percentage weight gain over the course of a seven hour winter day from 0930 to 1630 G.M.T. (c.f. Owen 1954), it is clear (Table 3.15.) that diurnal weight gain is particularly marked in both sexes in the first two years of the study and is more characteristic of females than of males.

Since season is already known to show a non-linear relationship with body weight in great tits (Haftorn 1976; Kluijver 1952; Owen 1954; van Balen 1967), its effects in this population are examined separately in Fig. 3.3. In both sexes, fluctuations in mean weight between August and April over the four seasons combined are minor and none of the month to month changes are statistically significant.

The inter-correlations between body size measures are analysed in more detail in Table 3.16. in which body weight has been corrected to 1200 for those captures in months in which significant relationships between weight and time of day exist. All three measures show significant but weak positive inter- correlations in all age-sex classes, with the exception of the absence of any correlation between wing and tarsus length in adult birds.

3.3.4.1. Discussion

The finding that male great tits are larger than females in all three body size measures corresponds with previous work as does the significant age effect on wing length within sexes (Haftorn 1976; van Balen 1967). The absence of an age effect on body weight within sexes occurs despite the fact that first-year birds (which might be expected to be lighter) were caught earlier in the day than adults, a fact that would be expected to accentuate any difference (Owen 1954). In comparison, Haftorn (1976) found adult males to be consistently heavier than first-year birds but found no age effect in females, and van Balen (1967) found age effects on body weight to be small and inconsistent in both sexes.

The absence of a significant negative correlation between wing length and inter-capture interval confirms that abrasion of the primaries is minimal during the winter, although it does become pronounced during the following breeding season (van Balen 1967). Body weight was not expected to show any simple, linear change with season (see below). A significant trend towards decrease in tarsus length is interesting but difficult to explain. One possibility is that a few birds caught early in the season still have disproportionately long, thick tarsi, a characteristic of nestling passerines that experience brood competition (O'Connor 1977, 1984). In great tits, this differential development is sufficiently marked for it to be necessary to fit nestlings with a larger ring size than that used on fully grown birds (Spencer 1984), so it is possible that some first-year birds still retained disproportionately large tarsi when ringed in August or September. These would later decrease in size (including the length component), perhaps through withdrawal of muscle water and mobilization of subcutaneous fat (O'Connor 1984).

The results of the multivariate analysis of possible influences on body weight suggest that other measures of body size, and time of day are important

- concurring with Kluijver (1952), Owen (1954), van Balen (1967) and Haftorn (1976) - but that current and preceding temperatures have little effect. Initially, this conclusion seems to be at variance with the results of Owen, van Balen and Haftorn who all find body weight to be generally inversely related to ambient temperature. They all suggested that body weight increased during the period of falling temperatures from October to December as birds accumulated energy reserves, but then decreased with generally increasing temperatures from January to March as food supplies became scarcer. However, in one of Haftorn's study winters (1948/49), weather conditions were "exceptionally mild, with little snow...". In that year, body weight correlations with temperature almost disappeared in both sexes, as did the seasonal pattern of weight change described above. In this study, all four winters are probably comparable with, or milder than, Haftorn's 1948/49 Norwegian winter (Appendix 2). Together with the fact that artificial food supplies were always available to great tits, this makes the apparently anomalous results of this study less surprising.

The single factor regressions of body weight on time of day suggest that females, being smaller, may suffer greater nocturnal weight losses than males (c.f. Kluijver 1952). The restriction of significant diurnal weight increases to October–December and February matches the higher capture rates in these months and supports the proposition that these are the months when great tits experience the greatest shortages of natural food, due to short daylength and genuine food scarcity. The higher rates of diurnal weight gain in the first two winters correspond with their greater severity (Appendix 2).

The finding of a definite seasonal pattern of weight change by Owen (1954), van Balen (1967) and Haftorn (1976) is derived, in each case, from a study population in which little, if any, artificial food was provided. As with the absence of a temperature correlation, the absence of a seasonal weight change pattern in this population probably reflects a combination of the relative mildness of the winters (Appendix 2) and the provision of artificial food.

The weaker inter-correlations between body size measurements in adult than in first-year birds is only described elsewhere by van Balen (1967). The result may mean that, subject to environmental constraints, experienced adults are able to achieve high weights irrespective of actual body size so that weight tends towards independence of more fixed measures of body size such as wing and tarsus length. In first-year birds, lacking experience and the intimate knowledge of an established territory, weight may remain a much closer correlate of intrinsic body size. The non-significance of the wing length – tarsus length correlations in adult birds may reflect small sample size rather than any genuine difference in the body size of the two age groups.

3.4. GENERAL DISCUSSION

The results discussed above correspond very closely with those of previous studies. Disappearance rates, patterns of feeder use, dispersal and biometrics all show similar patterns across age and sex classes. These conclusions are summarized below.

1) Disappearance rates decline with age, are generally higher in females than in males, and are not influenced by body size.

2) First-year birds tend to be attracted to artificial food sources both earlier in the season and earlier on a given day than adults.

3) Dispersal distances are generally over only a few hundreds of metres which results in a very restricted breeding season distribution of colour-ringed birds around the study site. Observations and recoveries of colour-ringed birds outside the study area indicate that some birds do undertake longer distance movements.

4) Males are significantly larger than females in three standard biometrics, but within sexes wing length is the only measure to change with age, being greater in adults. Body weight is significantly positively correlated with wing and tarsus length, especially in first-year birds and tends to increase over the course of the day. This diurnal weight change pattern only occurs at times of the year when food shortage has been suggested to be most acute, and rates of weight gain are greater in females than in males, being highest in harder winters.

The only differences between this population and others can be interpreted by reference to the mild winter weather conditions experienced during this study. These are summarized below.

1) Over the population as a whole, there is a female bias in captures of birds at artificial food sources; the reverse of the findings of a long-term Dutch study. This may reflect a higher availability of natural food which allows males to devote a greater proportion of their winter time budget to territorial activities, at the same time allowing socially subordinate females greater access to provided food.

2) Date of ringing is not related to the probability of a bird's return in a subsequent season. This suggests that winter weather conditions are not harsh enough to be a major agent of mortality or dispersal in this population. This conclusion is supported by data on the dispersal of colour-ringed birds from the site of ringing, which provide no evidence that winter conditions extend the radius of dispersal of colour-ringed birds beyond that expected after autumn juvenile dispersal.

3) Body weight analyses show no effect of current or preceding air temperatures. These data conflict with those of all other studies of

great tit body size, except those derived from exceptionally mild winters. The absence of a significant seasonal pattern of weight change also conflicts with the findings of previous studies. Its explanation probably lies in the extensive provision of artificial food in this study, as well as the mildness of winter weather conditions.

The general mildness of the winters during this study, with a low incidence of frost and snow cover as well as relatively high temperatures, is probably the most significant factor which distinguishes the ecology of this great tit population from those studied by others in western Europe. This difference may be of some importance in the interpretation of data presented in succeeding chapters and casual observations of flocking behaviour of tits at Ormiston Hall illustrate this point. Although activity at feeding stations involved the periodic passage of groups of tits through the site, followed by intervals of relative inactivity, it was rarely possible to find discrete flocks of tits moving in an integrated manner (Hinde 1952, pp. 15–16) in the surrounding woodland. Difficulty in discerning flocks or winter territories and in distinguishing flock members from 'floaters' has also been reported by Butts (1931), Desrochers & Hannon (1989), Odum (1942) and Smith & van Buskirk (1988) in black- capped chickadees, and by Saitou (1982) in great tits. In contrast, most other studies of great tits (e.g. Saitou 1978) and other parids (e.g. Condee 1967; Dixon 1965; Ekman 1979; Glase 1973; Hartzler 1970; Samson & Lewis 1979; Smith 1984) show evidence of winter flocks with stable membership, occupying discrete, non-overlapping home ranges. This sorting of the population into distinct social groups is especially marked in Ekman's (1979) study of willow tits *P. montanus* wintering in Sweden. In some species, these flock ranges have even been termed 'winter' or 'group' territories being defended either by the dominant male of the flock (e.g. Hartzler 1970 in the black-capped chickadee) or by all members of the group (e.g. Glase 1973 in the same species).

The mild winter and relatively abundant food throughout this study are probably at least partially responsible for the lack of flocking behaviour observed in tits. For example, Desrochers *et al* (1988) found that black- capped chickadee flocks became more clear-cut in years of high winter mortality and low food availability. However, in Smith &

van Buskirk's (1988) study of the same species, flocking behaviour remained indistinct even in very harsh winter conditions, and they suggested that this situation might be typical of years when the resident adult population was low or was swamped by large numbers of winter immigrants. As they pointed out, unstable flock structure may be relatively common in wintering parids but stability may vary with a variety of factors, including population structure and the availability of breeding habitat and food.

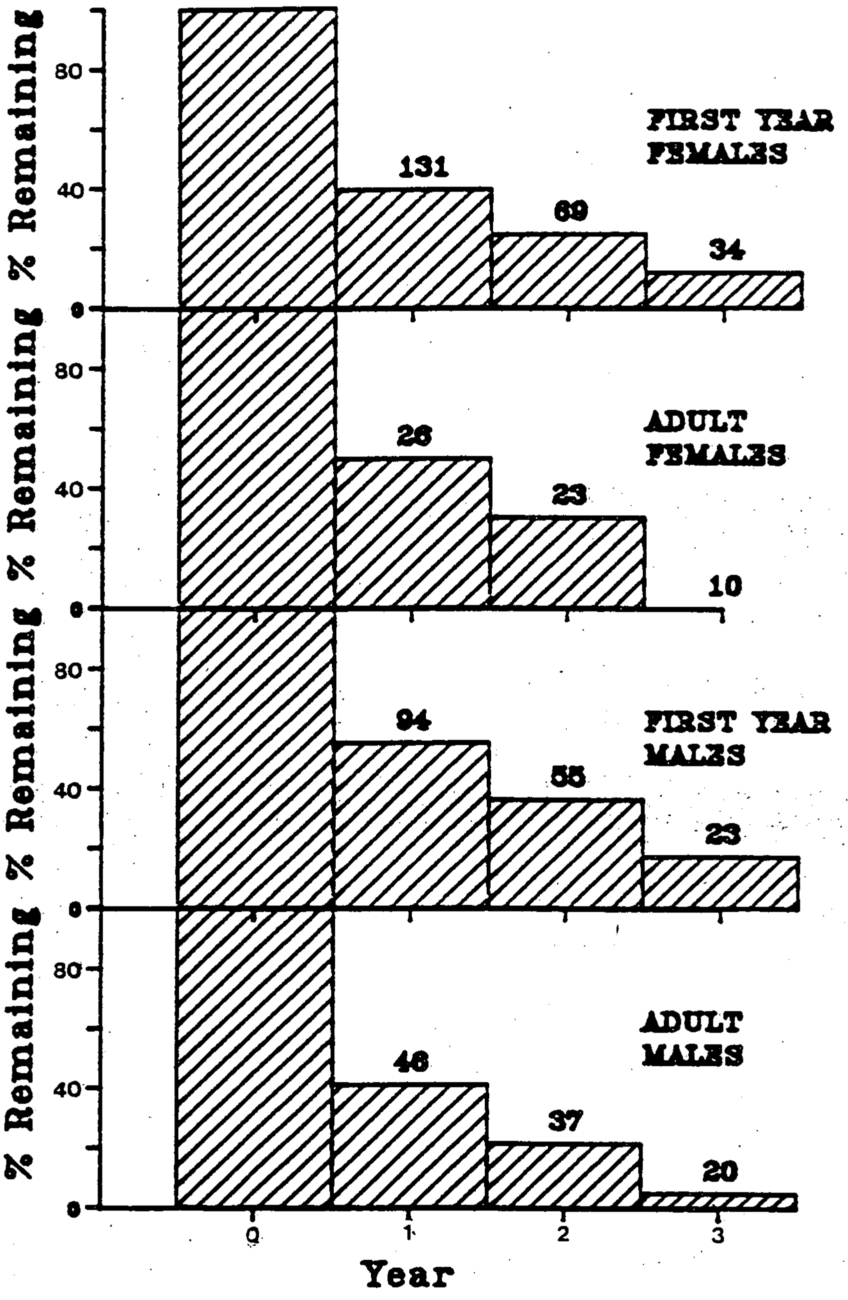


Fig. 3.1. Percentage of birds of each age-sex class surviving 1-3 years after ringing (Year 0). Sample sizes upon which percentages are based are annotated. For example, for Year 3 only birds ringed in 1985/86 provide a Year 0 cohort. For Year 1, the pooled total of birds ringed in 1985/86, 1986/87 and 1987/88 provides a Year 0 cohort.

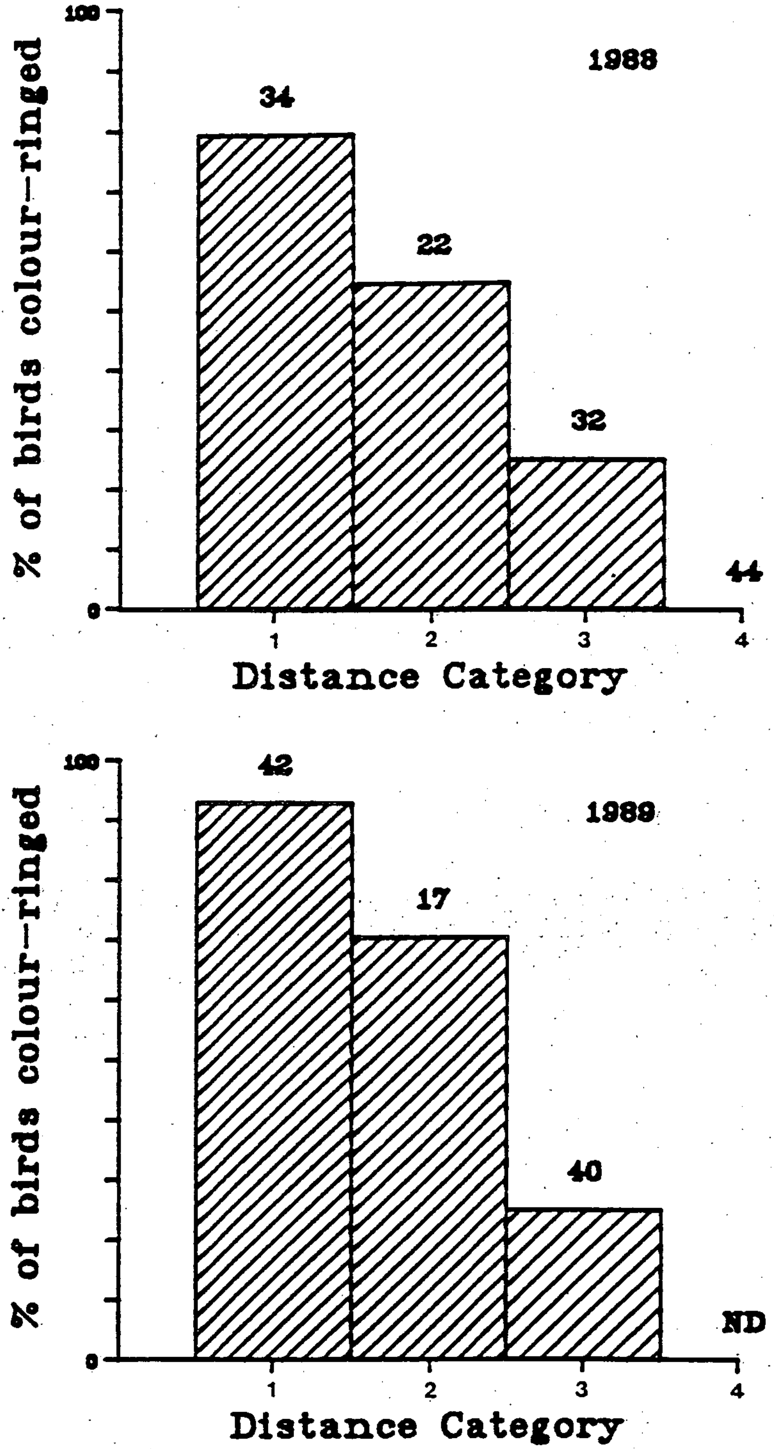


Fig. 3.2. Distribution of territorial, colour-ringed birds around the Garden in the 1988 and 1989 breeding seasons. Distance Category 1 = within 0-500m radius of the Garden. 2 = within 501-1000m. 3 = within 1001-2000m. 4 = over 2000m. Total sample of territorial great tits seen within each distance category is annotated.

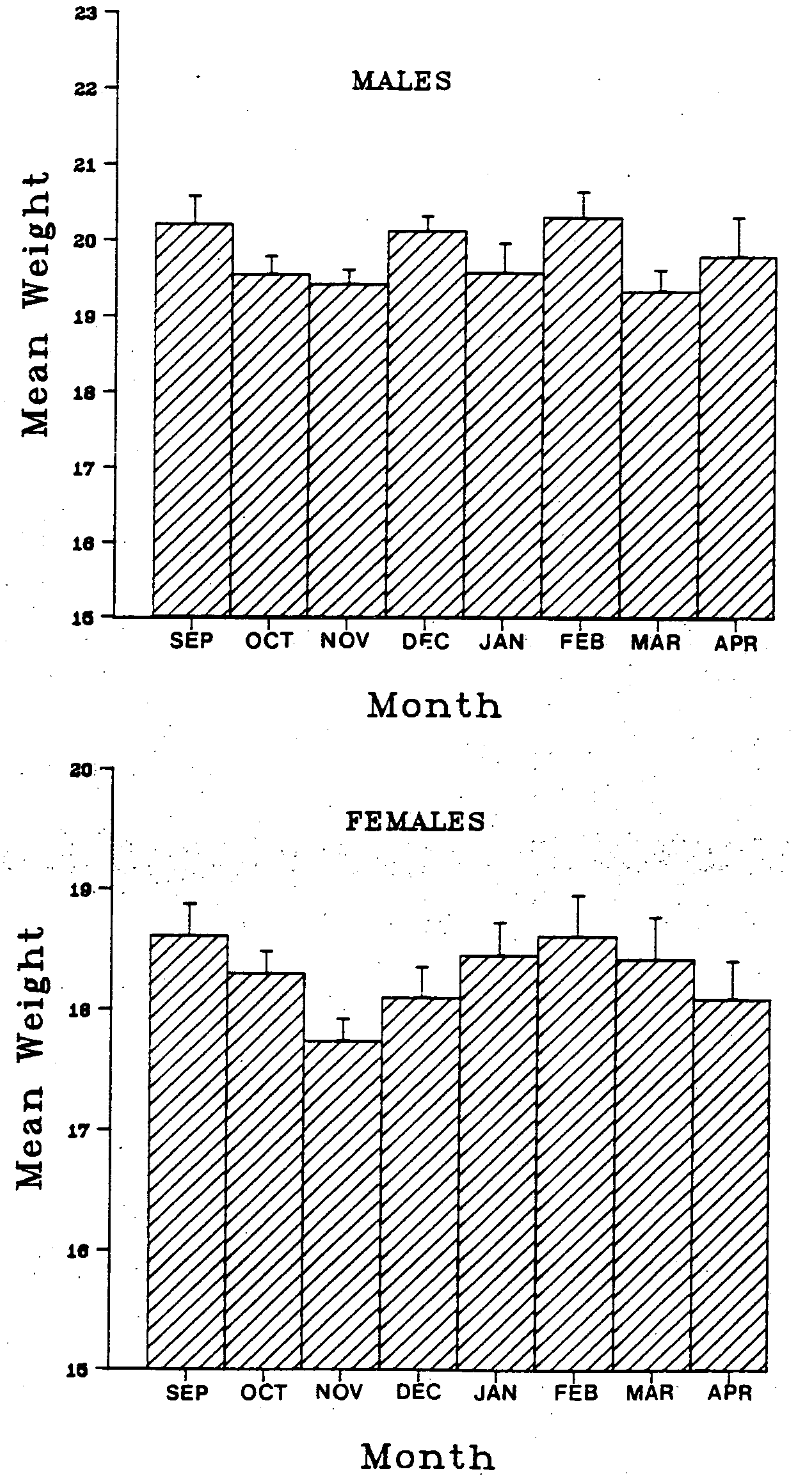


Fig. 3.3. Seasonal variation in mean weights of male and female great tits. Each month's sample includes all captures pooled over all three years. All weights are corrected to expected weight at 1200h for captures in those months where weight varied significantly with time of day. Error bars are 95% confidence limits.

	AM	FM	AF	FF	TOTAL	%ADULT	%MALE
1985/86	20 6.0	23 6.9	10 3.0	34 10.2	87 26.1	34.5	49.4
1986/87	17 1.5	32 2.9	13 1.2	35 3.1	97 8.7	30.9	50.5
1987/88	9 0.4	39 1.6	3 0.1	62 2.6	113 4.8	10.6	42.5
1988/89	11 0.1	58 0.6	18 0.2	66 0.7	153 1.7	19.0	45.1
TOTAL	57 0.4	152 1.2	44 0.3	197 1.5	450 3.4	22.4	46.4

TABLE 3.1. Distribution of initial captures of fully-grown great tits, classified by age-sex class and year of capture. AM = adult male, FM = first-year male, AF = adult female, FF = first-year female. These conventions are used hereafter. Each entry shows total captures (above) and total per 100 net-metre hours of effort (below). The final two columns show the age and sex ratios of newly captured birds in each year.

	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	TOTAL
AM	0	3	5	20	23	27	9	22	15	4	128
	0	0.3	0.3	0.9	1.2	3.5	0.8	1.9	1.0	0.3	1.0
FM	1	3	27	57	72	37	21	38	16	9	281
	0.3	0.3	1.7	2.6	3.8	4.7	1.8	3.2	1.1	0.6	2.2
AF	0	1	7	13	34	13	16	19	11	6	120
	0	0.1	0.4	0.6	1.8	1.7	1.4	1.6	0.8	0.4	0.9
FF	0	5	36	76	104	56	24	48	27	11	387
	0	0.6	2.3	3.5	5.5	7.2	2.1	4.1	1.8	0.7	3.0
TOTAL	1	12	75	166	233	133	70	127	69	30	916
	0.3	1.3	4.7	7.7	12.4	17.0	6.0	10.9	4.7	1.9	7.0
%MALE	-	-	42.7	46.4	40.8	48.1	42.9	47.2	44.9	43.3	44.7
%ADULT	-	-	16.0	19.9	24.4	30.1	35.7	32.3	37.7	33.3	27.1

TABLE 3.2. Distribution of total captures of fully-grown great tits classified by age-sex class and month of capture. Each entry shows total number of birds (above) and total per 100 net-metre hours of effort (below). Sex and age ratio of each month's total catch are given in the final two rows.

	1985/86	1986/87	1987/88	1988/89
AM	20	23	21	24
FM	23	32	39	58
AF	10	19	17	41
FF	34	35	62	66
TOTAL	87	109	139	189
%MALE	49.4	50.5	43.2	43.4
%ADULT	34.5	38.5	27.3	34.4
%F(M)	40.3	47.8	38.6	46.8
%A(M)	66.7	54.8	55.3	36.9

TABLE 3.3. Distribution of total number of captured individuals classified by year and age-sex class.
%F(M) = % of males in total first-year birds.
%A(M) = % of males in total adult birds.

YEAR OF RINGING	AGE-SEX CLASS	YEAR OF OBSERVATION/RECAPTURE			
		85/86	86/87	87/88	88/89
1985/86	AM	20	4(4)	1(1)	1(0)
	FM	23	13(4)	5(2)	4(0)
	AF	10	4(3)	2(3)	0(0)
	FF	34	12(5)	7(3)	4(1)
1986/87	AM		17	10(2)	7(1)
	FM		32	20(11)	15(5)
	AF		13	8(6)	7(4)
	FF		35	16(6)	10(5)
1987/88	AM			9	5(1)
	FM			39	19(6)
	AF			3	1(1)
	FF			62	24(12)
1988/89	AM				11
	FM				58
	AF				18
	FF				66
TOTAL RINGED POPULATION		87 (87)	130 (113)	182 (147)	250 (189)

TABLE 3.4. Survival rate of ringed great tits as estimated by observation and recapture (in parentheses), classified by year and age-sex class. The first column for each year gives the 'initial population' of birds first ringed in that year. The final two rows give the total colour-ringed population at the study site in each year, as estimated by observation and recapture (in parentheses).

	MEAN RINGING DATE		
	BIRDS REAPPEARING IN SUBSEQUENT SEASON	BIRDS DISAPPEARING	T-TEST
AM	176.1 19	161.0 27	$t = 1.06$ $p > 0.1$
FM	150.6 52	162.4 43	$t = 1.28$ $p > 0.1$
AF	176.2 13	164.6 13	$t = 0.63$ $p > 0.1$
FF	149.4 50	150.4 80	$t = 0.12$ $p > 0.1$

TABLE 3.5. Mean date of ringing (July 1 = 1) of birds which are observed in a subsequent season and those which are not, classified by age-sex class. The lower entry in each row gives sample sizes and significance level of t-test.

		MEAN SIZE	
		BIRDS REAPPEARING IN SUBSEQUENT SEASON	BIRDS DISAPPEARING
AM	a)	x=77.0, n=20	x=76.4, n=26
	b)	x=19.9, n=20	x=20.0, n=25
	c)	x=21.8, n=8	x=21.9, n=6
FM	a)	x=76.3, n=52	x=76.4, n=42
	b)	x=19.8, n=49	x=19.8, n=41
	c)	x=22.3, n=21	x=22.4, n=21
AF	a)	x=74.1, n=13	x=74.2, n=13
	b)	x=18.5, n=13	x=18.7, n=12
	c)	x=21.6, n=4	x=21.5, n=2
FF	a)	x=73.5, n=51	x=73.7, n=79
	b)	x=18.4, n=50	x=18.6, n=77
	c)	x=21.6, n=22	x=21.5, n=39

TABLE 3.6. Mean size at initial capture of birds which were observed in a subsequent season, and those which were not. Size estimated by three variables: a) wing length (mm), b) weight (g), c) tarsus length (mm). Birds classified by age-sex class. There are no statistically significant size differences between reappearing and disappearing birds of any age-sex class.

	NUMBER PRESENT IN YEAR n	NUMBER KNOWN TO BE ALIVE IN YEAR n+1
AM	99	52 (52.5%)
FM	94	52 (55.3%)
AF	75	43 (57.3%)
FF	131	52 (39.7%)

TABLE 3.7. Year-to-year survival rate of each age-sex class as estimated by observation. Cumulative data for 1985/86>1986/87, 1986/87>1987/88, 1987/88>1988/89. For example, a first-year female surviving from year 'n' to year 'n+1' is then classified as a year 'n' adult female.

AGE & SEX AT RINGING	DATE RINGED	DATE RECOVERED	TIME (days)	PLACE RECOVERED	DISTANCE (km)	DIRECTION
?M	NOV 85	NOV 85 (observed)	<30	Pathhead	4	SW
?M	?	NOV 88 (observed)	?	Peebles	32	SW
FF	17/4/88	23/5/88 (recovered)	36	Cousland	3.5	WNW
FM	13/11/85	27/2/87 (recovered)	472	Pencaitland	3	NE
FM	28/5/89 pullus	3/12/89 (controlled)	189	Oxenfoord Castle	3	W
(*)FM	14/2/88	27/2/88	13	Ormiston Hall	35	NE

TABLE 3.8. Recoveries and observations of colour-ringed great tits outside the study area. The record marked (*) refers to a bird ringed at Castlecraig, Blyth Bridge, Borders (55^{o} 42' N, 3^{o} 23' W) and colour-ringed at Ormiston Hall when controlled there 13 days later.

	MEAN+/-(SD)	SAMPLE SIZE	T-TEST
WING LENGTH(mm)			
AM	76.9(1.56)	86	3.43
FM	76.2(1.30)	153	p=0.0008
AF	74.1(1.43)	86	3.53
FF	73.4(1.40)	196	p=0.0005
ALL MALES	76.5(1.44)	239	22.82
ALL FEMALES	73.6(1.44)	282	p<0.0001
TARSUS LENGTH(mm)			
AM	21.9(0.63)	52	1.07
FM	22.0(0.58)	104	p=0.29
AF	21.1(0.65)	60	1.59
FF	21.2(0.66)	135	p=0.12
ALL MALES	22.0(0.60)	156	11.96
ALL FEMALES	21.2(0.66)	195	p<0.0001
WEIGHT(g)			
AM	19.9(1.08)	126	0.60
FM	19.8(0.88)	277	p=0.55
AF	18.4(0.82)	119	0.12
FF	18.4(0.94)	380	p=0.91
ALL MALES	19.8(0.95)	403	23.83
ALL FEMALES	18.4(0.91)	499	p<0.0001

TABLE 3.9. Mean sizes of age and sex classes of colour-ringed great tits. For wing length and tarsus length, each datum is the mean of all captures of a bird in one season. For weight, each capture is treated as an independent datum. All three biometrics are normally distributed.

MEASURE	SAMPLE SIZE	r	r^2
WING LENGTH	385	0.883	77.9%
TARSUS LENGTH	289	0.797	63.6%
WEIGHT	380	0.727	52.9%

TABLE 3.10. Repeatabilities of body size measures given by Pearson product-moment correlation coefficients of measurements from pairs of captures within one season. Age-sex classes combined.

MEASURE	SAMPLE SIZE	r	p
WING LENGTH	385	-0.115	<0.05
TARSUS LENGTH	289	-0.222	<0.01
WEIGHT	380	-0.103	0.05

TABLE 3.11. Relationship between degree of change and within-season inter-capture interval for three measures of body size. Age-sex classes combined.

	SIGNIFICANCE OF REGRESSION COEFFICIENTS			
	AM (n=72)	FM (n=196)	AF (n=85)	FF (n=273)
WING LENGTH	t=2.45 $p<0.05$	t=3.16 $p<0.01$	t=3.24 $p<0.01$	t=5.94 $p<0.001$
TARSUS LENGTH	t=2.60 $p<0.05$	t=3.22 $p<0.01$	t=2.77 $p<0.01$	t=5.41 $p<0.001$
TIME OF DAY	t=0.92 p=NS	t=2.22 $p<0.05$	t=2.11 $p<0.05$	t=5.09 $p<0.001$
"MINTEMP1"	t=0.52 p=NS	t=0.34 p=NS	t=0.83 p=NS	t=0.32 p=NS
"MINTEMP5"	t=0.17 p=NS	t=0.15 p=NS	t=1.91 p=NS	t=0.65 p=NS
"MEANTEMP"	t=0.77 p=NS	t=0.70 p=NS	t=0.50 p=NS	t=0.09 p=NS
"MEANTEMP5"	t=0.60 p=NS	t=0.01 p=NS	t=1.37 p=NS	t=0.16 p=NS
R^2	23.7%	15.3%	27.7%	32.4%

TABLE 3.12. Multiple linear regression of body weight on seven dependent variables in each age-sex class. Entries show t-value and significance of regression coefficients. R^2 = coefficient of determination (i.e. % of variation in body weight that is accounted for by variation in the specified independent variables.
"MINTEMP1" = minimum temperature in previous 24 hours.
"MINTEMP5" = mean minimum temperature of previous five days.
"MEANTEMP" = mean temperature on day of capture.
"MEANTEMP5" = mean temperature of previous five days.

	LINEAR REGRESSION EQUATION OF WEIGHT(Y) ON TIME OF CAPTURE(X)	SIGNIFICANCE
MALES		
1985/86	$y=18.0+0.00363x$ (n=64)	$t=3.87$, $p<0.001$
1986/87	$y=17.0+0.00373x$ (n=76)	$t=2.78$, $p<0.01$
1987/88	$y=20.2-0.000262x$ (n=83)	$t=0.35$, p=NS
1988/89	$y=19.2+0.000813x$ (n=179)	$t=1.63$, p=NS
POOLED	$y=18.9+0.00140x$ (n=402)	$t=3.58$, $p<0.001$
FEMALES		
1985/86	$y=15.7+0.00475x$ (n=54)	$t=5.16$, $p<0.001$
1986/87	$y=15.9+0.00374x$ (n=85)	$t=2.84$, $p<0.01$
1987/88	$y=17.4+0.00191x$ (n=130)	$t=3.03$, $p<0.01$
1988/89	$y=17.4+0.00126x$ (n=226)	$t=2.75$, $p<0.01$
POOLED	$y=17.0+0.00214x$ (n=498)	$t=6.17$, $p<0.001$

TABLE 3.13. Relationship between weight (g) and time of capture (minutes after 0000) in male and female great tits in each year.

	LINEAR REGRESSION EQUATION OF WEIGHT(Y) ON TIME OF CAPTURE(X)	SIGNIFICANCE
MALES		
SEP	$y=20.2+0.00004x$ (n=29)	$t=0.02$, p=NS
OCT	$y=18.6+0.00178x$ (n=75)	$t=2.59$, $p=0.01$
NOV	$y=18.1+0.00243x$ (n=92)	$t=2.64$, $p=0.01$
DEC	$y=20.3-0.00034x$ (n=61)	$t=0.29$, p=NS
JAN	$y=19.2+0.00053x$ (n=29)	$t=0.23$, p=NS
FEB	$y=17.4+0.00400x$ (n=59)	$t=3.25$, $p=0.002$
MAR	$y=19.9-0.00075x$ (n=30)	$t=0.55$, p=NS
APR	$y=17.5+0.00351x$ (n=12)	$t=1.62$, p=NS
FEMALES		
SEP	$y=17.2+0.00274x$ (n=42)	$t=1.92$, p=NS
OCT	$y=18.2+0.00016x$ (n=87)	$t=0.24$, p=NS
NOV	$y=15.6+0.00409x$ (n=134)	$t=5.02$, $p<0.001$
DEC	$y=15.7+0.00408x$ (n=66)	$t=3.02$, $p<0.01$
JAN	$y=16.5+0.00284x$ (n=39)	$t=1.43$ p=NS
FEB	$y=14.8+0.00547x$ (n=64)	$t=5.51$, $p<0.001$
MAR	$y=16.9+0.00218x$ (n=37)	$t=1.42$, p=NS
APR	$y=18.7-0.00092x$ (n=16)	$t=0.64$, p=NS

TABLE 3.14. Relationship between weight(g) and time of capture (minutes after 0000) for male and female great tits in each month for all years pooled.

	MALES	FEMALES
1985/86	7.6	10.8
1986/87	8.2	8.7
1987/88	-	4.3
1988/89	-	2.9
POOLED	3.0	4.9
OCT	3.8	-
NOV	5.2	9.6
DEC	-	9.5
FEB	8.5	12.8

(regression equations for all other months were not statistically significant)

TABLE 3.15. Estimated % weight gain of male and female great tits between 0930 and 1630, calculated from statistically significant regression equations in Tables 3.13. and 3.14.

	AM	FM	AF	FF
WING LENGTH/WEIGHT	r=0.283 n=86 p<0.01	r=0.326 n=150 p<0.001	r=0.249 n=87 p<0.05	r=0.304 n=195 p<0.01
WING LENGTH/TARSUS LENGTH	r=0.177 n=49 p=NS	r=0.261 n=99 p<0.01	r=0.162 n=60 p=NS	r=0.320 n=126 p<0.001
TARSUS LENGTH/WEIGHT	r=0.281 n=49 p<0.05	r=0.279 n=99 p<0.01	r=0.276 n=60 p<0.05	r=0.418 n=126 p<0.001

TABLE 3.16. Pearson product-moment correlation coefficients for the relationships between all three biometric variables in each age-sex class. Wing length and tarsus length are expressed as the mean of all captures of each bird within one season. All seasons pooled. Weight is expressed in the same way but with weights corrected to expected weight at midday for captures in those months where body weight was significantly correlated with time of day (Table 3.14.).

CHAPTER 4.

CORRELATES OF SOCIAL DOMINANCE.

4.1. GENERAL INTRODUCTION

4.1.1. The Concept of Dominance and Subordination

A basic task in studies of competitive social organization has been the assignment of the roles 'dominant' and 'subordinate' to animals engaged in dyadic competition over resources. Inevitably, this procedure is to some extent subjective and an initial problem is to define criteria which allow the assignment of dominance and subordination in a way that is functionally relevant (e.g. Richards 1974). For example, it would be possible to make this assignment to dyads of competing great tits on the basis of either degree of aggression shown, or eventual priority of access to the resource under competition (Syme 1974). Although intuition might suggest that the results of these two approaches would be highly correlated, this is not always the case (Bernstein 1981; Francis 1987; Syme 1974), so how do we choose between alternatives ?

Attributes which allow an animal to establish dominance over another individual can only be selected for if fitness benefits accrue to dominant members of dyads (Bernstein 1981) or if dominance and subordination are behavioural 'strategies' which can be maintained polymorphically in populations by frequency-dependent selection (Maynard Smith 1982; Rohwer & Ewald 1981). At a proximate level, fitness benefit is usually equated with priority of access to resources, so that the establishment of dominance over a conspecific increases fitness by definition. This correlation has been demonstrated empirically many times (e.g. Baker 1978; Banks *et al* 1979; Eden 1989; Ekman 1987; Ekman & Askenmo 1984; Geist 1971; Kikkawa 1980a,b; Lamprecht 1986a; Robinson 1986; Wiley 1973) and is one of the few points of consensus in theories of social dominance. Often, the mere fact that animals are seen to *compete* for access to a resource is used to justify the assumption that dominance, as abstracted from observation of that competition, is a biologically significant, fitness-related quantity. The resource may be any commodity, physical or social, gained immediately or after a time lag, that increases fitness (e.g. food, mates, territory).

A final point to be established is the difference between a dominant – subordinate 'asymmetry' and a dominant – subordinate 'relationship'. The former may be identifiable in a single dyadic interaction on the basis of who gains priority of access to the resource concerned. The latter develops over the course of time and repeated encounters between two particular individuals, and is characterized by predictability of outcome based on previous experience and individual recognition, and the immediate adoption of dominant and subordinate roles without escalated contest (e.g. Glase 1973). Selection pressures for the development of a dominant – subordinate relationship from an initial asymmetry might include savings in time, energy and risk of injury for both dominant and subordinate (Kaufmann 1983). This important distinction is made by Bernstein (1981) and is crucial to the studies of correlates and determinants of dominance in Chapter 4.2.

4.1.2. Introduction to the Study

This chapter uses the operational criterion of priority of access to resources to assign dominance and subordination to great tits involved in dyadic competition over resources (Chapter 2). In most cases, that resource was the food provided at the feeding stations. However, some competitive interactions were observed in which food was not the apparent goal resource. In these cases, there was evidence (Chapter 6) that the birds were competing over the control of territorial space. Hereafter, the terms 'dominant' and 'subordinate' refer to the roles adopted by two birds in respect of a particular dyadic encounter or a longer term dominant – subordinate relationship. Similarly, the corresponding abstract nouns 'dominance' and 'subordination' will be used to express the relational attribute possessed by each member of the dyad.

Chapter 4.2. investigates the importance of various physical, social and experiential attributes of great tits as correlates of dominance in dyadic competition, as a basis for the study of the function of display elements in Chapters 6 & 7. The possible development of dominant – subordinate relationships is also investigated as evidence bearing on the question of whether individual recognition develops in winter populations of great tits.

Chapter 4.3. expands the concept of dominance and subordination in individual dyads to that of dominance hierarchies and social status within the population as a whole. The value of dominance hierarchies and social status indices is explored in relation to the fitness consequences of dominance and high status, and the pinpointing of determinants of dyadic dominance as begun in Chapter 4.2.

Chapter 4.4. introduces location as a variable that is of considerable importance in determining dominance and social status in other great tit populations (Drent 1983). Its importance in the Ormiston Hall population is investigated and the relationship between site-related dominance and territoriality is discussed. For comparison, the attributes studied in Chapter 4.2. are also analysed as correlates of territorial status.

Chapter 4.5. provides an overall discussion of social organization in the Ormiston Hall great tit population as an introduction to the analyses of display function in Chapters 6 & 7. Social structure in this population is also compared with the results of studies of other tits.

4.2. CORRELATES OF DOMINANCE IN INTERACTIONS

4.2.1. Introduction

There is a large literature pertaining to social dominance and its determinants across a variety of animal taxa (e.g Allee 1942; Gauthreaux 1978). A brief scan of literature restricted to birds revealed 62 papers explicitly stating the success or failure of at least one of seven variables in either predicting the outcome of dyadic encounters or correlating with an index of social status. Many techniques have been used to create an index of an individual's overall degree of dominance across all dyads (e.g. Boyd & Silk 1983). This process is discussed later but could be summarized as the measurement of the probability that an individual will be dominant in its next interaction with an opponent 'selected' randomly from the population. The seven variables considered by these papers were size (as measured by wing length, tarsus length or body weight), age, sex, territorial status, prior residence, prior agonistic experience and aggressiveness. Table 4.1. shows the proportion of studies considering each variable that found it to be a significant correlate of dominance. No distinction is made with respect to the *direction* of these correlations. It should be emphasized that in some cases it was not clear whether inter-dependence between variables (e.g. age/size, sex/size) had been controlled for in presenting conclusions as to their relative importance.

Across the studies (mainly of passerines), social and experiential variables, and sex, are more consistent correlates of dominance than are physical attributes. It is also noteworthy that aggressiveness (measured by either frequency or intensity of overt aggression) is a relatively poor correlate of social status, as also noted by Francis (1987). A selection of studies best demonstrating the importance of each of these seven variables as dominance correlates is listed in Table 4.2. An aviary study by Popp (1987b) which found that changing hunger levels were capable of reversing dominant – subordinate asymmetries in dyads of captive American Goldfinches *Carduelis tristis* emphasizes that more rapidly varying factors might also be influential.

In this study, sex, age, body size (as measured by wing length, tarsus length and weight), territorial status, site familiarity and aggressiveness are all taken into account.

4.2.2. Methods

4.2.2.1 Summary

For each dyadic interaction, dominance and subordination are assigned to the two birds according to the criteria described in Chapter 2.4. For each dyad, the total number of interactions recorded over the course of a season (Sep-Apr) is summed to yield an overall outcome, and the bird dominant in the majority of interactions is considered the dominant member of the dyad. Dyads where each bird was dominant on the same number of occasions are excluded from further analysis. For each potential dominance-correlated attribute, this data set is categorized according to whether the attribute is positively or negatively related to outcome. (e.g. number of dyads in which longer-winged bird dominant versus number in which shorter-winged bird dominant). Chi-square tests are used to compare the categorized data with the random expectation of 50% of dyads falling into each category. In this study, the male bird was dominant in 97% of intersexual interactions ($n = 1865$) comprising several hundred dyads. Sex and correlated physical asymmetries are therefore considered to be the main asymmetries determining the outcome of dyadic interactions, and all analyses are carried out independently on the two intrasexual data sets. Initial analyses are carried out on the overall data set for each year, without controlling for site of observation, goal resource, resource ownership, behaviour or environmental conditions. Subsequent analyses take into account these factors where appropriate. One such factor is prior familiarity between opponents. If individual recognition exists then we might expect to find a consistent effect of repeated encounter on the importance of certain attributes as correlates of dominance. For example, as two birds become more familiar with each other then a predictable dominance relationship may develop based on mutual experience rather than on simple external cues such as size or plumage. In order to investigate the possible influence of repeated encounter on the factors determining the outcome of dyadic interactions, a measure of pairwise association was developed as an index of mutual familiarity.

The chosen association index was the Coherence Index (Ekman 1979) or Twice-Weight Index (Cairns & Schwager 1987) which is given by

$$T_t / (T_a + T_b + T_t)$$

where T_t is the number of observations of individuals A and B in the same group, T_a is the number of observations of A without B, and T_b is the number of observations of B without A. Both this and the Half-Weight Index,

$$T_t / (0.5(n_a + n_b))$$

where n_a is the total number of observations of A and n_b is the total number of observations of B (Ficken *et al* 1981) may give biased results. This happens if the probability of observing individuals A and B is not independent of whether or not they occur in the same group (spatial proximity) or time unit (temporal association). Specifically, if animals A and B are more likely to be observed when together than when apart, the Twice-Weight Index is more accurate because it reduces the weight of associated observations. If the pair are more likely to be observed when in separate spatial or temporal groups then the Half-Weight Index is more appropriate because it reduces the weight of independent observations. Both indices are simple modifications of Dice's (1945) measure of association ($T_t/(n_a + n_b)$) (Cairns & Schwager 1987). In this study, the main objective of field observation sessions was to record the occurrence and outcome of social interactions. Consequently, associated birds were probably more likely to be identified than lone individuals simply because of their propensity for social interaction. Any observer error was therefore most likely to be failure to record occurrences, alone, of one member of an AB pair. This led to the choice of the Twice-Weight Index as the most appropriate association index for this study.

The ideal data collection technique would have been to record the precise times of arrival and departure of every great tit visiting a feeder site during an observation session and to enter every visit thus scored for each member of a dyad in the Twice-Weight Index formula. However, because the observer's attention was directed primarily at the scoring of social interaction, this quality of data was impossible to collect. Instead, the chosen unit of occurrence at a feeder site was the 'observation day'. Thus T_t is the number of observation days on which both A and B were recorded. As a unit, the observation day is crude but reasonably consistent since most sessions were between 120 and 180 minutes in duration. Such a coarse definition of association will tend to create spuriously high association indices but is objective. Any finer division of observation days into, for example, 5-minute or 30-minute groupings proved impracticable due to the quantities of data generated. In any case, the turnover of great tits at the feeding stations was high (Appendix 4) and suggested considerable movement and mixing of birds within the immediate area. This fairly rapid movement of flocking great tits was also noted by Hinde (1952) who recorded average speeds of 85-150 metres per hour during autumn and winter mornings, the time during which most observation sessions in this study were carried out. In this context it seems reasonable to suppose that many of the birds recorded at a feeding station during an observation session would have made social contact during that time. As a measure of mutual familiarity, the chosen association index and unit of occurrence may therefore be appropriate. With reference to the use of "percentage of observation days on which a bird was observed" as a measure of frequency of occurrence at a site, it is worth noting that Oberski (1989) found very strong positive correlations (r_S always > 0.900) between this and an alternative measure ("percentage of 5-minute observation periods in which observed") for both sexes at the Yew and Wood sites in 1988/89. His analyses are reproduced in Appendix 5 and provide some justification for the use of the chosen measure as an index of frequency of occurrence at a given site.

4.2.2.2. Justification

Two analytical procedures fundamental to this chapter need justification. Firstly, there is the adoption of a 'majority of wins' criterion for assigning an overall dominant - subordinate asymmetry to a dyad. Secondly, the use of a dyad-by-dyad approach to the analysis of dominance correlates differs from the usual practice of ranking individuals on the basis of a dominance index calculated from all the dyadic interactions of each animal. The rank assigned to each individual is then used as an ordinally scaling attribute whose relationship with possible dominance correlates can be tested using either univariate or multivariate correlation statistics.

If individuals A and B interact 15 times over a specified period and A is dominant on all 15 occasions, it is more reasonable to state that A is the overall dominant of that dyad than if A was dominant on eight and B on seven occasions. The problem is that the point at which one chooses to abandon a dyad as inconclusive is arbitrary. In their study of white-throated sparrows *Zonotrichia albicollis*, Piper & Wiley (1989) excluded dyads where the 'dominant' bird won less than 75% of the interactions. This problem is particularly important with respect to studies of avian social organization where the social groups may not be so rigid, nor repeated encounters so frequent that dyadic dominance relationships become completely fixed (i.e. dominance relationships tend to be of the 'peck- dominance' type - Allee 1942; Masure & Allee 1934).

This contrasts with many mammalian (e.g. primate) societies (e.g. Dunbar 1988; Harcourt & Stewart 1987) where the members of social groups remain together almost continuously and interact so frequently that dyadic dominance relationships become completely predictable (i.e. 'peck-right' - Schjelderup-Ebbe 1935). These points are discussed in more detail in Chapters 4.3. and 4.4. A second problem is that dominance is sampled by only one observation in a very high proportion of dyads (males 51.5%, n=515; females 59.2%, n=250 in this study in 1988/89; 39% of 4107 dyads in Piper & Wiley's study). It is therefore important to demonstrate that a single, sampled interaction is representative of the true dominant - subordinate asymmetry in that dyad. Fig. 4.1. divides the total number of dyads for which interactions were recorded in 1988/89, according to the number of interactions observed (n_i). This is plotted against 'mean percentage of interactions won by the overall dominant' as a measure of the overall dominant - subordinate asymmetry in dyads of various n_i. This varies from 50%, if there is no overall asymmetry in any dyad, to 100% if all interactions have the same outcome in every dyad. Line X shows the relationship expected if the outcome of any interaction is random with a 50% probability of dominance for each individual. This represents a binomial distribution of overall outcome for each n_i which is asymptotic to 50% on the y-axis. Sample sizes (number of dyads) are annotated. For each n_i, the difference between the observed overall proportion of wins by overall dominants and random expectation (line Z) was tested for significance. Binomial tests gave $p<0.00001$ in all cases and support the hypothesis that an observed dominant - subordinate asymmetry is real for any $n_i > 1$. For this reason I have accepted the 'majority of wins' criterion for assigning the direction of dominance to a dyad, though noting that slightly asymmetric overall results (e.g. 3-2, 4-3) become more unreliable as n_i increases. I have also included single observation dyads in further analyses since Fig. 4.1. suggests that a single, randomly chosen interaction correctly predicts the overall dominant - subordinate asymmetry in a dyad in at least 78% of cases (females, $n_i = 5$) and as many as 97% of cases (males, $n_i > 11$).

The use of a dyad-by-dyad approach to the analysis of dominance correlates is exemplified by the studies of Balph *et al* (1979) on dark-eyed juncos *Junco hyemalis*, Harper *et al* (in press) on great tits, and Roberts & Searcy (1988) on red-winged blackbirds *Agelaius phoeniceus*. Although the technique is limited in that it does not lend itself to the multivariate analysis of several possible correlates simultaneously, it is logically preferable to the creation of a dominance index or rank as an attribute of each individual. The validity of assigning ranks is discussed in Chapter 4.3. but the basic problem is that the process involves the *assumption* that there is higher order social organization above the level of dyadic relationships. If this is not the case then social organization is no more than a set of independent dyadic relationships and rank is an artificial attribute with no biological reality. In other words, we could not expect a top dominant individual (rank 1) to distinguish between animals occupying ranks 3 and 30. It is simply dominant to both.

A difficult problem in the investigation of social interactions is ensuring that data points are statistically independent (Martin & Bateson 1986). Whenever animals are ranked according to social status, the ranks attributed to individuals are based on index values that cannot be independent because they are derived from social interactions between the individuals concerned. Similarly, in a dyad-by-dyad approach, to treat each interaction as an independent event would be to commit the pooling fallacy (Machlis *et al* 1985) since many interactions are between the same individuals and, moreover, may occur in rapid sequence so that there is also dependency in time. At the other extreme is to accept only the overall outcomes of dyads, neither of whose members occur in any other dyad in the final data set. This circumvents all problems of the repeated sampling of individuals but leaves no objective criterion for deciding which one of the dyads A-B, A-C and A-D should be included and which two excluded. The intermediate solution is to use the overall outcomes of all different dyads (*sensu* 'pairwise combinations'). This avoids repeated sampling of the same pairs of birds but does mean that any one individual may be sampled repeatedly as it interacts with different opponents. Nonetheless, the *interactional* element of each dyad *is* independent of all others because no one pair is ever sampled more than once. Since it is the causal influences on social interaction that are being studied, I consider that this approach meets the requirements of statistical independence and use it in preference to the assignment of dominance ranks for the logical reasons discussed above.

4.2.3. Results

Table 4.3. presents the raw data set showing the correlation between three independent measures of body size, and dyadic dominance for both sexes in each year. Interactions from all sites and all contexts (e.g. interactions at food versus those not at food and, in the case of interactions at food, occupant of feeder versus intruder) are pooled to give the overall outcome for each dyad. Because body size has already been shown to be age-related (Table 3.9), only dyads involving birds of the same age are included in this initial analysis. At this level of analysis, body size is unrelated to dominance in male dyads. In female dyads body size, as measured by tarsus length and body weight, is weakly but significantly related to dominance with larger birds tending to dominate smaller birds. The only significant difference between the sexes is that weight is a significantly better positive correlate of dominance in females than in males ($X^2 = 7.43$, df = 1, $p < 0.01$).

Table 4.4a. presents the same analysis for two experiential variables – age and prior territoriality. The latter is categorized as possession or non-possession of a breeding territory in the previous breeding season, in males, and as pairing with or not pairing with a territory holding male in the previous breeding season, in females. Analysis is based on the same data sets as Table 4.3., using all dyads where the two birds differ in either of these attributes. Body size is not controlled for due to its apparently marginal significance in affecting dominant – subordinate asymmetries. Clearly, age and prior territoriality are inevitably highly correlated because first-year birds cannot have had prior territorial experience. The results show a strong tendency for older/previously territorial males to be dominant over younger birds or those without prior territorial experience. The same relationship also exists in females but seems to be dependent on prior territorial experience rather than age *per se* . Accordingly, older males are significantly more likely to be dominant to younger males than older females are to be dominant to younger females ($X^2 = 3.86$, df = 1, $p = 0.05$). This effect is explored further in Table 4.4b. where the relationship between age difference and dominance is re-analysed using only dyads of first-year birds, which can have had no previous territorial experience. Again, all contexts and sites are pooled to give overall outcomes. The results show considerable between-year variation in both sexes (males: $X^2 = 10.69$, df = 1, $p < 0.01$, females: $X^2 = 8.70$, df = 1, $p < 0.01$). The pooled data set shows that there is no consistent, direct effect of age on dyadic dominance in either sex, but that the prior residence and territorial experience of some older birds is a strong positive correlate of dominance in both sexes.

The importance of prior territoriality as a correlate of dominance in birds surviving to their second winter is clear, and is also documented by Drent (1983) in a Dutch population. However, both Drent and Kikkawa (1980b) found that social status was also related to prior residence on a much finer scale, with status decreasing in the following order amongst first-year birds: early-hatched local birds > late-hatched local birds > early immigrants during post-juvenile dispersal > later immigrants. Table 4.4c. investigates this possibility in the Ormiston Hall population by treating date of ringing as an index of date of arrival in the local population. Thus, many of the first-year birds ringed in September or earlier were probably born locally, whilst those ringed later in the season are assumed to represent progressively later immigrants to the population. Since this approximation can only produce misleadingly short estimates of a bird's prior residence in the population, any errors will have only conservative effects on this analysis. Again, all contexts have been pooled to give overall outcomes for dyads but in this case, the three sites are treated as independent data sets before pooling in order to generate adequate sample sizes. This has the consequence that a given dyad may be represented more than once in one year's pooled total. The results show that, in first-year males, length of prior residence is a strong, positive correlate of dominance. Amongst females, the same relationship exists but is much weaker.

Prior residence and territoriality are evidently important dominance correlates in this great tit population, especially amongst males. The following analyses explore further the contrastingly weak correlations between body size and dominance. A particular problem with the initial analyses in Table 4.3. is that they may be influenced by opposing effects of body size or weight in different contexts such as season, resource type and value, prior experience of opponent and so on. For example, one scenario might be that an effect of body size on the outcome of agonistic interactions early in the season is gradually nullified as increasing asymmetries in prior residence and the development of individual relationships and territoriality become of overriding importance. The following analyses do not seek to test specifically this and alternative scenarios as working hypotheses. Rather, they simply test the null hypothesis – so far supported – that size and weight are of no importance in any intraspecific, competitive situation in which great tits find themselves. With the exception of Table 4.4c, analyses so far have pooled interactions from Garden, Yew and Wood to give overall outcomes for each dyad. This has advantages in terms of both sample size and avoidance of recurrence of the same dyad in a single sample. However, if site-related dominance is as much a feature of this population as it is of others (Brian 1949; De Laet 1984; Drent 1983; Saitou 1979b), then pooling of interactions from different observation sites is misleading because dominant – subordinate asymmetries are only meaningful with respect to a particular locality. Clearly, if site-related dominance is prevalent in this population, the likelihood of relatively fixed attributes such as body size and plumage being important determinants of social status is reduced. However, without pre-empting the study of site-related dominance in Chapter 4.4, the following analyses are restricted to overall dyad outcomes recorded at a single site – the Garden – in order to avoid repeated sampling of dyads.

Tables 4.5a. (males) and 4.5b. (females) compare the correlation of the three body size measures with dyadic dominance, across the following contexts:

i) interactions over food in which the 'intruding' bird was dominant,

ii) interactions over food in which the 'occupying' bird was dominant,

iii) interactions away from food which are assumed to reflect competition over territorial space (Chapter 6).

Interactions in each of these contexts were separated to give three independent data sets. In view of results presented above, age differences were not controlled for. The results show no significant deviations from null expectation in males, in any context, and there are no significant differences between contexts. In females, body weight is a weak, positive correlate of dominance in interactions at food, but only where the intruding bird is dominant. Approximately the same proportion of dyads are won by the heavier bird in interactions away from food, but the sample sizes are too small for statistical significance. As with males, there are no significant differences between contexts.

Table 4.6. introduces date (from October 1) as a potential positively covarying index of mutual familiarity and territoriality in the population. Here, the contextual variable is continuously distributed so, in this analysis, each interaction is treated as an independent datum. The results show a scattering of weak, marginally significant, negative correlations between date and the dominant-minus-subordinate size difference. This suggests that a very weak tendency for larger birds to dominate earlier in the season disappears during the winter, perhaps as experiential factors become more important. There is no consistent evidence of a change in the absolute physical asymmetry of interacting birds over the course of the winter.

Table 4.7. uses interaction rate (number of interactions per hour) on the day of observation as an index of the value of the provided food resource to the great tits. The hypothesis here is that physical characteristics may only be of importance in conditions where resources (in this case, food) are at a premium and physical strength in escalated encounters is required to achieve dominance. Again, each interaction is treated independently in this analysis. The results provide no evidence of such an effect, despite the fact that interaction rates varied over a wide range, from less than 1 per hour to over 1 per minute. The use of interaction rate as an index of resource value depends upon the assumption that the condition of birds visiting the feeders is random with respect to interaction rate. For example, if the

few birds visiting the feeder on days of low interaction rate are simply those in poorest condition, then it may be that resource value is always high, *from the point of view of those birds that do visit the feeders*. In another population of great tits, Gosler (pers. comm.) has found that social status is a relatively good index of physical condition. At one end of the spectrum, dominant males have a high pectoral muscle mass and carry relatively little extra weight in the form of fat as an energy reserve. At the other extreme, juvenile females show high fat scores with some showing evidence of metabolism of pectoral muscle as an energy source, a sign of severe energy deficit. The results in Table 4.7a. correlate the social status of birds interacting at the Garden feeders with interaction rate on the day of observation, in 1986/87 and 1988/89. The mostly negative correlations in female data sets imply that, if anything, subordinate birds do tend to visit the feeders on days when interaction rates are low, but that the reverse is the case for males. The conclusion is that poor condition, subordinate females may be the first to visit artificial food sources and that it may be the increased use of artificial food by juvenile males that is largely the cause of 'high interaction rate' days. Consequently, interaction rate may be viewed as quite a good index of resource value with respect to male-male interactions, but is less realistic for those between females.

Tables 4.8. and 4.9. use two measures of repeated encounter - number of interactions comprising overall dyad outcome, and the Twice-Weight Index - as estimates of the degree of mutual familiarity between dyad members. As discussed above, one hypothesis here is that if individual recognition does develop between birds as a consequence of repeated encounter then simple external cues such as size or plumage might be expected to be superseded as determinants of dominance by the more detailed information gained during previous encounters. The percentage values in Table 4.8. do suggest that larger males become less likely to be dominant as encounter frequency increases, and that a reverse trend might exist in females. However, only one of the data sets shows a significant deviation from random expectation. Table 4.9. shows no relationship between association index and either the dominant-minus-subordinate size difference or the absolute size asymmetry between dyad members, in either sex. In addition, there is no correlation between absolute size asymmetries and association index when all possible dyads (i.e. including those never seen to interact) are included in the analysis. The conclusion that variation in encounter frequency does not influence the relationship between size and dyadic dominance is important, but should not be taken as evidence against the existence of individual recognition since earlier analyses provide very little evidence of *any* involvement of body size in the outcome of agonistic interactions.

4.2.4. Discussion

In this study, sex and its associated physical asymmetries are the most striking correlates of dominance with 97% of agonistic, intersexual interactions being won by the male. Within the sexes, male dominance is correlated with prior territorial status and, in first-year birds, length of prior residence in the local area. Correlations between measures of body size and dyadic dominance are negligible in all contexts. That this is not due to gradual reduction in the size variance of the population as result of size-related mortality over the course of the winter is suggested by Table 3.6. Female dominance shows the same correlations with local prior residence and territorial status but these are weaker and there is also a weak, positive correlation with body weight which tends to decline in significance over the course of the winter.

These results compare well with those of other studies. Drent (1983) found that males always dominated females and that locally territorial males always occupied the highest positions in the winter rank hierarchy at a site. Amongst non-territorial birds, social status depended largely on length of prior residence in the local area rather than on age *per se*. Consequently, amongst locally-born males those earliest fledged tended to be dominant to others and all locally born males tended to be dominant to immigrants during autumn juvenile dispersal. Drent did find that body size determined dyadic dominance between birds symmetrical in terms of age and prior residence. This study does not have sufficiently accurate knowledge of prior residence to test this conclusion, but it should be noted that size differences consequent on fledging date may be important correlates of dominance in local birds in the immediate post-fledging period (Garnett 1976, 1981). Unfortunately, Drent makes little comment on determinants of dominance in females, except to suggest that social status amongst females does determine their chances of becoming paired to a territorial male. Fig. 4.6. does show a strong, positive correlation between the prior winter social ranks of breeding pairs in the Ormiston Hall population, though there are other explanations for this (Chapter 4.3.4.).

Saitou's (1979b) study of a Japanese population of great tits does provide some interesting contrasts with these results. He found that age was a consistent correlate of dominance within the sexes and noted that "the important factor is the prior occupancy of the area in adults". However, although he also found that males were consistently dominant over females, within age classes, and that adult males consistently dominated first-year females, the proportion of adult females dominating first- year males and vice versa was roughly equal with each individual dyad having a fixed relationship. Clearly, dominance of males over females is not as universal in Japanese populations as it is in western Europe. This difference is difficult to explain. However, Saitou's population does seem to show less sexual and age dimorphism in body size than found in this study (Saitou 1979b). and this may be a contributory factor. In this context it is interesting to note that no mixed-species flocking of tits occurred in Saitou's population (Saitou 1978) and other tit species (varied tit *Parus varius*, coal tit *P. ater*, willow tit *P. montanus* and long-tailed tit *Aegithalos caudatus*) were very rare visitors to the study area. If absence of other species of the pariform guild and a tendency towards monospecific flocking are characteristic of Japanese great tit populations then a lack of selection pressures for foraging niche specialization and separation, through lack of interspecific competition, may be responsible for a weaker sexual dimorphism in body size (e.g. Lack 1947; Schluter *et al* 1985). Saitou (1979b) also notes that prior residence effects on dominance in first-year birds may ultimately depend upon fledging date and correlated asymmetries in body size, but provides no data bearing upon this point.

The important conclusion of this section for succeeding chapters is that it is experiential variables, especially prior territoriality and prior experience of the local area that are likely to be the most significant asymmetries to great tits engaged in agonistic interactions. Body size may be of secondary importance, but only amongst females.

4.3. DOMINANCE HIERARCHIES AND THEIR LINEARITY

4.3.1. Introduction

As introduced in Chapter 4.2., the assignment of each individual in a population to a rank position within a dominance hierarchy usually assumes that rank, as derived from the total of an animal's dyadic dominance relationships, is a biologically relevant attribute. But as Bernstein (1981) warns "If a group is only a product of individual relationships then there may be no organizational principles transcending individual relationships". Since dominance hierarchies were first described by Schjelderup-Ebbe (1922) in chickens, their use on the basis of this assumption has been widespread (e.g. Clutton-Brock *et al* 1979 & refs. therein; Jarvi & Bakken 1984; Syme 1974 & refs. therein). One way of testing the assumption is to see whether rank is an independent variable influencing other attributes of animals (Bernstein 1981). Studies which do this are few and far between (e.g. Wiley & Hartnett 1980) but, especially in the primate literature, there are studies which show that aspects of social behaviour vary according to the magnitude of rank differences between opponents (Cheney 1978 a,b; Fairbanks 1980; Johnson 1989; Seyfarth 1976, 1980; Stammbach 1978; Stamps 1984). Although purely correlational, this study will test for the existence of rank difference - related behaviour in the dominance hierarchies of Ormiston Hall great tits in Chapter 6.

Secondly, the degree of linearity exhibited by the dominance hierarchies will be investigated. A linear hierarchy is one in which individuals can be ranked unambiguously according to their dyadic dominance relationships (e.g. A> B>C>D etc.). Such hierarchies have been described (e.g. Schjelderup-Ebbe 1922) but are rare (Manning 1979), often due to incomplete information or the method of calculation.

For example, at the level of individual interactions linearity may be rare simply because most dyadic relationships are not completely unidirectional (i.e. reversals occur) even though they may be highly asymmetrical. At the level of overall dyad asymmetries, however, linearity might be maintained (i.e. there is 'stochastic transitivity' – Chapter 4.3.2). A common practice has been to arrange individuals in a rank hierarchy which assumes the existence of linearity and is ordered to conform as closely as possible to that assumption (Lott 1979). This is usually achieved by ranking animals such that instances of animals dominating others of higher rank (i.e. reversals) are minimized (e.g. Beilharz & Mylrea 1963; Brown 1975; Drent 1983). Reversals or 'circular triads' (Appleby 1983) are cases where transitivity in the hierarchy (i.e. A>B>C and A>C) is broken by circularities (e.g. A>B>C but C>A). A hierarchy is only significantly linear if the proportion of circular triads exhibited is less than that expected by chance. Tests for the significance of linearity of hierarchies have been developed by Kendall (1962) where the relationships of all dyads are known, and by Appleby (1983) where information is incomplete. These tests show that small hierarchies may display linearity by chance, but at larger sizes the persistence of linearity demands explanation. One possibility is that the direction of dyadic dominance is determined by some transitively distributed attribute of the competing individuals. Physical characteristics such as size or age may be relevant in this respect (e.g. Fagen 1977; Landau 1951a; Wilson 1975 chapter 13) as may social factors such as prior residence (e.g. Landau 1951b). In large populations such as are considered here, the existence of significant linearity may be strong evidence that some transitively distributed factor is important in determining dyadic dominance. Its absence would indicate that a non-transitive factor such as prior social experience or territorial status, or a rapidly fluctuating variable such as hunger is worthy of further investigation. However, determinants of outcome may often interact (Collias 1943; Hinde 1978; Hinde & Datta 1981) and the antagonistic interaction of only two transitive determinants can lead to intransitivity in dominance relationships (Petraitis 1981). Consequently, a lack of linearity in hierarchies may have no easy interpretation whereas its presence might indicate the overriding importance of a single, transitive determinant.

When considering either the mathematical validity of a rank hierarchy, as assessed by its linearity, or its biological significance, it should be remembered that a large proportion of the literature concerning social dominance and rank hierarchies is set against a background of primate research (e.g. Bernstein 1981; Gartlan 1968; Richards 1974; Rowell 1974 & refs. therein). These studies mainly concern discrete, closely-knit social groups where repeated encounter and individual recognition are likely to be much more consistent features of social organization than in a large population of unstable membership, as is being studied here. This fundamental difference between primate 'societies' and avian 'populations' or 'flocks' has considerable implications for the likelihood that social relationships will display transitivity or that rank represents a biologically significant attribute of a bird. For example, the concept of rank as a meaningful attribute in a population of constantly changing membership is difficult to imagine. Similarly, in such an unstable group rare interactants or newcomers are unlikely to 'slot' immediately into a set of dominance relationships which maintain overall linearity if experiential or other non-transitive combinations of variables determine the outcome of dyadic encounters.

Here, dominance hierarchies will be used purely as intervening variables to help pinpoint [illegible] [illegible] determinants of dyadic dominance by studying their linearity. Their use does not necessarily imply their biological reality.

4.3.2. Methods

The same data sets that have been analysed in Chapter 4.2. are used here. In this case, however, the data are broken down by site, sex and year to give two sets for 1986/87 (Garden only) and six in each of the years 1987/88 and 1988/89 (Garden, Yew and Wood). The dominance index chosen for construction of the hierarchies was the cardinal index of Boyd & Silk (1983). This method has the following advantages over other indices reviewed by Boyd & Silk (1983), Clutton-Brock *et al* (1979) and Richards (1974).

i) It allows more precise measurement of rank differences between individuals than do ordinal ranks.

ii) It takes into account the fact that dominance relationships in some dyads are more ambiguous than in others (Chapter 4.2.2.2.) and uses the criterion of stochastic transitivity to assign transitivity to each triad. Thus if the probability of A being dominant to B (pAB) is greater than 0.5 and $pBC > 0.5$ and $pAC > pAB > 0.5$ over all interactions then the triad is considered transitive even though at an interaction-by-interaction level there may be reversals (i.e. transitivity is not absolute). If all possible triads fulfil this criterion then the hierarchy is considered to represent a linear series of dyadic relationships ($A > B > C$ .... n). Output files generated by the program also calculate the number of interactions which are reversals of the rank order produced on the assumption of stochastic transitivity. As a percentage of the total this provides a measure of the extent to which it is possible to order the individuals into a linear hierarchy according to this assumption.

iii) It allows for the fact that any individual's success in terms of number of interactions in which it is dominant or subordinate depends on the social status of the subset of others with which it competes. The iterative algorithm which calculates the cardinal indices takes into account all interactions simultaneously to produce an index value for each individual that is derived from p_i - the probability of being dominant in any given interaction. This index could be termed 'social status'. In the next iteration, each individual's p_i is adjusted according to the p_i of each opponent until all p_i values converge to constant values.

iv) Equilibrium values of p_i and the cardinal index tend towards a normal distribution which makes them easier than ordinal ranks to use in parametric statistical techniques.

v) The FORTRAN program listing of the cardinal index calculation (provided by courtesy of Dr Joan B. Silk) outputs a dominance matrix of all interactions that is based on the equilibrium cardinal indices. This facilitates assessment of the linearity of a hierarchy using the method of Appleby (1983).

vi) Cardinal index values range from zero to infinity. As with the rank orders derived from them, a tendency of the cardinal index value to zero reflects an *increase* in social status.

Practical problems with the method are:

i) that p_i values will not converge if there are any individuals which never lose an interaction because there is no means of determining to what extent such individuals are dominant over those below them in the hierarchy.

ii) The program fails to run if there are individuals which lose all their interactions - i.e. the method assumes that transitivity in dyads is always stochastic, never absolute.

In all matrices analysed in this study in which there were birds which were never subordinate, it was found that cardinal index values converged towards equilibrium sufficiently that no significant change was noticeable between 1000 and 10,000 iterations of the algorithm. Consequently, all matrices were analysed for a maximum of 1000 iterations, after which stability at a resolution of 0.01 index units was always achieved.

The problem of birds which were always subordinate was circumvented by introducing two imaginary birds (A and B) to the real hierarchy. 'A' was scored as being subordinate to all real individuals in one interaction, whilst being dominant to 'B' once and vice versa, once. This manipulation does not alter the relative ranks of the real individuals and produces an analysable matrix without any loss of real data. It is probable that the cardinal index values are influenced by the manipulation since the effect of dominating imaginary individual 'A' is greater for a real subordinate than for a real dominant. However, for the purposes of this study it is the advantages of the method in producing accurate rank orders that are of most value and, in any case, the effect of the manipulation should be consistent across all matrices analysed.

Annotated examples of input and output files are given in Figs 4.2. and 4.3. to illustrate the cardinal index calculation.

4.3.3. Results

Summaries of the output files for all fourteen matrices are given in

Appendix 6. These present total number of interactions, number of reversals of the overall rank order, the rank order and cardinal index value for each bird for which four or more interactions were recorded, and whether that bird a) survived to the next winter, b) held a territory or was paired to a territory holder in the next breeding season, and c) the distance of that territory from the site of observation. It was considered unreliable to use the rank/cardinal index values of individuals recorded in less than four interactions so the ranks given are corrected after their removal. Such individuals do, however, contribute a significant proportion of the observed interactions so they were never omitted *before* calculation of the cardinal indices.

The number of interactions reversing the overall rank order varies widely, from zero in two female hierarchies to over 20% in a third. The proportion of reversals in male hierarchies varies less, from 3 to 13%. Linearity (as measured by this proportion) decreases with increasing number of individuals in the hierarchy (n_i) (Fig. 4.4.) and with increasing number of interactions recorded (n_x) (Fig. 4.5.). However, n_i and n_x are also strongly correlated ($r_s = 0.864$, $n = 14$, $p<0.001$). A stepwise multiple regression of linearity on n_i, n_x and the sex of the hierarchy shows that 51% of the variation in linearity is explained by n_i but that this only increases to 52.5% when n_x and sex are taken into account. There is no overall difference between the sexes in hierarchy linearity (Mann-Whitney-Wilcoxon Test: males, $u = 10.0\%$, $n = 7$; females, $u = 9.1\%$, $n = 7$, $W = 57$, $p = 0.61$).

Appleby (1983) shows that a completely linear hierarchy will have a probability of chance occurrence of less than 0.1% in any hierarchy of more than seven individuals. Consequently, the fact that these data only produce hierarchies with more than 10% reversal of complete linearity in cases where more than 40 individuals and 150 interactions are involved, argues strongly that genuinely high levels of linearity exist in the dominance relationships of these great tits. The force of this argument is weakened by the fact that these hierarchies are very incomplete (i.e. a very high proportion of possible dyads are never seen to interact), and the probability of chance linearity is increased by incomplete information (Appleby 1983). This is because the number of observable dyads increases by n for every new bird added to a hierarchy of n individuals, so incompleteness of information will tend to increase at a constant rate of observation of interactions. Despite this, there is a strong tendency for linearity to decline with n_i in this data set.

Social status, as measured by either cardinal index or rank order does have fitness correlates. Although social status at a site is unrelated to the probability of a bird's reappearance there during the next winter (an index of survival), males of higher social status are more likely to establish a local breeding territory (Table 4.10.), i.e. within the area shown in Fig. 2.3. The same trend is is found in females, with higher status birds tending to become paired to territory holders, but is never statistically significant (Table 4.10.). In this context, it is interesting that the ranks of paired males and females are strongly, positively correlated (Fig. 4.6.), as also found by Brown (1963) in Steller jays *Cyanocitta stelleri* and Röell (1978) and Wechsler (1988) in jackdaws *Corvus monedula*. Beyond the relationship between social status and subsequent territoriality, there is also a tendency for birds of higher social status to establish territories closer to the site of observation. This correlation applies equally to all age-sex classes Fig. 4.7.).

4.3.4. Discussion

The degree of linearity in the dominance hierarchies of this population of great tits is difficult to test formally but seems sufficient to demand explanation. Though there are exceptions (e.g. Hamerstrom 1942), this linearity is characteristic of most studies of parids (e.g. De Laet 1984; Dixon 1965; Drent 1983; Glase 1973; Smith 1976) and other passerines (e.g. Brown 1963; Dilger 1960; Kikkawa 1961; Sabine 1959; Tordoff 1954; Watson 1970). In addition, studies of tits which have compared dominance hierarchies derived from observations at natural and artificial food sources have generally found that the hierarchies are similar for the same population in the same area (e.g. Glase 1973). Possible causes of hierarchy linearity in this study are discussed below, and the implications of reduced linearity as hierarchy size increases is discussed in Chapter 4.5.

In addition to generating linear dominance hierarchies, measures of a great tit's social status are closely related to the probability and proximity of territory establishment (males) or pairing with a territory holder (females). Similar fitness correlates have been reported for other species. Smith (1976, 1984, 1987) has found that in the event of a territorial vacancy in a population of black-capped chickadees *Parus atricapillus* it is the highest-ranked, non-territorial, 'floating' juveniles that are most likely to take over the area as a territory. In the same species, Dixon (1965) also noted that low ranking birds were unlikely to become established on local breeding territories. Knapton & Krebs (1976) and Arcese & Smith (1985) have shown that song sparrows *Melospiza melodia* of high winter social status obtain higher quality breeding territories.

If we accept that failure to establish a local breeding territory equates with either failure to breed or with the necessity for longer distance dispersal and its attendant risks, then the finding that winter social status is unrelated to the probability of return in (= survival to) the following winter is at first sight surprising. However, other studies of great tits have shown that winter home ranges and breeding territories may often overlap (De Laet 1984; Saitou 1979b) or even be indistinguishable except by seasonal variation in intensity of defence (Drent 1983). This implies the existence of site-relationship in the social status of great tits throughout the year, with distance from the centre of some activity range (whether it be defined as a 'territory' or a 'home range') being an important determinant of dyadic dominance. If such site-related dominance were to operate on a sufficiently small scale then lack of correlation between survival and social status would not be surprising. Low status at a site might simply reflect a bird at the edge of its range and high status might be characteristic of birds in the centre of their ranges.

The covariance of male and female social status (Fig. 4.6.) has several possible interpretations. Drent (1983) suggests that female social status is independent of that of males and that high status allows females to pair with dominant males. However, Saitou (1979c) has shown that pair formation generally occurs between birds that have been associated with each other in foraging flocks throughout the winter. So, it may be that both members of a future pair independently achieve a high, site-related social status due to their common home range, and that subsequent pairing is consequent on spatial and temporal association rather than high, local social status. Once paired, the status of the two birds may become mutually reinforcing if opponents associate the presence of one member of the pair with the proximity of the other during territorial establishment. This process has also been postulated to occur in the jackdaw (Röell 1978; Wechsler 1988).

The importance of prior territoriality and length of prior residence as dominance correlates (Chapter 4.2.) and the findings of this section lead into a more detailed investigation of site-related dominance in this population in Chapter 4.4. Prior residence /territoriality and site-related dominance also provide a covarying set of factors which might act to promote transitivity in the overall dominance structuring of the population. This is discussed further in Chapter 4.5. However, Chase (1974, 1982, 1985, 1986) and Jackson (1988) have suggested that a positive feedback effect of the outcome of one agonistic encounter on the probability of being dominant in a subsequent interaction may be the fundamental cause of linearity in dominance hierarchies. Results of experiments on unacquainted triads and tetrads of captive chickens (Chase 1982, 1985) suggested that the pattern of initial agonistic encounters within these groups was such as to ensure overall transitivity (Fig. 4.8.). Thus, in those experiments, double dominance and double subordinance were by far the most common initial interaction sequences, comprising around 90% of the data set. Subsequent reversals of the outcome of initial encounters were very rare so that the transitivity of dominance relationships in these small groups persisted. Chase (1982) concluded that "hierarchy formation can be best viewed as a developmental process where preceding dominance interactions influence succeeding ones." The form of this influence is that winners are more likely to win again and losers to lose again, a process which then maintains the transitivity of dominance relationships irrespective of the factors responsible for the outcome of initial interactions. If the larger social groups of animals that exist in the wild are seen as concatenations of these component triads, then the result is a linear dominance hierarchy. This 'winning begets winning' and 'losing begets losing' hypothesis is believed by Drent (1983) to be largely responsible for the development of site-related dominance, territoriality and dispersal in great tit populations by virtue of the birds' association of past agonistic experience with its spatial context. In other words, birds remain dominant in areas where they became dominant and subordinate in areas where they were initially subordinate. The dependence of future social behaviour on past experience is believed to be so strong that the life of a great tit is to a large extent determined by its initial social experiences after fledging. This far-reaching hypothesis is also discussed in Chapter 5 in relation to its implications for the existence of badge signalling in great tit populations. Empirical evidence in its support would go a long way to explaining the development of hierarchy linearity, prior residence effects and site-related dominance as features of avian social organization and would leave only the determinants of initial encounters to be explained. Chapter 7 goes on to consider dependency between successive interactions in terms of eventual outcome, in captive groups of great tits.

4.4. SPATIAL STRUCTURE OF GREAT TIT POPULATIONS: THE RELATIONSHIP BETWEEN TERRITORIALITY AND SITE-RELATED DOMINANCE

4.4.1. Introduction

In a review of territoriality and dominance systems, Wilson (1975) distinguished between three categories of social structure.

i) Absolute hierarchies. Rank changes only occur through social interactions and are otherwise stable in time and space.

ii) Relative hierarchies. Hierarchies in which individual ranks vary with location, being highest near some site of value such as a roosting or nesting site.

iii) Territoriality.

Wilson's classification establishes relative hierarchies or 'site-related dominance' as an intermediate phenomenon between the extremes of absolute dominance hierarchies and territoriality, a dichotomy which had long been considered to be oversimplified (e.g. Brown 1963; Sabine 1959).

Many studies, from Masure & Allee (1934a), Shoemaker (1939), Odum (1942) and Brian (1949) onwards, have referred to site-related dominance in the social system of a bird species and the phenomenon has also been reported from mammalian populations, an example being Taylor's (1966) study of home range and agonistic behaviour in the grey squirrel *Sciurus carolinensis*. Many early studies (e.g. Castoro & Guhl 1958; Glase 1973; Marler 1956; Masure & Allee 1934a; Ritchey 1951) referred to site-related dominance as a form of peck-dominance where the success of the subordinate in a minority of interactions was an effect of location, and Dixon (1965) suggested that in wild populations of birds peck- dominance is only a meaningful concept when framed in terms of site-related dominance. However, in very many cases it is unclear whether site-related dominance simply represents territoriality (i.e. a bird is dominant over all others within its territory but may not be outside it) or whether it is a distinct phenomenon. For example, Brown (1963), studying Steller jays, refers to a gradual decline in rank with distance from the nest site, without the existence of a defended territory boundary or line of discontinuous change in rank. Brown considered territoriality and site -related dominance to be two aspects of the same phenomenon. Similarly, Brian (1949) suggested that, in spring, male great tits could be said to possess a field of influence diminishing outwards from a locus in which they were most frequently present. In contrast, Piper & Wiley (1989) found clear, gradual, site-related changes in social status in wintering flocks of white-throated sparrows, a context far removed from that of breeding territories in both space and time. They concluded that "site dependence is a fundamental aspect of aggressive behaviour in species that establish localized ranges" irrespective of the presence or absence of territories. Similarly, Desrochers & Hannon (1989) reported the existence of site-related dominance in a winter population of black-capped chickadees even though flocks were neither using nor defending non-overlapping home ranges.

This section first attempts to clarify the conceptual tangle surrounding the terms 'site-related dominance' and 'territoriality' by emphasizing territoriality and site-correlated dominance (Oberski 1989) as two distinct forms of site-related dominance. This is followed by an investigation of site- related dominance in the great tit population at Ormiston Hall and a final discussion which uses these and other data from other species to exemplify the concepts introduced above.

4.4.2. What is the Relationship between Site-related Dominance and Territoriality ?

Without an adequate definition of the term 'territory' or 'territoriality' as the possession of a territory, this relationship is difficult to establish. Unfortunately, a universally acceptable definition of 'territory' has yet to be found (Kaufmann 1983), perhaps due to the great variety of taxa and social systems in which the term is used. Territories have been considered as 'defended areas' (Brown & Orians 1970; Brown 1975; Wilson 1975), 'areas of exclusive use' (Pitelka 1959) and 'areas of dominance' (Emlen 1957). Modern approaches have focused on functional consideration of the territory as an area/volume containing resources to which priority of access results in fitness gain. This fitness gain might be immediate, as in the case of the food content of a winter territory, or after a time lag, as in the case of successful reproduction after the establishment of a breeding territory. However, the concept of priority of access establishes the relationship between territoriality and social dominance (Kaufmann 1983). From this viewpoint, exclusive use is not a necessary criterion for the existence of a territory, and overt defence may be irrelevant since whether or not a territory boundary is actively defended depends on the cost/benefit payoff of aggressive interaction to both territory holder and intruder. For example, subordinates may simply avoid confrontation with territory holders at boundaries and territory holders may permit a degree of trespass due to the energetic costs and risks of expelling intruders. The concept of a territory as no more than an area of "spatially localized dominance" (Owen-Smith 1977) or an area in which "the resident controls or restricts use of one or more environmental resources" (Wolf 1970) has thus become established. Wiley & Wiley (1980) suggested that the existence of site-related dominance is the single best criterion for the existence of territoriality, whilst Dixon (1965) concluded his study of the mountain chickadee *P. gambeli* by stating that "the principal ecological consequence of a system of site-related dominance is the reservation by the individual of an area for his own use" (c.f. Pitelka 1959). However, he accepted that site-related dominance and territoriality could not always be equated. Similarly, Guhl (1961) noted the overlap between these two phenomena and other studies have equated the existence of site-related dominance during the non-breeding season with the persistence of less overt forms of territory maintenance (e.g. Drent 1983).

In the latest review, Kaufmann (1983) emphasizes the need to depart as little as possible from the derivation of the word 'territory' as a "specific geographical location - an identifiable volume...". He explicitly excludes ephemeral, moving territories and the defence of individual space (Conder 1989; Wilson 1975) although accepting that there may be no hard and fast line to be drawn. Kaufmann defines a territory as "a fixed portion of an individual or group's range in which it has priority of access to one or more critical resources over others who have priority elsewhere or at another time. This priority of access must be achieved through social interaction." In this study, we are concerned solely with territories established by individuals or breeding pairs. Though group territories have been reported in winter flocks of tits (e.g. Glase 1973), there is little evidence that an apparent 'group territory' reflects anything more than an independent tendency to defend the same area by each bird in a flock occupying a roughly common range (e.g. Hartzler 1970).

Taking this definition as a baseline, it is clear that territoriality is a form of site-related dominance. However, are there others ?

If a territory is a fixed area, as implied by the derivation of the word, then the change from priority of access to deference to others is expected to occur suddenly, at the territory boundary. If, instead, the social status of an animal decreases gradually with increasing distance from its nest area or other site of value, as in Brown's (1963) study of Steller jays, then no distinguishable territory exists according to the definitive criteria of fixed area and priority of access. The difference between these two scenarios is illustrated in Fig. 4.9. Of course, there could exist an infinite series of graded intermediates between these two extremes but the final criterion for deciding whether or not animals have territories is whether the animals themselves perceive boundaries. As observers, we might be able to map territory boundaries using singing behaviour, scent marking or confrontation between neighbours as indicators. However, if the immediate manifestation of territoriality is social dominance within a fixed area, then it is the existence of a contour marking an abrupt fall in social status that is diagnostic of the position of a territory boundary. If individuals do not show this discontinuity in social status at a certain distance from the centre of their activity range, then site-related dominance may still exist in the form of continuous rank changes across space, but territoriality does not.

Hereafter, I refer to the phenomenon of continuous, site-related variation in social status as site-correlated dominance after Oberski (1989). Site- correlated dominance is distinct from territoriality on the basis of a dichotomy between continuous and discontinuous social status changes. Both are forms of site-related dominance. The distinction between continuous and discontinuous status change may occur at different levels. For example, continuous changes in social status may still result from abrupt reversals in the dominant - subordinate relationships of individual dyads. This raises the theoretical possibility of a complex of bounded areas of social dominance, each marking a line of dominant - subordinate reversal for a particular pair of birds. However, this scenario involves much speculation as to the extent of individual and site recognition in different animals. In great tits, it seems likely that territory boundaries represent an exception to a general rule of gradual change in the relative probabilities of dominance for dyad members. In any case, priority of access as a function of a territory is determined by the whole spectrum of an individual's social interactions. Dominance indices or ranks, as estimates of this, are more relevant variables for evaluating the continuity/discontinuity criterion than are individual dominant - subordinate asymmetries.

Territoriality and site-correlated dominance are not mutually exclusive processes, either in time or space. A length of territory boundary is generally established through social interaction with one neighbour, and the whole territory is delineated as a result of interactions with a relatively small number of territorial neighbours. Therefore, the social status of a territory holder falls suddenly at the territory boundary due to abrupt reversals in its dominant - subordinate relationships with its immediate territorial neighbours. However, the bird's social relationships outside its territory may reflect site-correlated dominance, with rank falling gradually as the bird moves further from its territory. Clearly, part of this fall is a consequence of the bird becoming more subordinate to an increasing number of intervening territory holders as it moves away. The co-occurrence of site-correlated dominance and territoriality in a hypothetical territorial system is illustrated in Fig. 4.10. Note the distinction between abrupt changes in relationship between neighbours at territory boundaries and gradual changes in all other contexts. Similarly, one can envisage a temporal transition from site-correlated dominance to territoriality, with territorial boundaries crystallizing as individuals within a population become increasingly sedentary, occupy smaller ranges and interact only with immediate neighbours but at high frequency. This scenario may be a rough approximation to the change in social structure of many tit populations as winter flocks break up, birds pair up, and males begin to defend breeding territories (Glase 1973; Hinde 1952; Kluijver 1951; Perrins 1979; Saitou 1978, 1979a,b,c). For example, Desrochers & Hannon (1989) concluded that in black-capped chickadees "dominance did not follow broad gradients but instead that there were relatively narrow 'boundaries' between adjacent home range centers in which the dominance of each neighbor changed rapidly. Such narrow interfaces between centers of adjacent home ranges could become true territory borders when conditions would favor use of exclusive, defended areas."

The distinction between site-correlated dominance and territoriality may not be simply of conceptual interest. A knowledge of the pattern of occurrence of territoriality, site-correlated dominance and absolute hierarchies both within and between species may provide valuable insights into the relative importance of different resources and their distributions and the causes and effects of population density, migration and mortality. Answering the question of to what extent birds perceive social boundaries within a spatial and temporal context may therefore have important ecological implications.

This study assesses the extent of site-related dominance in the winter population of great tits at Ormiston Hall and relates this to prior and subsequent territorial status and an index of location winter home range. The aim is to determine whether great tits should be considered territorial throughout the year as Drent (1983) believed, or whether absolute hierarchies or site-correlated dominance exist outwith the seasonal establishment of breeding territories (e.g. Hinde 1952; Kluijver 1951; Perrins 1979; Saitou 1978, 1979a,b,c).

4.4.3. Methods

The use of overall dyad outcomes and the cardinal index of social status is combined in this section since we are concerned with the correlates and consequences of the totality of a bird's social experience. The study uses the same data sets as in Chapters 4.2. and 4.3. to investigate site-related dominance in the study population. Cardinal indices are not known to be comparable between sites and are only used for analyses employing data collected at a single site. For analyses which pool data from different sites, the ordinal ranks derived from ranking the cardinal indices are used but are expressed as relative ranks (i.e. rank divided by the number of birds in the hierarchy) so that a bird ranked 1 in a hierarchy of 40 has a higher relative rank (i.e nearer to zero) than a bird ranked 1 in a hierarchy of 10. For interpretation of Figures and correlation coefficients, it is important to remember that a low cardinal index or rank reflects high status so that if, for example, social status increased with size, this relationship would be expressed by a *negative* correlation coefficient.

4.4.4. Results

Chapter 4.3. has already established that birds of high winter social status are more likely to establish local breeding territories or become mated to local territory holders and, moreover, that within a radius of only a few tens of metres (Fig. 2.2.) an index of winter social status decreases with increasing distance from the territory in both sexes. These findings beg the question: does achievement of a high social status at a site during the winter reflect, a) continuous attachment to the area of a former breeding territory in adults (Saitou 1979a), and/or b) the development of territoriality in first- year birds ? If the answer to these questions is "yes", then we should expect significant variation in a bird's social status across the study area during a single winter, and that this variation is related to some measure of its preferential use of ('attachment to') part of its winter home range. It is assumed that those birds captured at the observation sites, which remain in the area sufficiently long for their social status to be estimated, represent a sub-population whose members have largely common home ranges. The alternative hypothesis would be that a fixed subset of the population shows site-independent high social status throughout this winter range and that this subset makes up the population of breeding pairs in the study area during the following spring. In this case, we would expect no site or 'area usage' - correlated variation in social status. Variation in status within this subset would have a cause unrelated to location and it would be this variation that is responsible for the distance of birds' territories from the sites at which winter social status was recorded. The latter scenario should be treated as the null hypothesis since there is already independent evidence that winter social status is affected by prior experience of a locality (Chapter 4.2.).

Appendix 7 gives a complete list of dyads for which overall outcomes were scored in 1988/89 at each of the three pairs of observation sites - Garden/Yew, Garden/Wood and Yew/Wood. This shows that between 20% and 50% of dyads had reversed outcomes between sites, despite their proximity (Fig. 2.2.), and that the proportion of reversals of overall outcome increased with distance between the sites.

Table 4.11. presents Spearman rank correlation coefficients of the relationship between frequencies of occurrence of birds at each pair of sites (expressed as the percentage of observation days on which a bird was observed, after its initial capture and colour-ringing). Not

surprisingly, there is evidence of strong, positive correlation in frequency of occurrence at sites very close to each other (Garden-Yew, Yew-Wood), but that this correlation disappears as the distance between the sites increases. With a hypothetical site, even further distant, we would expect this correlation to become negative. In this context, it is interesting that when age-sex classes are considered separately, the more sedentary adult birds (Chapter 3) do show negative correlations between frequencies of occurrence at the two sites in two of the three pairings. Although these negative correlations are not statistically significant, they do differ substantially from the positive correlations found in the more mobile first-year population.

So far, two important points have been established. Firstly, social status is site-related in the broadest sense. Secondly, birds' frequencies of occurrence at the feeding stations vary in the manner predicted by the occupation of a winter home range. If the attraction of continuously available, concentrated food sources had appreciably distorted ranging behaviour (i.e the home ranges of the birds became centred on the three feeding stations), then correlations between frequencies of occurrence at the three sites would have remained consistently positive for all age-sex classes. In other words, we have some justification for using frequency of occurrence at a feeding station as a measure of the site's proximity to the centre of a home range which has not been radically altered by the provision of food at the site. Further support for the use of this index of home range is provided by Appendix 4 which demonstrates the rapid turnover of birds at a given site and suggests that birds simply incorporated the feeding stations into their daily, 'routine' circuit of reliable feeding sites, a phenomenon previously reported by Hinde (1952) and Perrins (1979).

Frequency of occurrence is related to winter social status in both sexes. Table 4.12. shows the proportion of dyads in which the more frequently occurring bird at the site was also the overall dominant. In both sexes and at all three sites, this proportion was significantly greater than random. This relationship was particularly marked amongst males. Fig. 4.11. expresses the same data in the form of correlations between frequency of occurrence and cardinal index for both sexes at each site. Accordingly, we would expect territorial fate in spring to be related to winter site attachment and this is the case (Table 4.13.) though the relationship is much stronger in males than in females. Fig. 4.12. expresses the same data in the form of correlations between frequency of occurrence and distance to territory for males and females at all three sites, pooled. Amongst territorial males, birds more frequently present at a site during the preceding winter tend to establish their breeding territories closer to that site than less frequent visitors. The same trend exists amongst females but is not statistically significant.

A final analysis investigates those birds occurring at more than one site to see whether social status changes are accompanied by the change in frequency of occurrence that would be predicted on the basis of the above results. All p-values attached to the following analyses are therefore one-tailed. Fig. 4.13. presents Spearman rank-correlation coefficients between difference in relative rank and difference in frequency of occurrence of males at each pair of sites. At two of the three pairs of sites, the predicted relationship holds, i.e. a decrease in status from site A to site B is correlated with a decrease in frequency of occurrence, and vice versa. The absence of this relationship between the Garden and Yew sites correlates with the fact that this pair of sites showed the lowest percentage of reversals of overall dyad outcomes (Appendix 7) and that the two sites are the closest together (Fig. 2.2.). Correspondingly, median relative rank change between Garden and Yew is less than that for either of the other pairs of sites, although the difference is not statistically significant (Garden-Yew, u = 0.14, Garden-Wood, u = 0.18, Yew-Wood, u = 0.23: Kruskal-Wallis, H = 0.98, df = 2, $p > 0.50$). Too few females have a measurable social status at more than one site to allow this analysis to be undertaken.

4.4.5. Discussion

The results of Chapters 4.3. and 4.4. have shown that the winter social status of a bird, as recorded from social interactions between October and March of each year, is related to its subsequent territorial fate and the proximity of any successfully established territory. These results are statistically significant in all age-sex classes, though especially so in males. Secondly, birds have a higher winter social status when in the areas which they occupy most frequently and there is evidence that status varies with location in a way that is at least partially predictable by variation in frequency of occurrence. Accordingly, the more frequently a bird visited the study area during winter, the more likely it was to become established on a breeding territory and the closer that territory was likely to be. The direction of causality between frequency of occurrence and social status (i.e. do more frequently occurring birds develop a higher social status, or does high social status in a particular area lead a bird to frequent it more often ?) is perhaps irrelevant at this stage since one of the aims of Chapter 6 is to examine the idea that it is prior social experience of individuals and sites that is an important determinant of each bird's pattern of agonistic behaviour. If this idea proves to be correct then social status and site attachment will be mutually reinforcing and it would be misleading to consider one as cause and the other as effect.

Thus, the Ormiston Hall great tit population does show site-related dominance during the winter months and this social structure is related to the subsequent distribution of breeding territories. Unlike De Laet (1984), who found site-related dominance only in adult birds, this study finds it in all age-sex classes, though the relationships with subsequent territory location are much stronger in males than in females. These conclusions are based on interactions recorded throughout the period October to March, so there are good grounds for believing that this result is more than simply an early manifestation of spring territory defence. Thus, the occupation of areas of local dominance coupled with age/prior residence (Table 4.14a.) constitute the main set of factors determining the successful establishment and location of a breeding territory. Very similar conclusions were made by Desrochers & Hannon (1989) in their study of winter flocks of black-capped chickadees. Morphological characteristics show virtually no correlation with territory establishment (Table 4.14b.).

What the above data do not enable us to do is to determine to what extent winter site-correlated dominance and spring territoriality are related but distinct phenomena or, alternatively, to what extent they are manifestations of the same pattern of social relationships, separated only in time. As discussed above, the argument hinges upon if and when the birds perceive a patchwork of bounded territories, outside which their owners show a sudden decline from a 100% probability of dominance in intrasexual agonistic encounters. The results suggest that breeding territories tend to be in the same areas in which the incumbent was socially dominant during the preceding winter. Chapter 6 illustrates the gradual increase, over the course of the winter, of spatial intolerance and agonistic interactions in which priority of access to the immediate area, rather than a specific material resource which it contains, appeared to be the goal. This change implies the gradual development of territoriality during the winter. However, boundaries of equal probability of dominance for territorial neighbours over which interactions 'see-sawed' with one male chasing the other to one side of the boundary followed immediately by the reverse process were not seen until April. By this time, nest-site selection had taken place and birds were to be seen carrying nesting material. The impression is that the birds' occupation of 'preferred areas' of local dominance (preference and dominance perhaps being mutually reinforcing) gradually crystallizes into a system of bounded territories, the time of this crystallization roughly corresponding to the end of any flocking behaviour but varying with the activity of neighbouring pairs. As Hinde (1952, p.52) put it, "preferred areas thus changed gradually into 'territories' in the classical sense". Whether or not site-correlated dominance persists amongst non-territorial birds and when territory owners are outside their boundaries is still an open question. It is also a question which may be difficult to answer since interactions which would answer it are less frequent during the spring when birds tend to remain within their territories and are difficult to attract to artificial food sources.

The change from winter social organization to the system of territories described here matches almost exactly Hinde's (1952) description of the process in the great tit population of Wytham Wood, England (pp. 50-53). Hinde also recognizes "birds becoming conditioned to places in which they had won on previous skirmishes" (p. 51) and states that "the area defended by the Great Tit is by no means rigid or precisely defined but consists in the first place of a fluid region around certain preferred stations..." (p. 52). Like De Laet (1984) and this study, Saitou (1979c) found that breeding territories usually overlapped prior winter ranges in his Japanese population. He also noted the advantage of previously resident, adult males in re-establishing their former territories, but did not recognize the process of gradual change linking winter social organization and the pattern of breeding territories (p.157, para. 8). Drent's (1983) study of a Dutch population of great tits is the most committed exposition of the idea that favourable prior social experience in, and preferred occupation of, a local area are mutually reinforcing determinants of the area in which a male will establish a territory. He also notes the importance of age and prior residence in influencing the probability of successfully establishing a territory but, in contrast to this study, considers large size to be advantageous in this process above a threshold of 16g body weight and 19.5mm tarsus length. In this study, virtually all males exceeded these size thresholds and no effect of size on territory establishment was observed. Drent also confounds territoriality as a set of behaviour patterns with the possession of a territory as a bounded area. He would consider a male's localized winter dominance simply as a more subtle manifestation of territory possession than spatial intolerance and the existence of observable boundaries. However, the development of spatial intolerance and a system of bounded areas of total dominance seem to be clear, gradual processes which represent large scale changes in social organization and behaviour and which link two quite distinct extremes - a system of site-correlated, continuously variable social status, and a patchwork of territories bounded by lines of discontinuous change in social status. To relegate all this change to no more than 'variation in intensity of territorial defence' seems to oversimplify a phase of the life cycle whose outcome is critical to successful reproduction. Hinde's (1952, p.53) summary of territoriality in the context of the annual cycle makes this point concisely:

> "Although some reproductive fighting occurs in the autumn, it does not usually result in the defence of an area, and territories are not established at this time. It is, however, possible that the birds do become conditioned to a particular area so that they are likely to establish their preferred areas there in Spring."

Similarly, Smith & van Buskirk (1988) and Desrochers & Hannon (1989) working on black-capped chickadees found that during winter individual territories were at most poorly developed, if present at all.

Finally, to put this study in the context of those of other *Parus* species, it is worth noting that site-related dominance is a general feature of the winter social organization of tits (e.g. Colquhoun 1942 working on blue tits *P. caeruleus*, Glase 1973, Hartzler 1970, Odum 1942, Smith 1976 and Desrochers & Hannon 1989 on black- capped chickadees, and Dixon 1965 and Minock 1971 on mountain chickadees *P. gambeli*). Though not all these studies distinguish between site-correlated dominance and territoriality, most make it clear that the dominance relationships between birds which flocked together (i.e. occupied a roughly common range) tended to be site-independent, whilst those between birds from different flocks (i.e. occupying largely non-overlapping ranges) tended to be site-dependent. The fundamental link between site-related dominance and the 'fitness value' associated with a particular location (whether it be a material resource such as food or a non-material resource such as the probability of territory establishment) is emphasized by many studies of social organization in captivity (e.g. Dunham 1966; Ellis 1966; Hardy 1965; Mc Bride 1969 et al; Masure & Allee 1934b) in which the 'range' was too small for individual variation in locations of interest to develop and site-related dominance was not found. Cases where site-related dominance does develop in captivity are almost always those where aviary conditions allow individuals or pairs to defend nest sites, as exemplified by Shoemaker's (1939) study of canaries *Serinus canaria*, Watson's (1970) work on house sparrows *Passer domesticus*, and Wechsler's (1988) two-year study of a captive flock of 26 jackdaws. An equivalent field study is that of Samson (1977) on Cassin's Finch *Carpodacus cassini* in which flock instability, mobility and lack of site attachment precluded the development of individual variation in the 'resource value' of particular areas so that site-related dominance was not seen. To use Drent's approach, residence times have to be long enough and activity ranges large enough for individuals to associate previous social experience with its location. Site-related dominance will then develop. The partially sedentary nature of most tit populations, coupled with their winter flocking behaviour, make them ideal candidates for the evolution of a site-related social organization. This organization determines its own development since it consists of individuals whose primary determinant of future status and experience is past status and experience.

4.5. GENERAL DISCUSSION

The purposes of this chapter have been to pinpoint the main correlates of dominance in great tits involved in agonistic competition over resources and to demonstrate the importance of social dominance in allowing territory establishment and reproduction.

As in the majority of other studies of social dominance in birds, sex and prior territoriality were found to be important dominance correlates in great tits. Age was found to be of relatively little importance except through its association with previous experience of sites and territories, but prior residence in an area was correlated with dominance even in first-year birds with no prior territorial experience. Measures of physical size were of negligible importance in males and made only a limited contribution to the probability of dyadic dominance in females.

This summary compares well with another major study of social dominance in European great tits (Drent 1983) but shows an interesting contrast with a similar study in Japan (Saitou 1978, 1979a,b,c). The almost universal dominance of males over females in this and Drent's populations was not found in Saitou's study where older females were often dominant over younger males. This may be a result of reduced sexual dimorphism in the Japanese population for which a possible explanation is the relative lack of ecological competition between the great tit and other parids in Japan. This may have resulted in reduced selection pressures for niche separation and specialization between the two sexes, and a consequent lack of sexual dimorphism.

Both Drent and Saitou suggest that many dyads of great tits encounter each other frequently enough that individual recognition develops. Preliminary evidence for individual recognition in this study is given by Fig. 4.1. which shows that the dominant - subordinate asymmetry of a dyad tends to become more predictable (i.e. more akin to the 'dominance relationship' of Bernstein 1981). as encounter frequency increases. The possibility of individual recognition is investigated further in Chapters 6 & 7 by looking at the effect of increased frequency of encounter or level of association on the behaviour shown by birds during agonistic interactions.

Social dominance is site-related throughout the year but the transition from site-correlated dominance to the patchwork of spring breeding territories is a gradual one. This process seems also to be typical of that of other parids (e.g. Glase 1973; Perrins 1979; Smith 1972; Smith 1976; Desrochers & Hannon 1989). Local social status is positively related to a bird's frequency of occurrence in that area and high winter social status is an important precursor to successful establishment of a breeding territory in the same area, for both sexes. This geographical overlap between breeding territories and areas of previously high social status is also found in other studies of great tits (e.g. Brian 1949; De Laet 1984; Drent 1983; Saitou 1979b,c). Successful establishment as a member of a territorial pair is, in turn, crucial to successful reproduction since birds failing in this must either disperse, with its attendant risks, or attempt to breed non-territorially, a process known to lead to reduced reproductive output (Dhondt & Schillemans 1983). In effect, the annual cycle of the great tit can be seen as a process of continuous positive feedback: social dominance in winter leads to territorial establishment leads to successful reproduction leads to continued social dominance in the following winter, and so on. Drent (1983) believes that this positive feedback also operates on a much finer scale, with the physiological and psychological effects of success or failure in one agonistic encounter having a strong influence on a bird's agonistic behaviour in succeeding encounters. Whatever the level to which we take this 'positive feedback' hypothesis, it seems to be crucially dependent on location with site attachment and agonistic success being mutually reinforcing. This 'winning begets winning' and 'losing begets losing' scenario could be invoked right from the day of fledging such that a great tit's entire life history is only explainable as a causal chain beginning with its first social interactions as a fledged juvenile. Alternatively, we could envisage that the significance of prior experience in determining current behaviour becomes weaker as it becomes more remote (either temporally or spatially). In other words, it might be more relevant to consider limited and moving time (and space) frames of prior experience as determining current behaviour, with events occurring prior to (or outside) them being irrelevant. Chase (1974, 1980, 1982, 1985) presents a formal, theoretical background for the effects of previous agonistic experience on current agonistic behaviour which suggests that for any triad of birds, the process will tend always to lead to transitive dominance relationships between the three, i.e, A>B>C and A>C. It is then simply a matter of extrapolation to reach the conclusion that the linear dominance hierarchies which were found in this study and so commonly in others, are perhaps better explained by the 'positive feedback' hypothesis than by invoking a single, transitively distributed attribute of the birds or a covarying set of such attributes as putative determinants of dominance and causes of linearity in hierarchies. Hierarchy linearity was found to decrease as the number of individuals in the hierarchy increased as also found by Brewer (1961) in both black-capped and Carolina *P. carolinensis* chickadees. If the progressive addition of birds to a hierarchy over the course of a winter's observation reflects observation of increasingly rare visitors to the site (i.e. the larger the hierarchy, the greater the proportion of rare visitors that it contains), these rare visitors might be especially likely to disrupt the linearity of the hierarchy. This would occur if linearity was dependent on the transitivity of component triads, which only develops as a consequence of mutual experience. This process is perhaps especially likely to occur at artificial feeding stations which may be attracting birds from other areas and thus inflating the proportion of 'rare visitors' in the population visiting the feeders. In his study of black-capped chickadees, Glase (1973) noted the effect of feeders in causing home range overlaps and reducing the level of linearity in dominance hierarchies recorded at such sites.

In the ideal situation where the life histories of all birds were known from day one, Chase's hypothesis would be testable. However, when observations begin at the arbitrary point in a bird's life when it hits a mist-net, how do we know whether a run of agonistic successes is caused by:

a) dependence of current behaviour on previous behaviour or,

b) some fixed, independent attribute of the bird (e.g. its size) ?

This study's data imply that Chase and Drent's ideas may indeed be correct since the only variables which correlate strongly with social dominance are experiential (prior territoriality and prior residence). Accepting this point, the important problem is then to discover what is communicated by the postural display which characterizes agonistic interactions. The variables most relevant to outcome are prior residence and territorial status operating, perhaps, through the effects of previous agonistic experience on current agonistic tendencies at the site of interaction. In contrast, it seems less likely that postural display in the great tit has an important RHP-signalling function since physical attributes have not been found by this study or others (Drent 1983; Saitou 1979b) to show strong correlations with dominance in agonistic encounters.

In summary, possible signal functions for postural display seem to be:

a) prior residence/prior territoriality.

b) Site-specific agonistic tendencies ('aggressiveness') based on some or all of previous agonistic experience at or near the same locality. Since calculations of social status or rank are based on the sum of a bird's previous agonistic experience at a particular locality, this possibility could be investigated by looking at postural display in relation to cardinal index or rank at a given site, calculated within different time frames of previous agonistic experience.

c) Size - of limited importance and only between females.

d) Immediate agonistic tendencies based on a proximate internal stimulus such as hunger. This remains an untested possibility, not touched upon by the work in Chapter 4.

It is noteworthy that in three out of four of these cases, the variable suggested as being communicated by postural display is not an intrinsic and costly attribute of the signaller but can be signalled conventionally without any cost except that associated with performance of the display concerned. In other words, these three cases might all be open to cost-independent, 'bluff' signalling and its evolutionary consequences, as discussed in Chapter 1. Chapter 5 goes on to consider one particular way in which conventional signalling of 'bluffable' attributes might have evolved, namely the proposed signalling of social status through plumage variation. Chapters 6 & 7 first consider the theoretical, evolutionary implications of the types of signal function suggested above and then move on to an observational and experimental study which uses the findings of this Chapter and Chapter 5 to attempt to explain the functions of the variety of postural displays seen in agonistic encounters between great tits. The study will also draw upon data from interspecific interactions with blue and coal tits. Chapter 6 is devoted to field observations, whilst Chapter 7 is based on an aviary study of small groups of captive great tits.

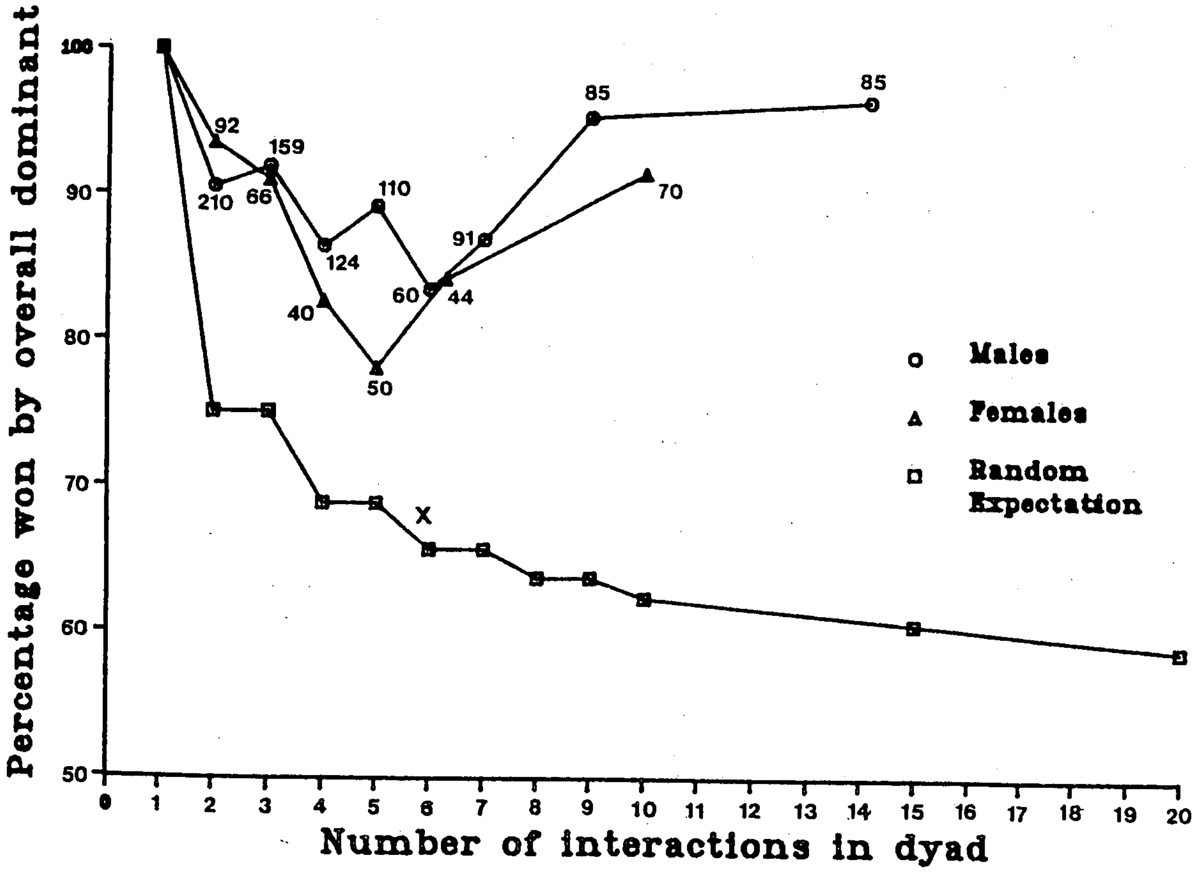


Fig. 4.1. The relationship between overall dyad asymmetry (% of interactions won by the overall dominant) and the number of interactions comprising overall dyad outcome. Sample size for each point appended. See text for full discussion.

```
006      0.001  1000  n/Critical value for resolution/max. iterations
01                    Identity of individual 1
02                    Identity of     "       2
03                    Identity of     "       3
04                    Identity of     "       4
05                    Identity of     "       5
06                    Identity of     "       n
 1      2      10     Id. of winner/Id. of loser/Number of interactions
 1      3      12
 1      4      4
 1      5      9
 1      6      5
 2      1      11
 2      3      9
 2      4      12
 2      5      22
 2      6      12
 3      1      9
 3      2      9
 3      4      6
 3      5      8
 3      6      2
 4      2      2
 4      5      7
 4      6      10
 5      1      1
 5      3      1
 5      4      5
 5      6      3
 6      1      1
 6      2      2
 6      3      2
 6      4      17
 6      5      16
```

Fig. 4.2. Input file for calculation of cardinal indices from a matrix of dominant-subordinate interactions. See text and Boyd & Silk (1983) for further explanation.

INITIAL MATRIX

```
          1      2      3      4      5      6

1         0     10     12      4      9      5     40
2        11      0      9     12     22     12     66
3         9      9      0      6      8      2     34
4         0      2      0      0      7     10     19
5         1      0      1      5      0      3     10
6         1      2      2     17     16      0     38

         22     23     24     44     62     32

  TOTAL NUMBER OF INTERACTIONS =     207
  NUMBER OF REVERSALS =     76
  PERCENT OF REVERSALS =  0.37
```

MATRIX BASED UPON COMPUTED RANKS

```
          2      1      3      6      4      5

2         0     11      9     12     12     22     66
1        10      0     12      5      4      9     40
3         9      9      0      2      6      8     34
6         2      1      2      0     17     16     38
4         2      0      0     10      0      7     19
5         0      1      1      3      5      0     10

         23     22     24     32     44     62

  TOTAL NUMBER OF INTERACTIONS =     207
  NUMBER OF REVERSALS =     55
  PERCENT OF REVERSALS =  0.27
  EQUILIBRIUM REACHED AFTER     22  ITERATIONS
  CRITICAL VALUE FOR SOLUTION =  0.0010
  MAXIMUM LIKELIHOOD ESTIMATE = -0.1031E+03
  TEST OF EQUALITY STATISTIC =   0.80736E+02  (WITH 5DF)

   RANK      ANIMAL ID          P(I)           DOMINANCE INDEX

    1            2           0.322E+00            0.113E+01
    2            1           0.310E+00            0.117E+01
    3            3           0.247E+00            0.140E+01
    4            6           0.706E-01            0.265E+01
    5            4           0.335E-01            0.340E+01
    6            5           0.172E-01            0.406E+01
```

Fig. 4.3. Output file from FORTRAN program for calculation of cardinal indices. See text and Boyd & Silk (1983) for further explanation.

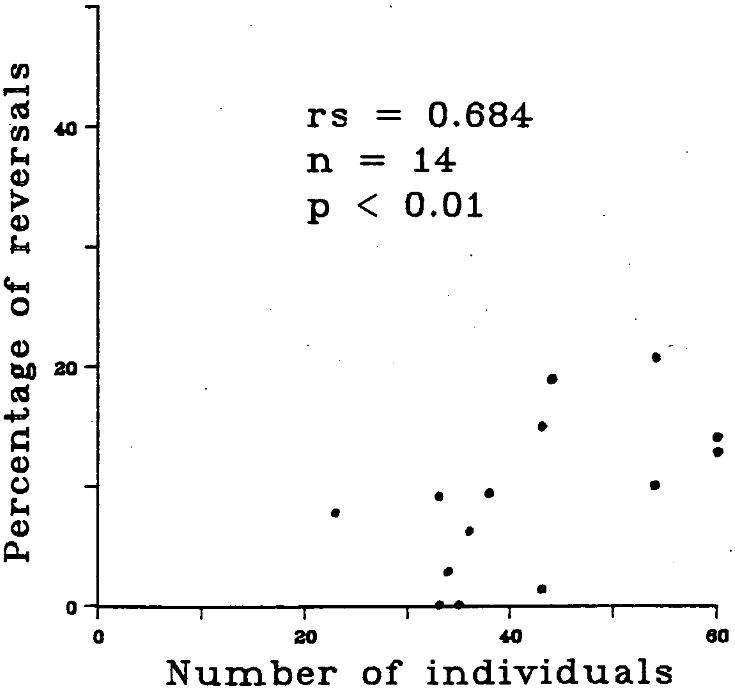


Fig. 4.4. Relationship between the number of individuals in a dominance hierarchy and its linearity. Data derived from fourteen dominance hierarchies in Appendix 6. See text for further discussion.

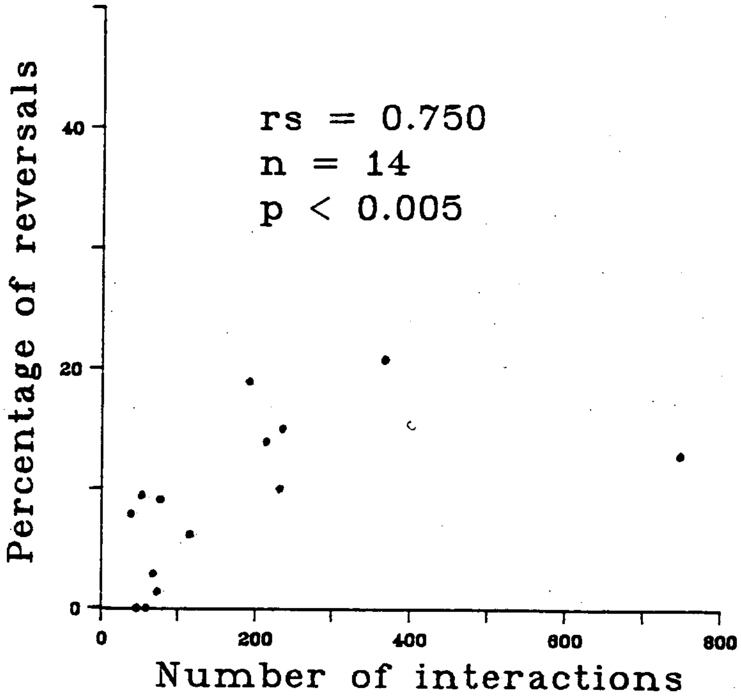


Fig. 4.5. Relationship between number of interactions recorded and linearity across the fourteen dominance hierarchies in Appendix 6. See text for further discussion.

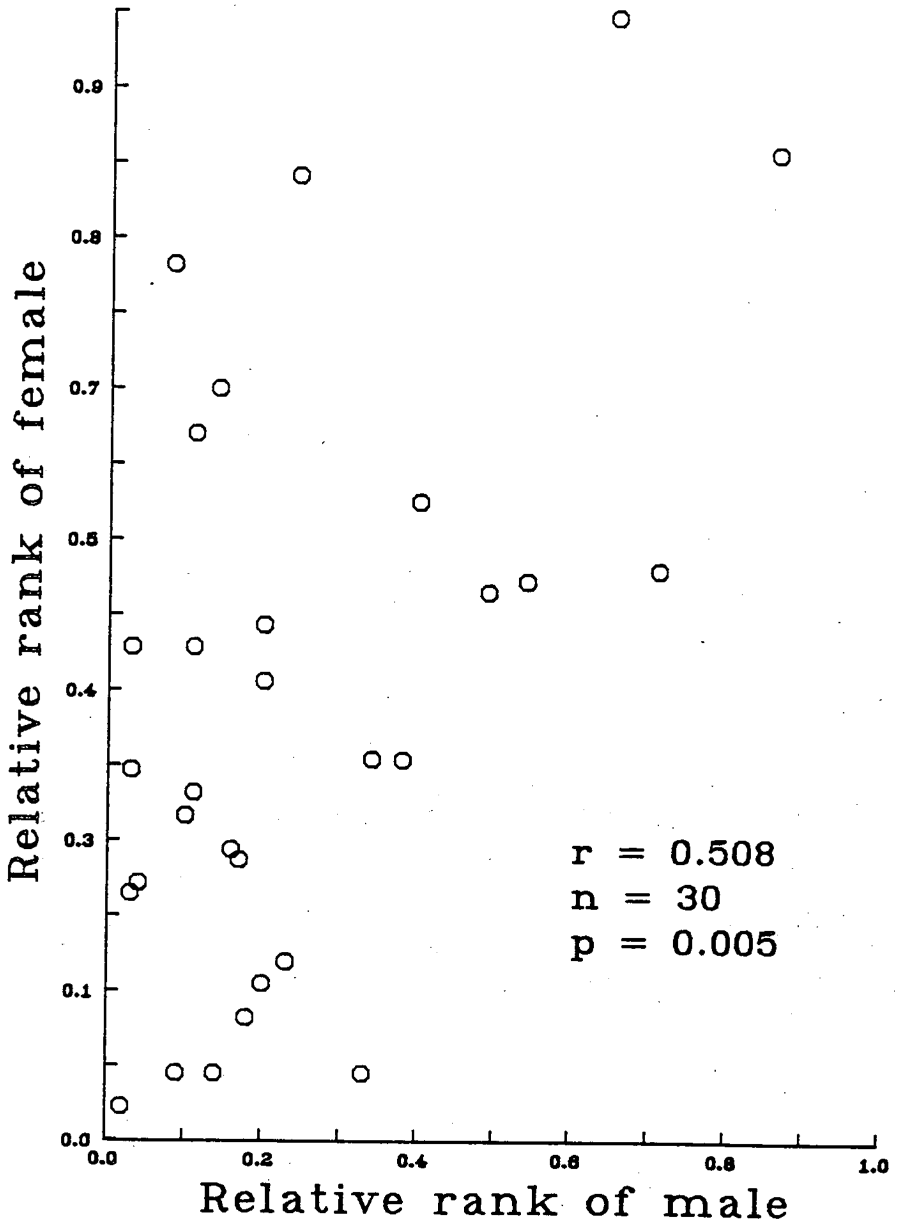


Fig. 4.6. Relationship between the ranks of the members of breeding pairs of great tits during the immediately preceding winter. Data pooled from all sites and all three winters. Relative rank = rank (derived from Appendix 6) divided by the number of individuals in the hierarchy.

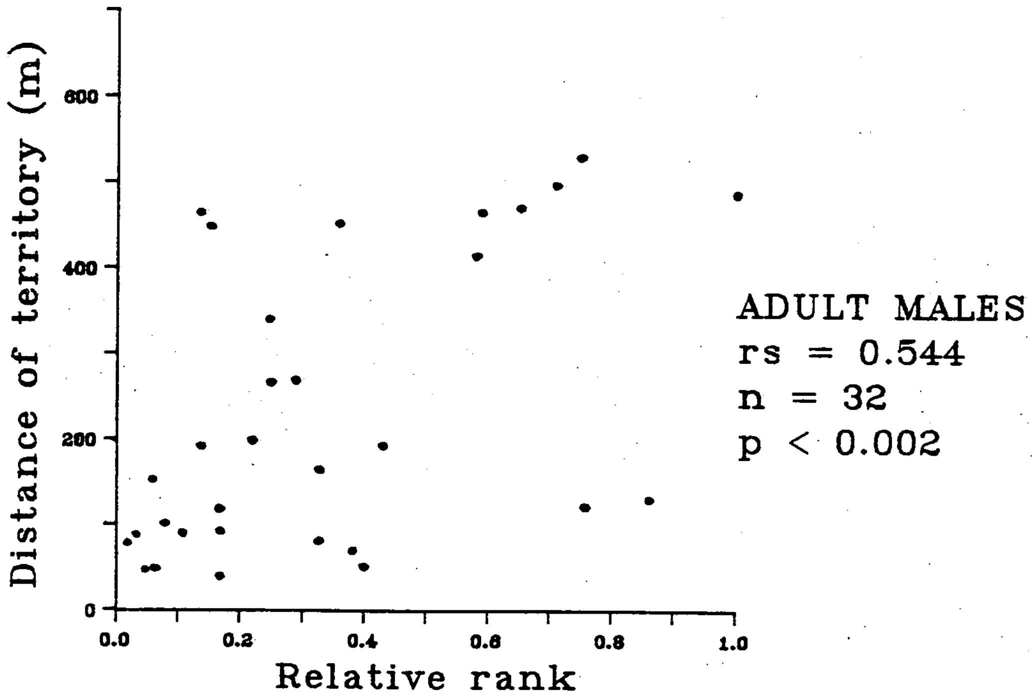


Fig. 4.7. Relationship between relative rank and distance to breeding territory (Chapter 2.4.) in the following spring, for each age-sex class. Data pooled from all three sites and all three winters.

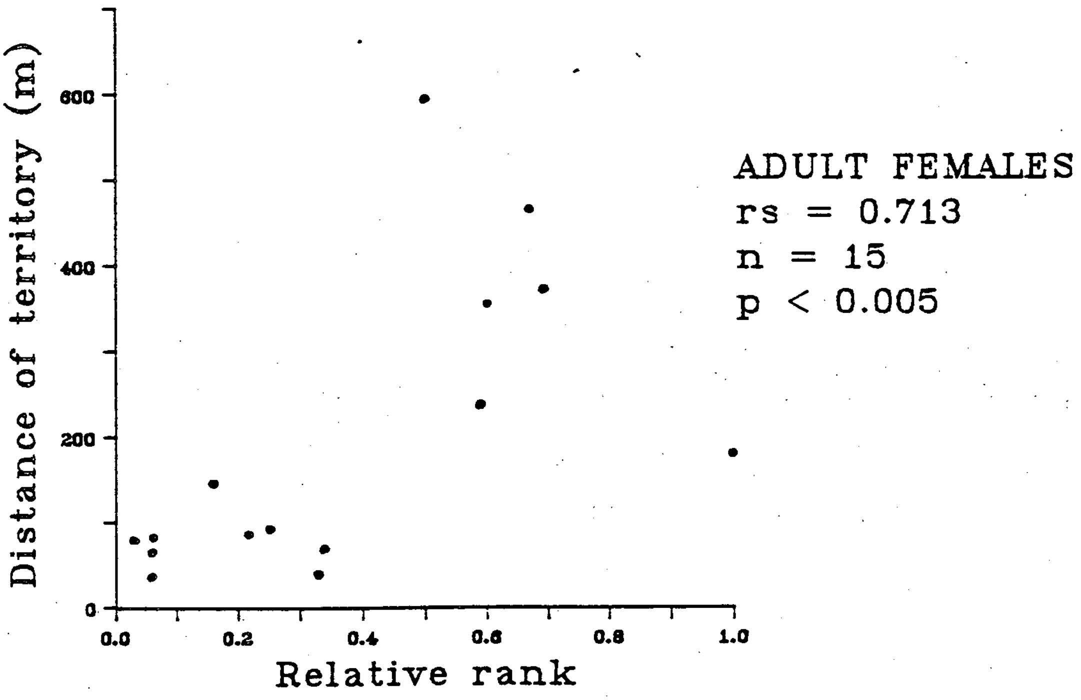


Fig. 4.7. continued.

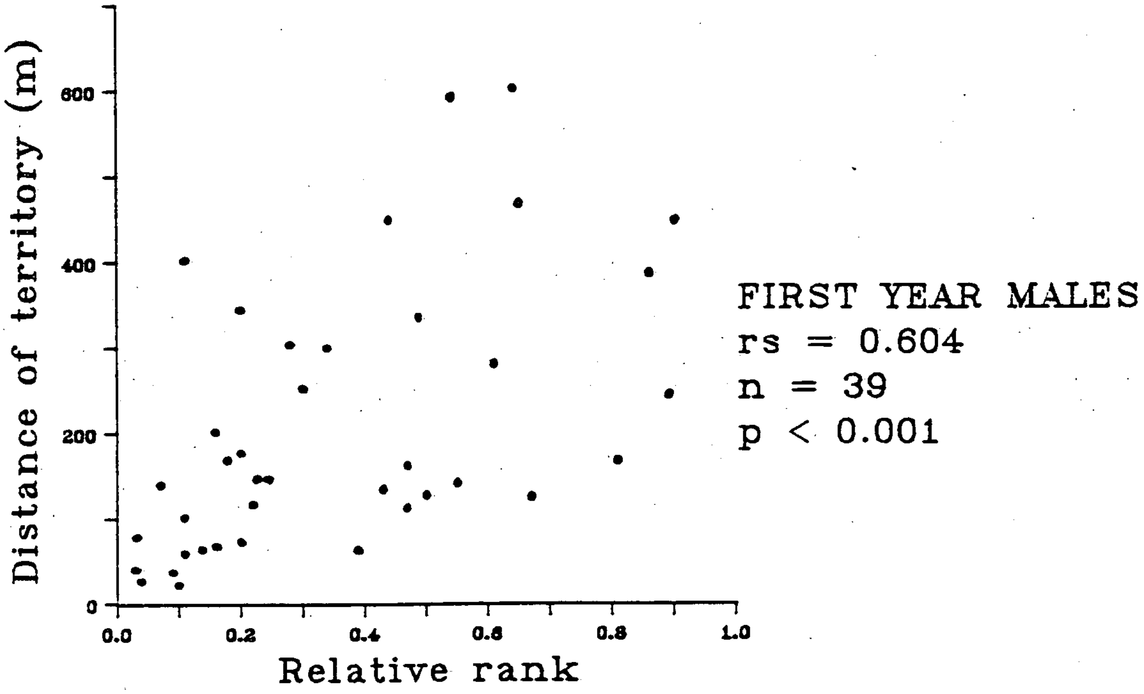


Fig. 4.7. continued.

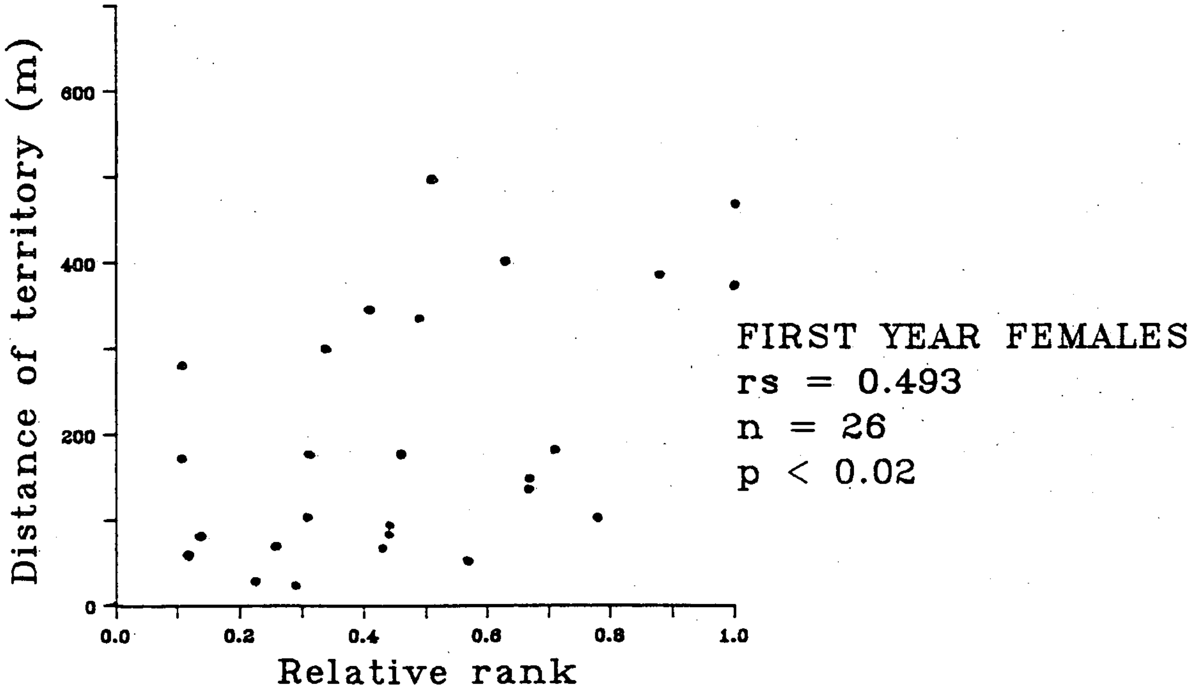
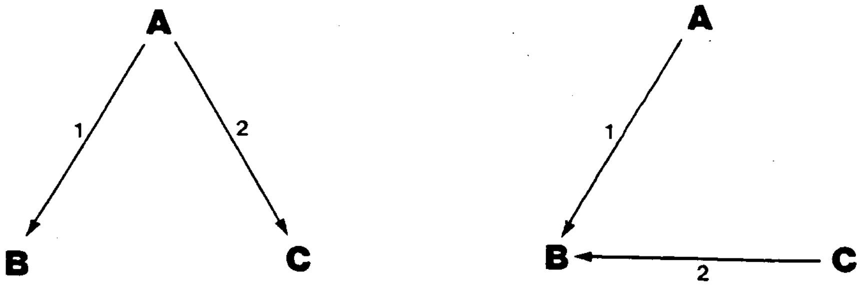
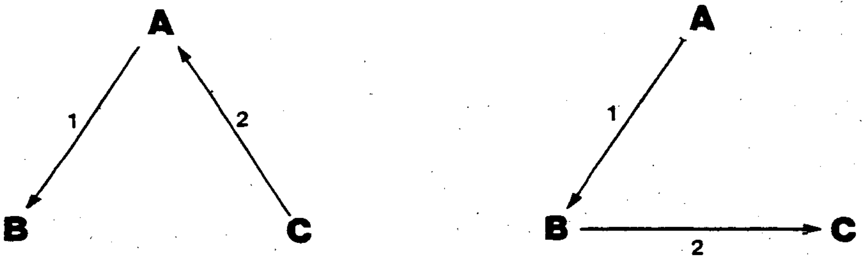


Fig. 4.7. continued.



Double Dominance

Double Subordinance



Bystander Dominates
Initial Dominant

Initial Subordinate
Dominates Bystander

Fig. 4.8. The four possible initial interaction sequences in the formation of dominance relationships in triads. Interactions are numbered in the order of occurrence. Only 'Double Dominance' and 'Double Subordination' ensure the transitivity of the dominance relationships in the triad. The other two sequences could lead to either a transitive or an intransitive triad, depending on the direction of the third relationship. Figure modified from Chase (1982, Fig. 1).

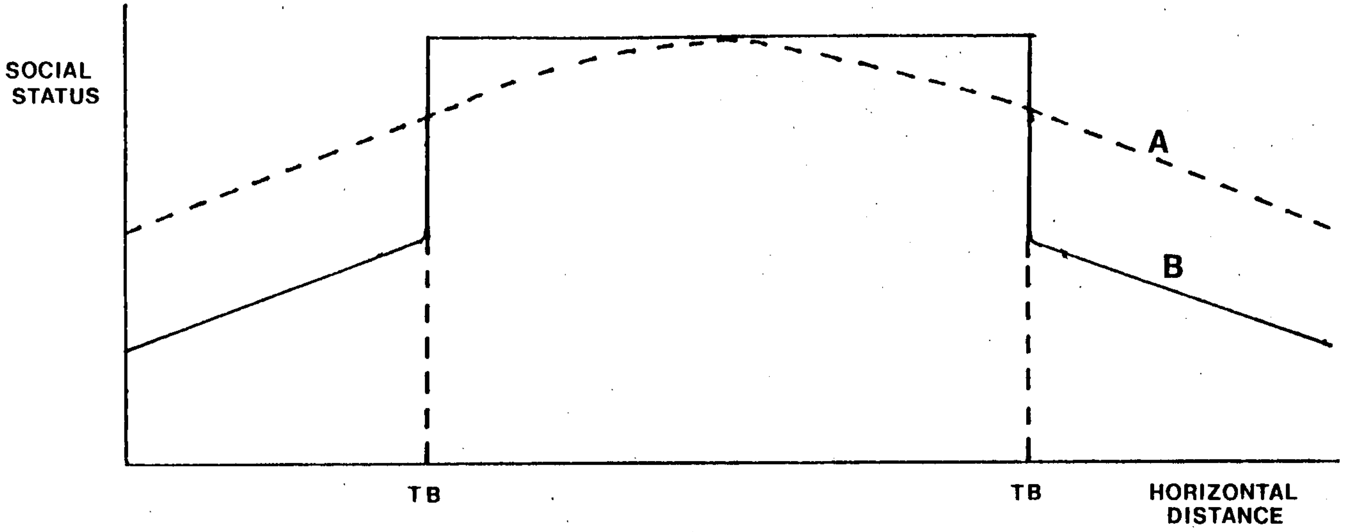


Fig. 4.9. Schematic representation of site-correlated dominance' and territoriality as spatial patterns of variation in social dominance. Line A represents site-correlated dominance over a horizontal distance represented by the x-axis. Line B represents the spatial variation in dominance associated with possession of a territory bounded at the points marked 'TB'. See text for further discussion.

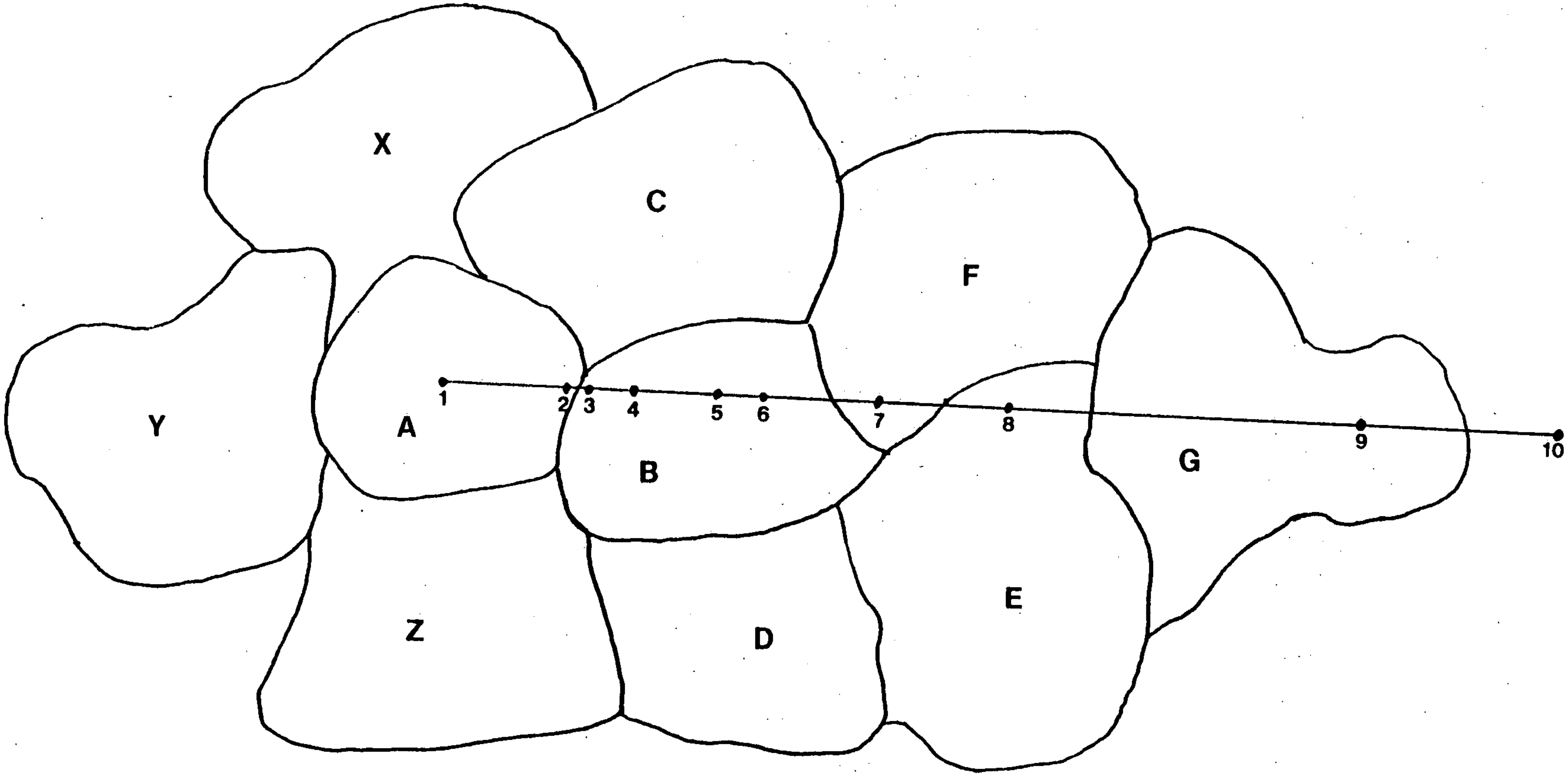


Fig. 4.10. A plan view of ten hypothetical territories occupied by males A–G and X–Z. The horizontal line marks a series of 10 stations at which the proportion of wins by male A over each of the others is recorded. Possible patterns of change in the overall social status of male A are depicted overleaf.

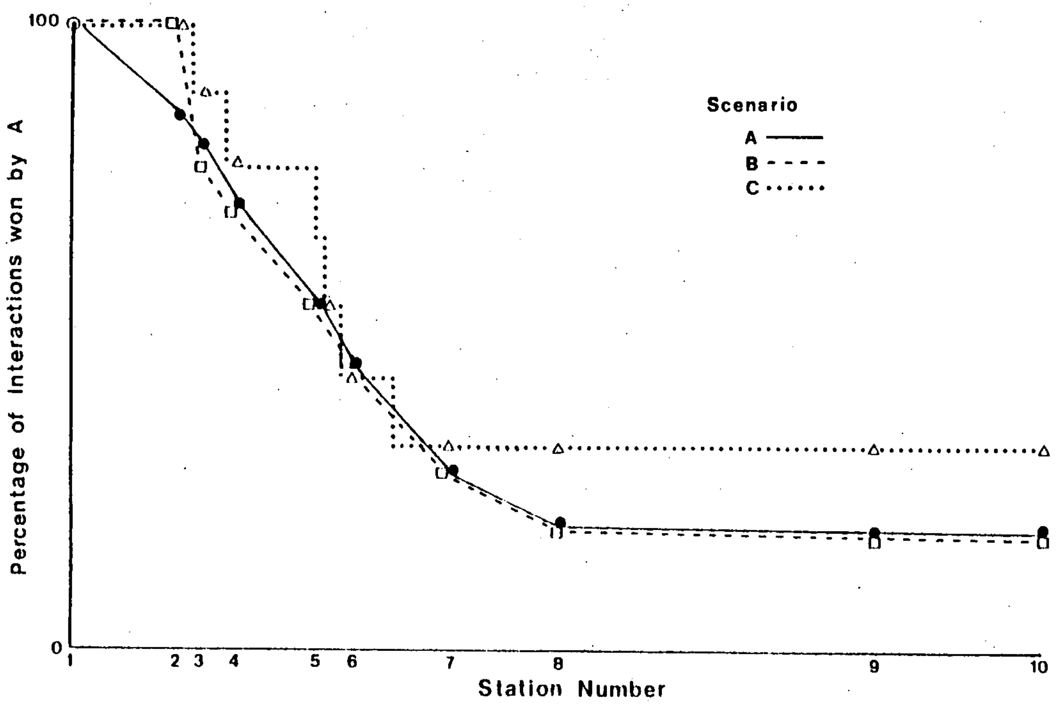


Fig. 4.10. continued. The proportion of wins by male A in competition with each other male. Overall social status is measured as the overall proportion of interactions won, . In scenario A, all changes in the overall dominant-subordinate asymmetry of each dyad are gradual from a point of total dominance. In scenario B, overall dyad asymmetries change gradually from a *bounded area* of total dominance (the territory) and thus reverse abruptly at mutual territory boundaries. In scenario C, all overall dyad asymmetries reverse abruptly, either at mutual territory boundaries or at a point where the territories of the dyad members are equidistant. These hypothetical data are presented graphically , with the line of stations as the x-axis.

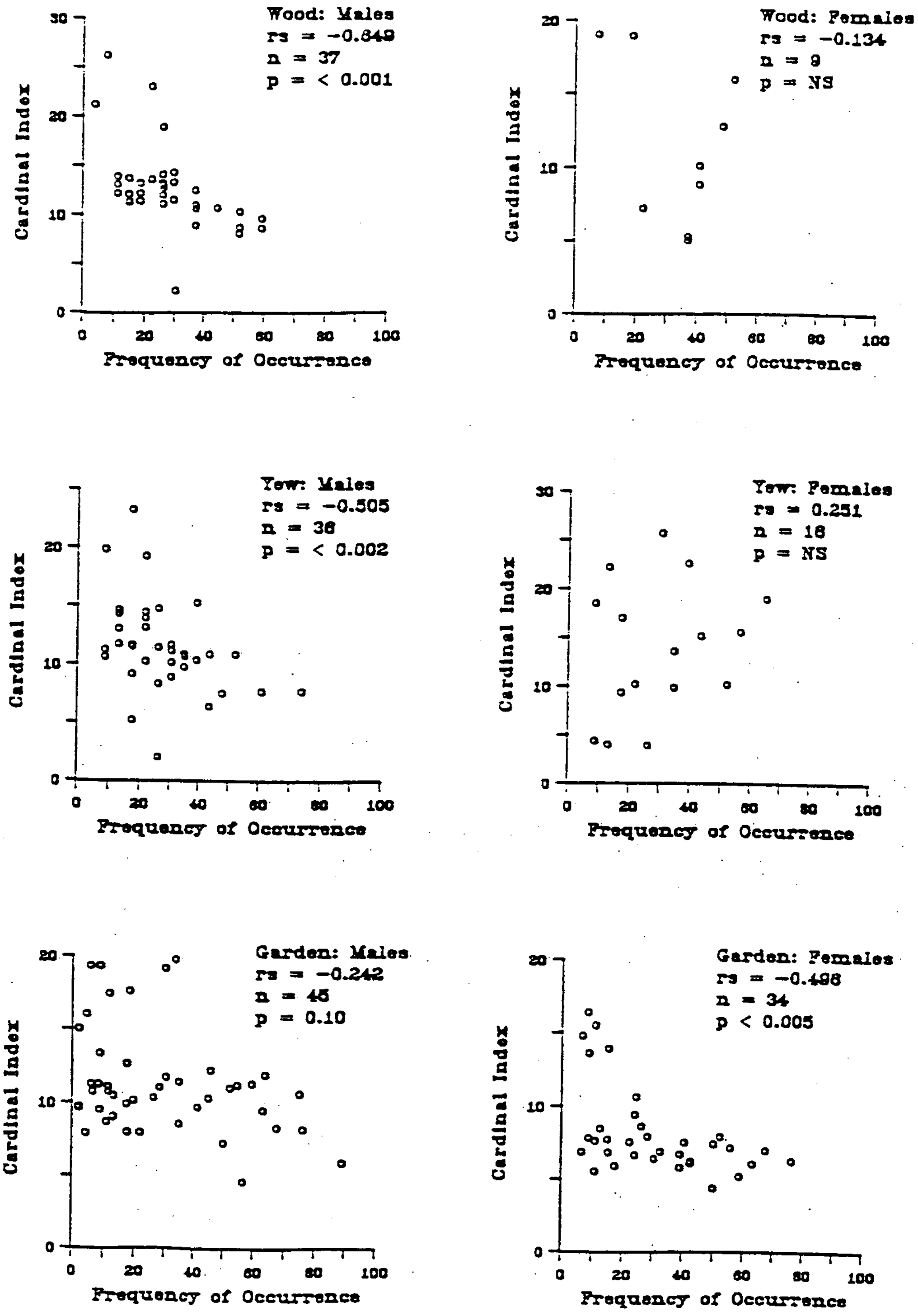
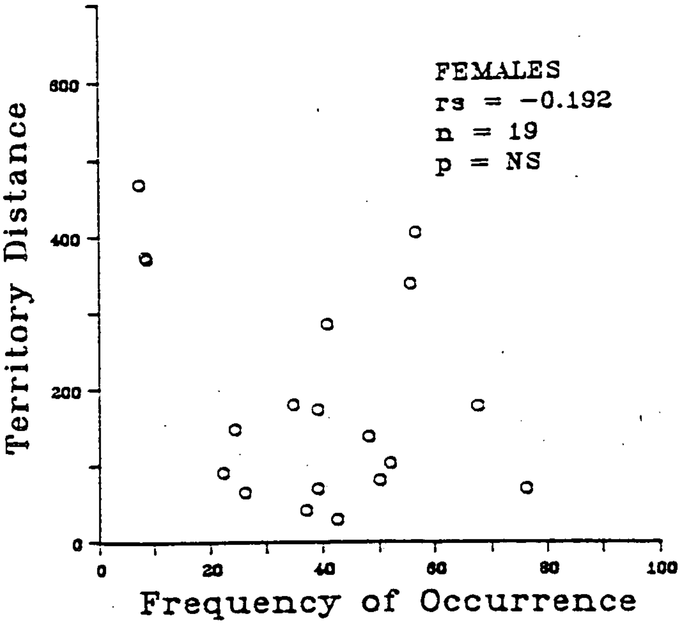


Fig. 4.11. Relationship between frequency of occurrence and social status for both sexes at each site during the 1988/89 winter. Frequency of occurrence is expressed as the proportion observation days on which a bird was seen. Cardinal indices are derived from Appendix 6.



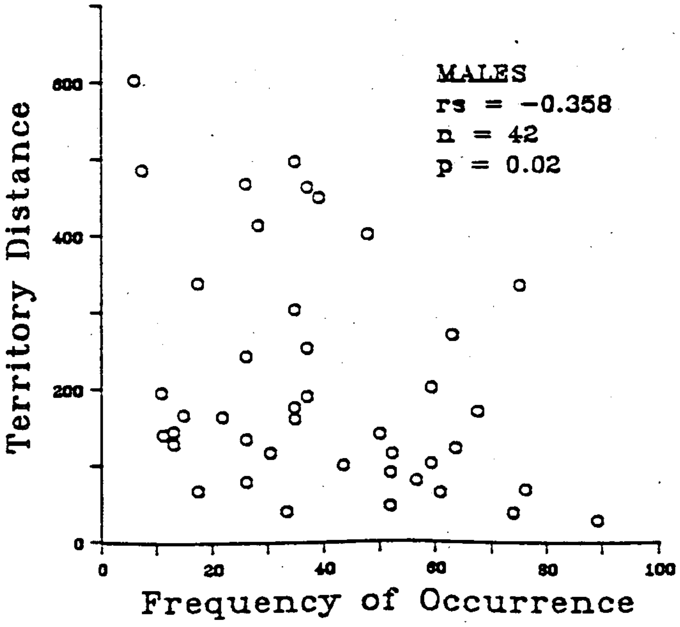


Fig. 4.12. Relationship between frequency of occurrence at a site during the winter and the distance of the breeding territory from that site during the following breeding season. Data pooled from all three sites and all three winters.

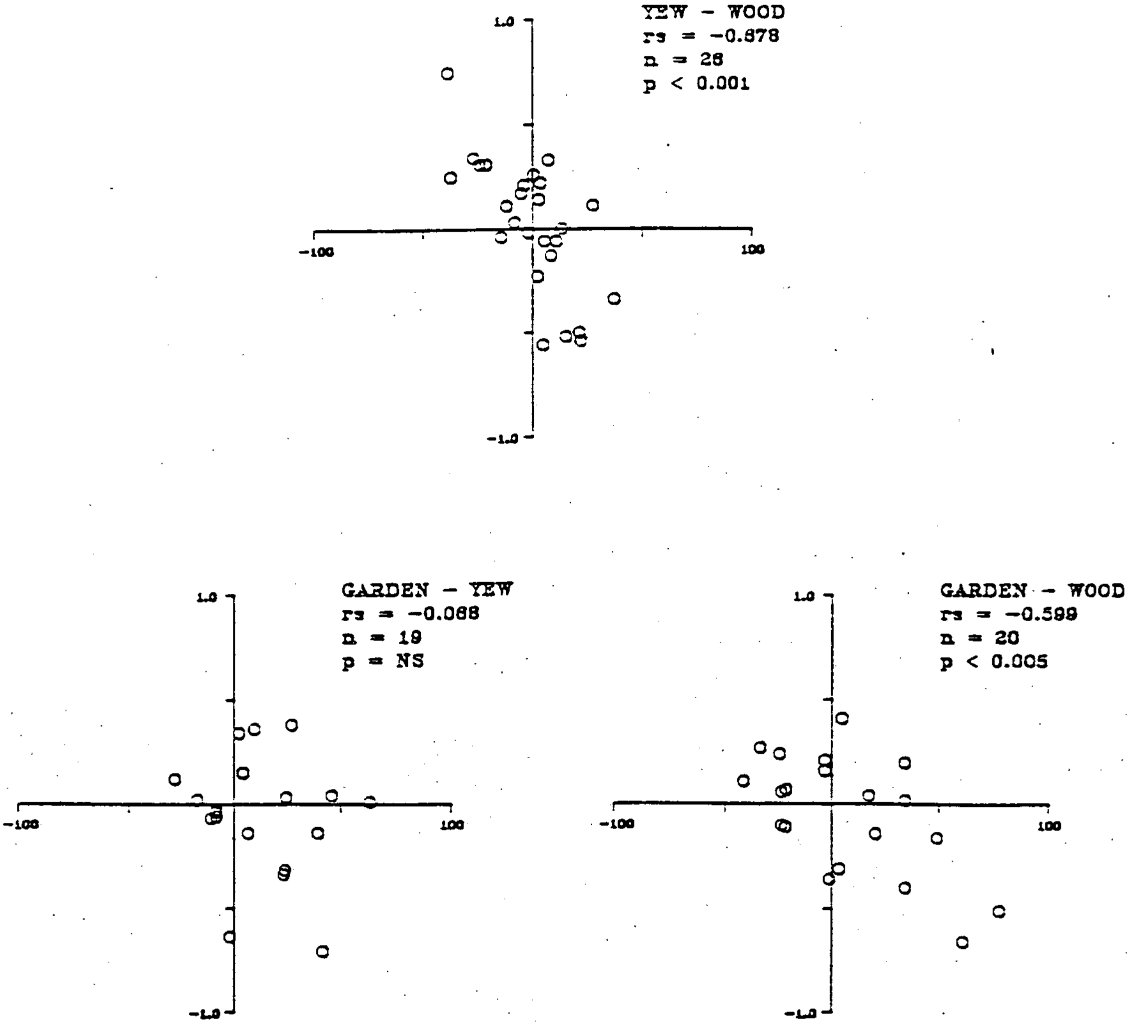


Fig. 4.13. Relationship between difference in relative rank and difference in frequency of occurrence of males recorded at both of two sites during the 1988/89 winter. Data for all three possible pairs of sites are presented.

	Number of studies considering variable	Number(%) in which variable a correlate
Size	30	16 (53.3)
Age	30	27 (90.0)
Sex	41	37 (90.2)
Territorial Status	11	11 (100.0)
Prior Residence	17	16 (94.1)
Experience of Agonistic Success	8	8 (100.0)
Aggressiveness	10	6 (60.0)

TABLE 4.1. Importance of physical, social and experiential attributes as correlates of dominance in birds. Data extracted from a scan of 62 papers.

SIZE	SPECIES STUDIED
Black & Owen (1987)	Brent Goose (*Branta bernicla*)
Collias (1943)	domestic hen
Garnett (1976)	Great Tit (*Parus major*)
Lamprecht (1986b)	Bar-headed Goose (*Anser indicus*)
Searcy (1979)	Red-winged Blackbird (*Agelaius phoeniceus*)
AGE & SEX	
Arcese & Smith (1985)	Song Sparrow (*Melospiza melodia*)
Balph et al (1979)	Dark-eyed Junco (*Junco hyemalis*)
Glase (1973)	Black-capped Chickadee (*Parus atricapillus*)
Hogstad (1987)	Willow Tit (*Parus montanus*)
Piper & Wiley (1989)	White-throated Sparrow (*Zonotrichia albicollis*)
TERRITORIAL STATUS	
Arcese & Smith (1985)	Song Sparrow
Beletsky & Orians (1987)	Red-winged Blackbird
Goforth & Baskett (1971)	Mourning Dove (*Zenaidura macroura*)
Hogstad (1987)	Willow Tit
Schjelderup-Ebbe (1922)	domestic hens & ducks
PRIOR RESIDENCE	
Arcese & Smith (1985)	Song Sparrow
Glase (1973)	Black-capped Chickadee
Krebs (1982)	Great Tit
Sabine (1959)	Dark-eyed Junco
Schjelderup-Ebbe (1935)	domestic hens & ducks
AGONISTIC EXPERIENCE	
Black & Owen (1987)	Brent Goose
Collias (1943)	domestic hens
Lamprecht (1986b)	Bar-headed Goose
Piper & Wiley (1989)	White-throated Sparrow
Schjelderup-Ebbe (1922)	domestic hens & ducks
AGGRESSIVENESS	
Balph (1977)	Dark-eyed Junco
Baptista et al (1987)	White-crowned Sparrow (*Zonotrichia leucophrys*)
Hegner & Wingfield (1987)	House Sparrow (*Passer domesticus*)
Shoemaker (1939)	Canary (*Serinus canaria*)
Watson (1970)	House Sparrow

TABLE 4.2. Selected studies demonstrating the importance of seven attributes as correlates of dominance.

		Dyads	Number(%) in which larger bird dominant	X^2	p
1986/87					
WING LENGTH	Male	69	39 (56.5)	1.18	NS
	Female	50	27 (54.0)	0.34	NS
WEIGHT	Male	76	37 (48.7)	0.07	NS
	Female	59	40 (67.8)	8.36	<0.01
1987/88					
WING LENGTH	Male	38	25 (65.8)	3.81	NS
	Female	58	27 (46.6)	0.30	NS
TARSUS LENGTH	Male	47	28 (59.6)	1.74	NS
	Female	50	26 (52.0)	0.10	NS
WEIGHT	Male	52	27 (51.9)	0.10	NS
	Female	66	27 (40.9)	2.20	NS
1988/89					
WING LENGTH	Male	174	79 (45.4)	1.48	NS
	Female	105	61 (58.1)	2.76	NS
TARSUS LENGTH	Male	193	100 (51.8)	0.26	NS
	Female	122	75 (61.5)	6.44	0.01
WEIGHT	Male	215	97 (45.1)	2.06	NS
	Female	138	86 (62.3)	8.39	<0.01
POOLED					
WING LENGTH	Male	281	143 (50.9)	0.09	NS
	Female	213	115 (54.0)	1.36	NS
TARSUS LENGTH	Male	240	128 (53.3)	1.07	NS
	Female	172	101 (58.7)	5.23	<0.05
WEIGHT	Male	343	161 (46.9)	1.29	NS
	Female	263	153 (58.2)	7.03	<0.01

TABLE 4.3. Proportion of dyads with the larger bird, estimated by three measures of body size, as the overall dominant. Data from all sites and all contexts pooled but only dyads involving birds of same age are included. Significance of deviations from random expectation (50%) analysed using chi-square tests. See text for further explanation.

1986/87		Dyads	Number(%) in which older/previously territorial bird dominant	X^2	p
AGE	Male	68	42 (61.8)	3.78	0.05
	Female	65	34 (52.3)	0.15	NS
1987/88					
AGE	Male	61	45 (73.8)	13.81	<0.001
	Female	43	30 (69.8)	6.75	<0.01
PRIOR TERRITORIALITY	Male	24	16 (66.7)	2.71	NS
	Female	25	17 (68.0)	3.28	NS
1988/89					
AGE	Male	238	135 (56.7)	4.31	<0.05
	Female	105	47 (44.8)	1.17	NS
PRIOR TERRITORIALITY	Male	136	98 (72.1)	26.50	<0.001
	Female	38	28 (73.7)	8.55	<0.01
POOLED					
AGE	Male	367	222 (60.5)	16.16	<0.001
	Female	213	111 (52.1)	0.38	NS
PRIOR TERRITORIALITY	Male	160	114 (71.3)	28.91	<0.001
	Female	63	45 (71.4)	11.59	<0.001

TABLE 4.4a. Correlation of age difference and difference in prior territorial status with overall dyadic dominance. Deviations from random expectation (50%) analysed using chi-square tests. Data from all sites and contexts pooled. See text for further explanation.

	Dyads	Number(%) in which older bird dominant	X^2	p
1987/88				
Male	43	32 (74.4)	10.28	<0.01
Female	23	16 (69.6)	3.56	NS
1988/89				
Male	131	60 (45.8)	0.93	NS
Female	75	26 (34.7)	7.07	<0.01
POOLED				
Male	174	92 (52.9)		
Female	98	42 (42.9)		

TABLE 4.4b. Proportion of dyads in which older bird was also the overall dominant. Deviation from random expectation (50%) analysed using chi-square tests. Analysis uses data pooled from all sites and contexts but omits dyads where either bird held a territory (male) or was paired to a territory holder (female) in the previous breeding season.

	1986/87	1987/88	1988/89	POOLED(%)	X^2	p
MALES	52/66	22/35	151/207	225/308 (73.1%)	65.47	<0.001
FEMALES	19/41	36/61	72/117	127/219 (58.0%)	5.65	<0.05

TABLE 4.4c. Proportion of dyads in which earlier-ringed bird was overall dominant. Analysis restricted to dyads of first-year birds. Data from all contexts pooled and all sites treated independently. Deviations from random expectation (50%) are analysed using chi-square tests.

	1986/87	1987/88	1988/89	POOLED	Difference from random expectation
WING LENGTH					
Food (intruder)	-	-	67/139	67/139	NS
Food (occupier)	-	-	31/62	31/62	NS
Food (total)	36/64	13/26	85/173	134/263	NS
'Territorial'	7/15	11/18	16/48	34/80	NS
TARSUS LENGTH					
Food (intruder)	-	-	86/173	86/173	NS
Food (occupier)	-	-	31/67	31/67	NS
Food (total)	-	19/23	92/192	111/215	NS
'Territorial'	-	16/21	28/54	44/75	NS
WEIGHT					
Food (intruder)	-	-	88/183	88/183	NS
Food (occupier)	-	-	36/80	36/80	NS
Food (total)	36/70	9/33	98/209	143/312	NS
'Territorial'	5/24	11/22	26/57	42/103	NS

TABLE 4.5a. Proportion of dyads in which larger male, as the estimated by three measures of body size, was the overall dominant. Analysis uses data pooled from all sites and does not control for age differences. Different resource types ('food' vs. 'territorial') and contexts (intruding bird wins vs. occupying bird wins) are treated as independent data sets. Deviations from random expectation (50%) of the pooled totals from the three years are analysed using chi-square tests and their significance given in the last column.

	1986/87	1987/88	1988/89	POOLED	Difference from random expectation
WING LENGTH					
Food (intruder)	-	-	43/80	43/80	NS
Food (occupier	-	-	30/48	30/48	NS
Food (total)	26/49	13/21	58/100	97/170	NS
'Territorial'	5/5	2/6	8/16	15/27	NS
TARSUS LENGTH					
Food (intruder)	-	-	58/100	58/100	NS
Food (occupier	-	-	34/57	34/57	NS
Food (total)	-	6/19	71/123	77/142	NS
'Territorial'	-	3/6	11/18	14/24	NS
WEIGHT					
Food (intruder)	-	-	67/102	67/102	<0.01
Food (occupier	-	-	31/61	31/61	NS
Food (total)	39/58	9/24	78/129	126/211	<0.01
'Territorial'	5/5	4/9	12/22	21/36	NS

TABLE 4.5b. Proportion of dyads in which the larger female, as estimated by three measures of body size, was the overall dominant. Analysis as for Table 4.5a.

		r_s	number of interactions	p
MALES				
WING LENGTH	Date vs. D-S Difference	-0.104	534	0.02
	Date vs. Asymmetry	-0.049	534	NS
TARSUS LENGTH	Date vs. D-S Difference	0.051	510	NS
	Date vs. Asymmetry	-0.004	510	NS
WEIGHT	Date vs. D-S Difference	0.042	534	NS
	Date vs. Asymmetry	0.163	534	<0.001
FEMALES				
WING LENGTH	Date vs. D-S Difference	-0.132	302	0.02
	Date vs. Asymmetry	-0.088	302	NS
TARSUS LENGTH	Date vs. D-S Difference	-0.112	300	0.05
	Date vs. Asymmetry	-0.081	300	NS
WEIGHT	Date vs. D-S Difference	-0.055	302	NS
	Date vs. Asymmetry	-0.067	302	NS

TABLE 4.6. Relationship between season and biometrics as correlates of dominance in individual interactions. Analysis based on data collected in 1988/89 in the Garden at food. Date = number of days from October 1 (=1). D-S Difference = size of dominant minus size of subordinate. Asymmetry = absolute difference in size between dominant and subordinate. See text for further explanation.

		r_s	Number of interactions	p
MALES				
WING LENGTH	Rate vs. D-S Difference	-0.088	534	0.04
	Rate vs. Asymmetry	0.063	534	NS
TARSUS LENGTH	Rate vs. D-S Difference	-0.036	510	NS
	Rate vs. Asymmetry	-0.087	510	0.05
WEIGHT	Rate vs. D-S Difference	-0.002	534	NS
	Rate vs. Asymmetry	-0.021	534	NS
FEMALES				
WING LENGTH	Rate vs. D-S Difference	0.050	302	NS
	Rate vs. Asymmetry	0.124	302	0.03
TARSUS LENGTH	Rate vs. D-S Difference	0.020	300	NS
	Rate vs. Asymmetry	0.100	300	NS
WEIGHT	Rate vs. D-S Difference	0.021	302	NS
	Rate vs. Asymmetry	0.074	302	NS

TABLE 4.7. Relationship between interaction rate on day of observation (number per hour) and biometrics as correlates of dominance in individual interactions. Analysis based on same data set as in Table 4.6. Interpretation as for Table 4.6. See text for further explanation.

Year	Sex	Class	Sample	r_s	p
1986/87	Male	Dominant	272	0.220	<0.001
1986/87	Male	Subordinate	237	0.321	<0.001
1986/87	Female	Dominant	204	-0.046	NS
1986/87	Female	Subordinate	199	0.135	0.014
1988/89	Male	Dominant	637	0.185	<0.001
1988/89	Male	Subordinate	578	0.044	NS
1988/89	Female	Dominant	317	-0.216	<0.001
1988/89	Female	Subordinate	306	-0.350	<0.001

TABLE 4.7a. Spearman rank correlation coefficients between cardinal index of the interacting bird and interaction rate on the day of observation, for intrasexual interactions at Garden feeders in 1986/87 and 1988/89, classified by year and sex. All interactions in the four data sets are treated as being independent and each data set is divided into two classes according to whether the bird providing the datum was dominant or subordinate in the interaction. See text for further discussion.

		Number(%) of dyads with larger bird as overall dominant			
	Number of interactions	Male	p	Female	p
WING LENGTH	1	44/81(54.3)	NS	36/63(57.1)	NS
	2	17/32(53.1)	NS		
	2-3			15/26(57.7)	NS
	3-4	18/36(50.0)	NS		
	4+			8/11(72.7)	NS
	5+	5/22(22.7)	<0.05		
TARSUS LENGTH	1	46/90(51.1)	NS	38/72(52.8)	NS
	2	16/34(47.1)	NS		
	2-3			24/38(63.2)	NS
	3-4	20/44(45.5)	NS		
	4+			6/14(42.9)	NS
	5+	10/24(41.7)	NS		
WEIGHT	1	49/97(50.5)	NS	42/76(55.3)	NS
	2	18/39(46.2)	NS		
	2-3			24/39(61.5)	NS
	3-4	22/47(46.8)	NS		
	4+			11/15(73.3)	NS
	5+	14/25(56.0)	NS		

TABLE 4.8. Relationship between interaction frequency (number of interactions constituting overall outcome) and biometrics as correlates of dominance. Analysis based on data collected in 1988/89 in the Garden at food. p = significance of difference from random expectation (50%), as analysed using chi-square tests. See text for further explanation.

		r_s	Number of dyads	p
MALES				
WING LENGTH	AI vs. D-S Difference	-0.043	207	NS
	AI vs. Asymmetry	0.060	207	NS
	(all dyads)	0.024	1431	NS
TARSUS LENGTH	AI vs. D-S Difference	-0.129	193	NS
	AI vs. Asymmetry	-0.017	193	NS
	(all dyads)	0.047	1326	NS
WEIGHT	AI vs. D-S Difference	0.025	207	NS
	AI vs. Asymmetry	-0.007	207	NS
	(all dyads)	-0.011	1431	NS
FEMALES				
WING LENGTH	AI vs. D-S Difference	-0.014	130	NS
	AI vs. Asymmetry	0.024	130	NS
	(all dyads)	0.000	2346	NS
TARSUS LENGTH	AI vs. D-S Difference	-0.056	129	NS
	AI vs. Asymmetry	-0.034	129	NS
	(all dyads)	0.028	2278	NS
WEIGHT	AI vs. D-S Difference	0.059	130	NS
	AI vs. Asymmetry	-0.030	130	NS
	(all dyads)	-0.005	2346	NS

TABLE 4.9. Relationship between association index (AI) and biometrics as correlates of dominance. Analysis based on overall dyad outcomes recorded from the Garden, at food, during 1988/89. Interpretation as for Tables 4.6. and 4.7, except that 'all dyads' entry refers to correlation between AI and size asymmetry for *all* dyads for which these two measures are available, irrespective of whether or not they were seen to interact. For further explanation, see text.

				n	mean cardinal index or rank	t/W	p
GARDEN	1986/87	Males	T:	12	4.80± 1.68	3.72	<0.001
			NT:	23	7.87± 3.21		
			S:	19	6.88± 2.72	0.12	0.90
			NS:	16	6.74± 3.63		
		Females	T:	11	8.57± 2.30	1.41	0.17
			NT:	21	10.11± 3.87		
			S:	21	9.16± 3.24	0.89	0.38
			NS:	11	10.38± 3.87		
POOLED	1987/88	Males	T:	18	0.39	300.5	0.03
			NT:	24	0.63		
			S:	25	0.60	580.5	0.68
			NS:	19	0.50		
		Females	T:	12	0.54	223.5	0.42
			NT:	29	0.53		
			S:	17	0.50	324.0	0.39
			NS:	24	0.55		
GARDEN	1988/89	Males	T:	16	9.13± 2.03	3.98	<0.001
			NT:	29	12.53± 3.72		
		Females	T:	11	7.78± 3.24	0.48	0.64
			NT:	24	8.33± 2.98		
YEW	1988/89	Males	T:	14	9.30± 3.23	2.92	0.006
			NT:	22	12.81± 3.92		
		Females	T:	3	9.78± 5.86	1.28	0.29
			NT:	13	14.76± 6.90		
WOOD	1988/89	Males	T:	12	11.22± 5.64	1.15	0.27
			NT:	25	13.24± 3.22		
		Females	T:	6	11.51± 5.35	0.04	0.97
			NT:	3	11.34± 7.03		
POOLED	1988/89	Males	T:	42	0.26	1673.5	<0.001
			NT:	76	0.63		
		Females	T:	20	0.45	539.0	0.27
			NT:	40	0.57		

TABLE 4.10. Relationships between winter social status, territorial status in the following spring (T = occupying a local territory; NT = not occupying a local territory) and reappearance in (= survival to) the next winter (S = did survive; NS = not known to have survived). For single site comparisons, social status is measured by cardinal index and a t-test is employed. For comparisons pooling data from all sites in one year, social status is measured by relative rank (rank divided by number of individuals in the hierarchy) and a Mann-Whitney-Wilcoxon test is used.

	n	r_s	p
GARDEN - YEW			
All birds	198	0.169	<0.02
Adult males	52	-0.023	NS
Adult females	49	-0.057	NS
First-year males	46	0.388	<0.01
First-year females	51	0.214	0.13
GARDEN - WOOD			
All birds	200	0.039	NS
Adult males	51	-0.041	NS
Adult females	51	-0.102	NS
First-year males	47	0.147	NS
First-year females	51	0.086	NS
YEW - WOOD			
All birds	193	0.463	<0.001
Adult males	55	0.549	<0.001
Adult females	49	0.289	<0.05
First-year males	40	0.428	<0.01
First-year females	49	0.505	<0.001

TABLE 4.11. Correlations between frequencies of occurrence at the three feeding stations in 1988/89. Frequency of occurrence measured as proportion of observation days after its initial capture and colour-ringing upon which a bird was seen.

		n	Number(%) of dyads with most frequently occurring bird as overall dominant.	X^2	p
GARDEN	Males	263	170(64.6)	22.54	<0.001
	Females	161	98(60.9)	7.61	<0.01
YEW	Males	120	84(70.0)	19.21	<0.001
	Females	49	32(65.3)	4.61	<0.05
WOOD	Males	144	93(64.6)	12.26	<0.001
	Females	35	24(68.6)	4.86	<0.05

TABLE 4.12. Proportion of dyads in which the bird most frequently occurring at the site was also the overall dominant and difference of this proportion from random expectation (50%). Data from 1988/89, and includes all contexts of interaction.

			n	mean frequency of occurrence	t	p
GARDEN	Males	T:	16	44.5%	3.37	0.003
		NT:	29	20.5%		
	Females	T:	10	41.1%	1.84	0.089
		NT:	24	26.0%		
YEW	Males	T:	14	37.3%	3.11	0.006
		NT:	22	21.9%		
	Females	T:	3	39.1%	1.20	0.32
		NT:	13	28.1%		
WOOD	Males	T:	12	35.5%	1.86	0.08
		NT:	25	24.1%		
	Females	T:	6	34.6%	0.15	0.89
		NT:	3	32.1%		
POOLED	Males	T:	42	39.5%	4.83	<0.001
		NT:	76	22.1%		
	Females	T:	19	38.7%	2.20	0.036
		NT:	40	27.1%		

TABLE 4.13. The relationship between frequency of occurrence at feeding stations (measured as in Table 4.11.) and subsequent territorial fate (as in Table 4.10.). All proportions were arcsine square root-transformed before being used in t-tests.

Year	Total observed in population during winter	Number(%) becoming established on local territory
1986/87		
AM	21	6(28.6)
FM	45	8(17.8)
AF	17	7(41.1) **
FF	47	5(10.6)
1987/88		
AM	20	12(60.0) ***
FM	64	8(12.5)
AF	13	8(61.5) ***
FF	85	9(10.6)
1988/89		
AM	24	16(66.7) ***
FM	96	11(11.5)
AF	26	10(38.5) **
FF	104	12(11.5)

TABLE 4.14a. Relationship between age and territorial status in subsequent breeding season. Significant differences from random expectation are indicated by asterisks (* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$) based on chi-square tests.

		ADULTS		FIRST-YEARS	
		n	mean	n	mean
WING LENGTH (mm)					
Males	T:	19	77.5 ± 1.7	29	76.6 ± 1.2
	NT:	67	76.8 ± 1.5	114	76.2 ± 1.3
			t = 1.61, p = 0.12		t = 1.50, p = 0.14
Females	T:	18	74.1 ± 1.3	25	73.4 ± 1.5
	NT:	69	74.0 ± 1.5	172	73.4 ± 1.4
			t = 0.19, p = 0.85		t = 0.02, p = 0.98
TARSUS LENGTH (mm)					
Males	T:	17	21.8 ± 0.7	22	22.1 ± 0.5
	NT:	32	21.9 ± 0.6	77	22.0 ± 0.6
			t = 0.58, p = 0.57		t = 0.50, p = 0.62
Females	T:	12	21.0 ± 0.7	20	21.2 ± 0.7
	NT:	48	21.0 ± 0.6	106	21.2 ± 0.7
			t = 0.07, p = 0.95		t = 0.28, p = 0.78
WEIGHT (g)					
Males	T:	19	19.5 ± 1.0	28	19.7 ± 0.7
	NT:	67	19.8 ± 1.1	122	19.7 ± 1.0
			t = 1.46, p = 0.15		t = 0.44, p = 0.66
Females	T:	18	18.6 ± 0.6	25	18.3 ± 0.9
	NT:	69	18.1 ± 1.0	171	18.3 ± 1.0
			t = 2.40, p = 0.02		t = 0.26, p = 0.80
VSI (mm)					
Males	T:	33	1070 ± 141		
	NT:	85	1066 ± 158		
			t = 0.13, p = 0.89		
Females	T:	26	704 ± 119		
	NT:	118	659 ± 117		
			t = 1.74, p = 0.09		

TABLE 4.14b. Relationship between morphological characteristics and territorial status in the subsequent breeding season. T = occupying local territory. NT = not known to be occupying local territory. VSI = ventral stripe index (see Chapter 5). Data from all years pooled with birds appearing in more than one year treated independently. All size measurements were expressed as the mean of all captures of a bird within one season. In the case of weights, these are first corrected to expected weight at 1200h for captures in those months where body weight was significantly correlated with time of day (Table 3.14.).

CHAPTER 5.

THE VENTRAL STRIPE – A MEANS OF AGONISTIC COMMUNICATION ?

5.1. BACKGROUND

Rohwer (1975) proposed that the position of a bird species along an axis of winter plumage variability is functionally related to the social system that determines access to resources. Specifically, given the fulfillment of three conditions, the evolution of continuously variable plumage characteristics as signals of social status could be favoured as a means of allowing potentially damaging competition over resources to be settled conventionally, without recourse to actual fighting. These conditions are:

i) that there is interference competition for resources,

ii) that there is variation in fighting ability,

iii) that repeated aggressive contacts are coupled with difficulty of individual recognition due to large flock size or instability of flock composition.

Rohwer found correlations between plumage variability, winter social structure and flock stability across a number of North American passerine species. Variability increased with flocking behaviour and decreased with dispersion and territoriality of the winter population. His studies on the most variably plumaged of these species, Harris' Sparrow *Zonotrichia querula* (Rohwer 1975, 1977, 1985; Rohwer & Rohwer 1978; Rohwer & Ewald 1981; Rohwer *et al* 1981), are now widely cited as pioneering evidence for the existence of status signalling (e.g. Krebs & Davies 1981; Maynard Smith 1982). However, with hindsight, both Rohwer's and others' tests of the status signalling hypothesis (SSH) leave little ground for confidence in the idea that plumage variability has evolved to signal social status. One problem is that in none of Rohwer's studies are the observed correlations between plumage and status independent of the sex and age of the birds concerned. Similarly, in experimental studies where plumage and hormonal manipulations of birds were carried out, these transcended the boundaries of the trait distributions of age-sex classes to create, for example, a false 'adult male' by manipulation of a juvenile male (e.g. Fugle *et al* 1984; Parsons & Baptista 1980; Rohwer 1977; Rohwer & Rohwer 1978). The same problems apply to other studies of Harris' Sparrows (Watt 1986a), white-crowned sparrows *Z. leucophrys* (Fugle *et* *al* 1984; Parsons & Baptista 1980; Watt 1986b), chaffinches *Fringilla coelebs* (Marler 1955), dark-eyed juncos *Junco hyemalis* (Baker & Fox 1978; Balph *et al* 1979; Ketterson 1979), penguins (Ryan *et al* 1987) and oystercatchers *Haematopus ostralegus* (Ens & Goss-Custard 1986). Secondly, several experimental studies (e.g. Parsons & Baptista 1980; Rohwer 1977; Rohwer & Rohwer 1978) have suffered from methodological flaws such as inadequate controls and the introduction of manipulated birds to established social groups so that prior residency effects and neighbour-stranger discrimination may have outweighed the effects of the manipulation itself (Roper 1986).

Watt (1986b) suggested the inclusion of age and sex-related plumage variation under a broad definition of status signalling. However, Balph *et al* (1979), Rohwer (1982) and Shields (1977) point out that differential predation risk (Baker & Parker 1979), sexual selection (Darwin 1871; Fisher 1930) and species recognition (Sibley 1957) may all be important selection pressures behind the evolution of age and sex-related plumage differences, especially in species with only one complete moult during the annual cycle. Jarvi *et al* (1987a) have tested eight such hypotheses on the pied flycatcher *Ficedula hypoleuca*, finding intersexual selection to be the most plausible cause of plumage variation in this species. Since these alternative explanations are less likely to apply to plumage variation within age-sex classes, the SSH is generally reserved for cases where status-plumage correlations occur between individuals of the *same* age-sex class (Whitfield 1987). Within these constraints, Whitfield found only two examples of species where there was evidence that continuous plumage variability signalled individual status - the great tit (Jarvi & Bakken 1984) and the pine siskin *Carduelis pinus* (Balph & Balph 1979). Indeed, Jackson *et al* (1988) now report that they find no support for the SSH in flocks of Harris' Sparrows of a single age-sex class.

There is now evidence that status signalling also occurs in the house sparrow *Passer domesticus* (Moller 1987a,b; Ritchison 1985), the red-winged blackbird *Agelaius phoeniceus* (Eckert & Weatherhead 1987a,b) and possibly in the greenfinch *Carduelis chloris* and corn bunting *Miliaria calandra* (Maynard Smith & Harper 1988), dark-eyed junco (Holberton *et al* 1989) and robin *Erithacus rubecula* (Harper pers comm.). With the exception of the pine siskin, all these species show a positive correlation between status and the size of a plumage patch. Further observational and experimental work (Harper *et al* in press; Jarvi *et al* 1987b; Maynard Smith & Harper 1988) has also been carried out on the great tit and is reported to support the existence of status signalling in this species. As a result of this published evidence, the great tit has replaced Harris' Sparrow as a much quoted example in support of the evolution of status signalling (e.g. Whitfield 1987). For reasons discussed below I felt that this situation might yet be premature and therefore carried out a further investigation of the social significance of plumage variability in the population at Ormiston Hall.

5.2. INTRODUCTION

The black ventral stripe of the great tit is a strongly sexually dimorphic character. In males it is wide, glossy and extends between the legs whilst in females it is narrower, duller and does not extend as far towards the tail or as widely between the legs (Perrins 1979; Svensson 1984; pers. obs.). Males also tend to be glossier in other areas of black plumage and to exhibit less white feathering in the ventral stripe than females (Harper *et al* in press; pers. obs.). In view of the great tit's winter flocking behaviour and the apparent continuous variation of ventral stripe size within the sexes, Jarvi & Bakken (1984) used it as a model to test both the SSH and the individual recognition hypothesis - IRH - (Collias 1943). The latter hypothesis suggests that plumage variability may have evolved to facilitate individual recognition. This would reduce the frequency of escalated fighting since birds would be able to associate individual phenotypes with fighting ability demonstrated in previous encounters. Support for this hypothesis would contradict the last of Rohwer's (1975) three basic conditions for the evolution of social status signalling. Jarvi and Bakken's conclusion that "the function of variation in the width of the breast stripe plumage is to proclaim the social status of the individual" was based on the following results.

i) Rank in the social hierarchy in both wild and captive birds was strongly positively correlated with ventral stripe width.

ii) Wild great tits aggressively approached a stuffed, radio-controlled dummy displaying a ventral stripe narrower than their own but retreated from one with a wider stripe than their own.

iii) A stepwise multiple regression analysis suggested that social status was the main independent variable explaining variation in ventral stripe width.

With the benefit of hindsight, these results can be seen to have the following weaknesses.

i) Sample sizes were very small (n=11 for both wild and captive flocks) and the sexes were mixed so that correlations between social status and ventral stripe width were confounded by sex since males are nearly always dominant to (Chapters 3 & 4) and have much larger ventral stripes than females (Svensson 1984).

ii) Stripe width was only measured at one point - the base of the sternum. Strong correlations of this measure with the birds' stripe width rank, as assessed from photographs, were again confounded by sex.

iii) The method of determining social rank in the captive flock was based on order of approach to a presented food item - top dominant first and so on. However, both Hegner (1985) working on blue tits and De Laet (1985) on great tits have shown that order of arrival at a food source may be *inversely* related to social status, especially after predator attacks. Jarvi & Bakken's social hierarchy in the captive flock may therefore be suspect.

iv) The stripe widths of the dummies were 5mm (1), 12mm (2) and 25mm (3). These correspond to 'female', 'male' and 'supernormal' respectively. Encounters between real birds and dummies may therefore have been confounded by apparent sex differences in the case of (1) and (2). Submissive behaviour towards dummy (3) was perhaps to be expected given its unrealistic appearance.

v) The five independent variables used in the multiple regression analysis show many positive inter-correlations (their data; Chapters 3 & 4). For example, the apparent power of stripe width in explaining social status again appears to be confounded by sex.

A further experiment by Jarvi *et al* (1987b) did show a positive correlation between social status and stripe width in ten small groups of male great tits. However, an attempt to confirm this experimentally by injecting the most subordinate, narrow-striped bird in each group with testosterone and artificially widening its stripe produced equivocal results. Although the manipulated subordinates did rise in rank, the other, untreated birds in the experimental groups changed in relative rank simultaneously.

Maynard Smith & Harper (1988) approach the evolution of status signalling as a game theoretical problem and point out that the necessary conditions depend upon whether the signal is a 'badge of status' (Krebs & Dawkins 1984). The term 'badge' is intended to imply that the hormonal and metabolic costs of developing a slightly larger plumage patch of a given colour at moult are negligible and that status signalling is thus exactly analogous to 'intention signalling' as discussed in Chapter 1. If this is the case, status signals are costless and open to intraspecific mimicry ('bluffing'). In other words, the invasion of populations by individuals of low fighting ability which signal a fraudulently high status is expected. Roper (1986) gives some interesting parallels between costless badge signalling in bird and human social groups. If 'honest' signalling of social status using costless badges is to become established, Maynard Smith & Harper (1988) predict that the following conditions must be met.

i) Escalation of conflict to true fights must be more likely as signalled status of the opponents becomes more similar and the cost of escalation must increase with the status being signalled.

ii) The cost of fighting must be high relative to the value of the resource being contested - i.e. status signalling is only expected to operate in competition over relatively trivial resources.

iii) Bluffing must be 'punished' - i.e. individuals signalling at a higher level than their actual ability warrants must pay disproportionately high costs due to becoming involved in more fights with genuinely high status individuals than do honest subordinates (Moller 1987b).

The constraints on the evolution of costless signalling systems are discussed further in Chapter 6. Alternatively, dominant birds may despotically attack birds whose behaviour and signalled status are incongruent since this may often reflect disease or illness in the incongruent bird such that it is easily chased off a resource (Jarvi *et al* 1987b; Rohwer 1977). Despotism towards incongruent birds may be selectively favoured if it reduces the chance of future contact with, and infection from, those individuals (Walso & Jarvi ms.).

In contrast, if status signals are costly to produce (e.g. Moller & Erritzoe 1988; Roskaft *et al* 1986; Silverin 1980) then they may be thought of as RHP-correlated signals which could be used in mutual assessment of fighting ability, a process with much less severe constraints on its evolution (e.g. Clutton-Brock & Albon 1979; Davies & Halliday 1978; Geist 1966). In this case, status signals are no longer distinct from RHP assessment signals in terms of their evolution.

The recent work by Harper *et al* (in press) supports Maynard Smith & Harper's (1988) 'badges of status' rationale for the evolution of status signalling. In a winter population of great tits, stripe width was found to be highly sexually dimorphic with no overlap between males and females. Older birds had significantly wider stripes than yearlings and stripe width was independent of body size (RHP) as measured by tarsus length. Within age-sex classes, the wider-striped bird was dominant in a significantly greater than random proportion of dyads but taking into account other correlated plumage characteristics (stripe gloss, crown gloss, stripe white, cheek yellow) did not significantly improve the predictive power of stripe width. The power of stripe width in predicting outcome declined as resource value (as measured by intake rate at the food source under competition) increased, whilst that of tarsus length increased. Fights and chases were more likely at these 'high value' sites and increased in probability with symmetry in the stripe widths of the opponents. However, no correlation was found between the probability of escalation and the mean stripe width of the competing birds.

The crucial questions that arise from the above studies are what is the typical social organization of wintering great tits, and what is the likelihood of the evolution of status signalling under these conditions? Jarvi & Bakken (1984) state without references that the species winters in large, unstable flocks yet Saitou (1978, 1979a,b,c) found a quite rigid, hierarchical flock structure in a Japanese population and Drent (1983) suggests that territoriality is a year-round feature of great tit social organization. In addition, Harper (pers. comm.) has pointed out that his study involved birds moving some distance from their normal home ranges to visit artificial feeding/observation sites that were within the territorial system of few, if any, resident great tits. This contrasts with Ormiston Hall where observations were carried out within the territorial system of 15-25 pairs. This study therefore investigates the possibility of status signalling in the great tit population at Ormiston Hall as follows.

i) Does status signalling of the 'badges of status' type exist and, if it does, are the three predictions of Maynard Smith & Harper (1988) fulfilled ?

ii) If status signalling does exist, how is it affected by variation in territoriality of individuals and of the population as a whole ?

iii) Does the winter social organization of the great tit at Ormiston Hall correspond with that predicted by Rohwer (1975) to be the most suited to status signalling, as *assumed* by Jarvi & Bakken (1984) and Harper *et al* (in press) ?

iv) Is there any evidence for the development of individual recognition in the winter population, a hypothesis rejected by Jarvi & Bakken (1984) but not since tested on great tits ?

Data presented in this chapter will be used to answer questions (i) and (ii). Chapter 5.5. considers questions (iii) and (iv) by drawing upon the conclusions of Chapter 4. The problem of individual recognition is also discussed as a preliminary to further investigation in Chapters 6 and 7.

5.3. METHODS

From November 1987 to April 1989, as many as possible of the great tits captured for colour-ringing or subsequently retrapped were photographed for the purpose of calculating an index of their ventral stripe size. Photographic equipment consisted of an Exakta Varex IIb camera bolted to a stand at a fixed distance from a white hardboard base, giving a white background to each photograph. The camera was fitted with a Hoya 50mm lens, a Sunpak GX8R ring flash and light control and a Sunpak AD-17 AC adaptor. Ektachrome 100ASA colour slide film was used throughout.

Each bird was laid on its back on the white background and held, fully extended, by its bill and legs such that the crown of its head and its feet were in contact with the base. The ventral plumage was then smoothed down from the neck to between the legs, five times, to control for plumage ruffling during handling and to facilitate subsequent measurement of stripe width. One photograph was then taken. The camera shutter release was attached to a lever system which enabled one person to release the shutter with their forehead whilst holding the bird with the fingertips of both hands. In most cases, the bird was not visibly distressed by this process and it was therefore repeated (including the smoothing procedure) before the bird was released. The following additional plumage measurements were also made before the bird was released.

i) STRIPE WHITE: the amount of white feathering in the ventral stripe, measured on an arbitrary scale of 0(none), 0.5, 1, 1.5, 2(much).

ii) CHEEK YELLOW: the amount of yellow feathering in the white cheek patch, measured on the same scale.

iii) CROWN GLOSS: the degree of gloss in the crown feathering, measured on the same scale.

The transparencies were subsequently projected from a fixed distance on to a screen marked with vertical lines at 5cm intervals. All films were analysed in random order during a single one-month period, using the same projector and screen, without any disturbance to their positions. The first vertical line was aligned with the points of inflexion at which the ventral stripe widens to become a throat patch and its boundaries with the yellow ventral plumage become perpendicular to the longitudinal axis of the body (Fig. 5.1.). From this reference point, stripe width was measured from the projected image (in mm.) at the eight successively more posterior vertical lines using a transparent ruler (Fig. 5.1.). These measurements were then summed to give a ventral stripe index (VSI). This index has the advantage of being calculated from much of the total length of the ventral stripe except the area around the base of the legs where it proved impossible to smooth down the plumage repeatably. A similar technique for the calculation of VSI was used by Harper *et al* (in press) but, in their study, each of five width measurements was scored in the field, using vernier calipers.

Except where otherwise stated, VSI refers to the overall mean VSI pooled from all days of capture within a season. Within each capture day, measurements from repeat photographs are pooled to give a mean value, before calculation of the overall mean VSI. Data from the 1987/88 and 1988/89 seasons are pooled except where stated. Repeat measurements of birds from different seasons are considered to be independent due to the occurrence of a complete moult in the intervening period.

5.4. RESULTS

5.4.1. Repeatability and Independence of Ventral Stripe Index Measurements

Table 5.1. shows the repeatability of VSI measurements for both sexes. The repeatability of duplicate photographs of a bird during one capture is very high. Inter-capture repeatability is still highly significant but is much lower. This relatively poor repeatability contrasts with that achieved by Harper *et al* (in press) but further analysis reveals that it may not be a consequence of measurement error. In 38 out of 55 individuals, mean male VSI was larger on the second day of capture (CD2) than on the first (CD1), a significant difference from random expectation ($X^2 = 8.04$, df = 1, $p < 0.01$). In 33 out of 54 cases, the same difference applied to females ($X^2 = 1.57$, df = 1, $p < 0.5$). Similarly, mean VSI of males on CD2 was significantly larger than on CD1 over the whole sample (mean VSI on CD1 = 1048, mean VSI on CD2 = 1135; $t = 2.74$, $n = 55$, $p = 0.0072$) but the same difference was not significant in females (mean VSI on CD1 = 662, mean VSI on CD2 = 688; $t = 1.14$, $n = 54$, $p = 0.26$). Table 5.2. shows that, within CD1, both sexes show a significant positive correlation between VSI and date, but that this correlation fails to reach significance for CD2. Correspondingly, there are negative correlations between rate of change

of VSI (i.e. (VSI on CD1)-(VSI on CD2) plotted against (CD2-CD1)) and CD1 in both sexes. Inter-capture interval varied between 2 and 154 days, with a mean of 49.7 ± 8.2 days over all 99 pairs of captures. Between years, seven out of nine females and five out of six males showed an increase in VSI.

VSIs of males are much larger than those of females (males: mean = 1067, n = 118; females: mean = 667, n = 144; t = 23.31, $p < 0.0001$) although there is some overlap between the sexes. These measurements are independent of the procedure used to sex birds in the field since the latter involves inspection of areas of the ventral stripe that were not used in the calculation of VSIs. There is no significant difference between the VSIs of first-year and older birds of either sex (Table 5.3.). Over the 1988 and 1989 breeding seasons, pooled, VSI is not significantly related to territorial status in either sex (Table 4.14b.). However, the trend towards larger-striped females becoming paired to territory holding males is interesting.

Table 5.4. presents the relationships between VSI and the three biometrics for both sexes. VSI is independent of body size except for a weak inverse relationship between VSI and tarsus length in males. Table 5.5. presents inter- correlations between all four plumage scores for each sex. In males, large- striped birds tend to be glossier and have less white feathering in the stripe. Glossy birds also tend to have less yellow feathering in the white cheek patch but cheek yellow varies independently of both VSI and stripe white. The same pattern exists in females, but correlations between VSI, stripe white and cheek yellow do not reach statistical significance. Amongst males, adults are glossier than first-year birds and tend to have less white in the stripe and less yellow in the cheek. In females, the same difference applies to glossiness and stripe white but the age classes do not differ in the extent of cheek yellow. Males are glossier, have less white in the stripe and whiter cheeks than females.

5.4.1.1. Discussion

The implication of the data on repeatability is that VSI increases at a decreasing rate over the course of the winter, especially in males.

Unfortunately, the data do not yield relationships that are sufficiently strong to allow the prediction of VSIs on the basis of measurements on a single capture day, using regression analysis. Consequently, overall mean VSIs are used in all subsequent analyses with the proviso that social interactions may be influenced by unaccounted for VSI changes. Directional error in the measurement of VSI seems unlikely in view of the measurement procedure (Chapter 5.3.).

Since males have larger VSIs than females, further analyses are carried out separately for the two sexes. Age is not controlled for since although VSI tended to increase in the small number of birds measured in successive years, there are no significant age-related VSI differences in the population as a whole. VSI is also largely uncorrelated with other biometrics so further analyses treat VSI as being independent of all the physical attributes considered in Chapter 4. Other variable plumage characteristics covary with VSI, but the strength of these correlations is less than that found in a similar study (Harper *et al* in press) and, in contrast to the latter, the extent of yellow feathering in the white cheek patch varies independently of other plumage characteristics. This independence is of interest, especially since the cheek patch is conspicuous and potentially functional as a signal. Due to its scale of measurement, it is not appropriate to investigate any relationship between social dominance and cheek colour using the dyad-by-dyad technique (i.e. there would be a very high proportion of ties). Instead, Fig. 5.2. presents correlations between cheek yellow and social rank as derived from cardinal dominance indices, for the two sexes at each site in the 1988/89 season. This analysis provides no evidence of any consistent relationship between cheek colour and social status in either sex.

5.4.2. VSI as a Correlate of Outcome in Dyadic Competition

VSI is being treated here as a dominance correlate in exactly the same way as the attributes considered in Chapter 4. Analysis uses the same rationale, for the same reasons, and is based on the same data set of observed dyadic interactions (Chapter 4.2.2.1.), though restricted to 1987/88 and 1988/89.

Table 5.6. gives the percentage of dyads in which the bird with the larger VSI was also the overall dominant. The overall data sets for the two sexes are divided according to year and the VSI difference between the dyad members. Data from all three sites are pooled in order to generate adequate sample sizes. Consequently, the analysis is conservative in that a few dyads are lost due to the effects of site-related dominance which may generate an equal number of wins for each bird as a result of pooling opposing overall outcomes (e.g. 2-0 vs. 0-2) from different sites (Chapter 4.4.). VSI is a weakly significant correlate of dominance in females with larger-striped birds dominant in 60% of intrasexual dyads. Surprisingly, this correlation disappears in the most VSI-asymmetric dyads (200+) but is stronger in the most symmetrical dyads (0-49) where measurement error, perceptual constraints on the birds and temporal VSI changes might have been expected to exert a randomizing effect. In males there is no evidence that VSI is a dominance correlate in intrasexual dyads. If anything, there is a trend towards smaller-striped birds being dominant in highly VSI-asymmetric dyads. Accordingly, larger VSI is a significantly better predictor of dyadic dominance in females than in males in one year (1987/88: $X^2 = 2.52$, df = 1, $p > 0.1$; 1988/89: $X^2 = 6.25$, df = 1, $p < 0.05$; pooled: $X^2 = 8.06$, df = 1, $p < 0.01$). There is no between-year difference in either sex (males: $X^2 = 0.77$, df = 1, $p > 0.1$; females: $X^2 = 0.38$, df = 1, $p > 0.5$).

Table 5.7. presents a similar analysis of the 1988/89 data set but divides it, firstly, into dyads recorded interacting at a feeder versus those interacting in a context where food was not the immediate goal resource. Secondly, the feeder subset is divided into a data set based on interactions where the bird first at the feeder was dominant ('owner' wins) versus a data set based on interactions where the incoming bird was dominant ('intruder' wins). This analysis does not take into account variation in VSI asymmetry since Table 5.6. fails to show any significant, consistent effect in either sex. Amongst males, VSI is a weakly significant correlate of dominance in 'non-food' dyads with smaller-striped birds being dominant in 40 of 61 cases. This is significantly different from the situation in 'feeder' dyads ($X^2 = 4.49$, df = 1, $p < 0.05$) where VSI asymmetry is random with respect to

outcome. In females, there is no such difference with respect to resource context with larger-striped birds being dominant in around 60% of dyads in both contexts. In neither sex is the relevance of VSI as a correlate of dominance affected by the 'owner-intruder' asymmetry. Amongst males, VSI remains a random predictor of outcome in both contexts. In females, larger-striped birds are again dominant in around 60% of dyads in both contexts.

Tables 5.8. - 5.10. consider the effect of three additional variables on the correlation between VSI and the outcome of dyadic competition.

Table 5.8: interaction rate on the day of observation. Interaction rate (number of dominant - subordinate interactions per hour of observation) at the site of observation is treated as a rough index of the value of the provided food as a resource (but see discussion in Chapter 4.2.). The analysis is restricted to data collected at the garden in 1988/89 and individual interactions are treated as independent events.

Table 5.9: Date of interaction (October 1 = 1). This is assumed to be a positive correlate of the degree of mutual familiarity between opponents and of the intensity of territoriality in the population (see Chapters 4.5. and 6). Again, individual interactions are treated independently and the three sites are analysed separately using all 1988/89 data.

Table 5.10: Total number of interactions comprising overall dyad outcome. This is used as another rough index of the degree of mutual familiarity between opponents. Data from all three sites and both years are pooled in this analysis.

None of these sets of results yields any consistent relationship with the VSI-dominance correlation, although Table 5.9. suggests that VSI may be a more reliable dominance correlate earlier in the season (i.e. October to December) than later, in males.

5.4.2.1. Discussion

Analyses so far indicate that VSI is a weak positive correlate of dominance in females, across a variety of contexts of social interaction. There is little evidence that VSI is related to dominance amongst males.

What there is suggests that territoriality and increasing familiarity between dyad members might be factors which override any positive correlations between VSI and dominance. Territoriality and prior residence / site attachment have already been found to be important dominance correlates, especially in males, both in this population (Chapter 4) and others (Drent 1983). Similarly, there is already evidence (Fig. 4.1., Chapter 4.5.) that increasing mutual familiarity may allow the development of highly predictable dominant - subordinate relationships between individual great tits. Since VSI is a relatively fixed attribute over the course of one moult cycle (but see discussion of 'coverable badges' in Chapter 5.5.), it is an unlikely candidate for the signalling of any form of site-related dominance. If status- related plumage signals do play any role in the social structure of male great tits, it may be necessary to look for it either by controlling for the powerful effects of territoriality and site-related dominance or by restricting analysis to contexts where the effects of these factors are weaker.

The final set of analyses reduces the screening effect of territoriality by considering only dyads in which neither bird held a territory within 100m of the observation site (Chapter 4.4.) during the subsequent spring. The confounding effects of site-related dominance are also reduced by considering each site separately. The Twice-Weight Index is applied to each dyad to test for any effect of familiarity on the importance of VSI as a dominance correlate in the refined data set. The first analysis is based on the 1988/89 data sets for all three sites. The second uses the 1987/88 and 1988/89 garden data sets.

5.4.3. The Effects of Territoriality and Repeated Encounter on the Strength of VSI as a Dominance Correlate

On the basis of the criteria established above, and after pooling the three independent data sets, the bird with the larger VSI was dominant in 119 of 243 male dyads (49.0%) and 89 of 147 female dyads (60.5%). The result for males simply confirms that a tendency for smaller-striped birds to be dominant in interactions over territorial space prevailed in 1988/89, but that outside this context there is no relationship between

VSI and dominance in male dyads over the winter as a whole. There was no overall tendency for territory-holding males in 1989 to be smaller-striped than others (territory holders: mean = 1079+/-134, n = 33; others: mean = 1066+/-158, n = 85) so the anomalous result in Table 5.8. may simply reflect the dominance of the local territory holder, a bird with a fairly small VSI, in very high proportion of interactions away from food at the garden. The result for females provides further confirmation that VSI is a weak, positive dominance correlate of dyadic dominance across all contexts.

Table 5.11. illustrates the relationship between VSI asymmetry and association index for each sex for the pooled total of dyads recorded at the garden feeder in 1987/88 and 1988/89, omitting those dyads where at least one bird was, or was paired to, a local territory holder. In neither sex is there any tendency for the direction of the dominant - subordinate VSI asymmetry to change with the level of association of the dyad members. In males, association index is not related to the magnitude of the VSI asymmetry. However, in females the more highly associated dyads show significantly more similar VSIs than birds less commonly associated - at least in those dyads for which a dominant - subordinate asymmetry was recorded.

5.5. GENERAL DISCUSSION

This study has shown that, as in other populations, the ventral stripe of the great tit is a strongly sexually dimorphic characteristic which is uncorrelated with body size and is continuously variable within age-sex classes. Stripe size does co-vary with other sex and age-related variable plumage characteristics but these relationships are much weaker than those found in a similar study (Harper *et al* in press). The extent of yellow feathering in the white cheek patch is a conspicuous, sexually dimorphic, age-related plumage feature which varies independently of VSI. However, it shows no consistent relationship with social status in either sex. Because juvenile great tits possess yellow cheek patches before the post-juvenile moult, it is possible that many 'cheek yellow' scores obtained during the autumn are determined primarily by the rate of completion of post-juvenile moult in the bird concerned. VSI may increase with age at each post-nuptial moult but, as with other studies (Harper *et al* in press), the evidence for this is inconclusive. It is shown for the first time that VSI is not constant between moults but increases over the course of the autumn and winter. Two effects may explain this seasonal change. Firstly, juvenile birds caught in late September or early October may be in the last stages of post-juvenile moult during which the ventral stripe becomes fully developed (Flegg & Cox 1969; Ginn & Melville 1983). Secondly, darkly pigmented feathers are known to abrade more slowly than lighter ones (Averill 1923; Ginn & Melville 1983). Consequently, there may be gradual abrasion of the pale yellow, ventral feathers over the course of the winter, revealing their darker bases and increasing the apparent size of the ventral stripe. However, this is not to suggest that the ventral stripe is a behaviourally 'coverable' badge which would potentially allow its bearer to signal short term changes in a given attribute. Hansen & Rohwer (1986) believe that such 'coverable badges' would be selectively advantageous over fixed badges by allowing signalling of a rapidly varying attribute such as aggressiveness and could evolve under the same conditions. Functional coverable badges have been demonstrated in the red epaulettes of the red-winged blackbird (Roskaft & Rohwer 1987) and possibly also occur in the white wing flashes of the chaffinch (pers. obs.). Brian (1949) implied and Harper *et al* (in press) suggest that the ventral stripe of the great tit may be partially coverable with VSI decreasing when birds adopt fluffed, 'subordinate' postures and increasing in erect, sleeked, 'dominant' postures. However, there is no significant empirical evidence bearing on this point.

There is no evidence that VSI is correlated with the outcome of competitive, dyadic interactions between male great tits in this population, except for a very weak tendency for larger-striped birds to have a greater probability of dominance early in the season (October-December). VSI is a weak but consistent correlate of dominance in interactions between females in all contexts and there is a significant tendency for females with very asymmetric VSIs to associate less frequently than those with similar VSIs. An index of resource value is not associated with the probability of larger-striped birds being dominant in interactions over food in either sex.

Several aspects of the population structure of the great tits at Ormiston Hall may contribute to these findings. The results of Chapter 4.4. and of other studies (Drent 1983) suggest that site-correlated dominance during the non-breeding season and its gradual crystallization into a territorial system during the spring are typical of sedentary great tit populations. Consequently, aspects of site attachment, site familiarity and prior residence are the most important dominance correlates in male birds in such populations. In relation to the conditions arrived at by Maynard Smith & Harper (1988) for the evolution of badge signalling, location - the occupation of an area of local dominance - may be seen as a resource critical for the establishment of a breeding territory and eventual reproductive success. In this context, the result of any interaction might affect this process, thus supervening the value of the resource (e.g. food) under immediate competition. Both Chase (1974, 1982, 1985, 1986) and Jackson (1988) also point out the possibly important effects of the outcome of previous encounters on an animal's behaviour in subsequent interactions. For example, an animal with a history of winning is likely to initiate further contests over resources and maintain high status in the future, but an animal with a poor history of agonistic success is likely to avoid contests and continue losing. Bronstein (1985c), Drent (1983) and Popp (1988) provide empirical evidence for this in Siamese fighting fish *Betta splendens*, great tits and American goldfinches *Carduelis tristis* respectively, and there is also evidence that such changes in aggressive behaviour are mediated by changes in plasma androgen levels (Baptista *et al* 1987; Ramenofsky 1985). Drent suggests that this positive feedback process combines with site-related dominance and leads to dominant male great tits actively seeking out new opponents within their home range for aggressive engagement, the adaptive function being reinforcement of both local dominance and its physiological basis. Conversely, the function of dispersal is seen as a mechanism by which unsuccessful birds break out of a vicious circle of 'defeat-begets-defeat' by moving to areas in which they are not conditioned to be subordinate and will meet individuals to whom they are not conditioned to be subordinate. In effect, the course of a great tit's life is seen as being controlled by its social fate in its first few weeks. This is perhaps an extreme view, and to suggest that great tits seek out aggressive encounters simply to serve the process of agonistic self-reinforcement flies in the face of consideration of the potential costs of aggressive behaviour, especially if it leads to actual fighting. This problem is discussed further in Chapter 6. However, acceptance of the general idea that the outcome of a social interaction may have consequences beyond success or failure to obtain access to the immediately contested resource casts doubt on the validity of treating any resource as 'trivial'. This is especially so if outcome affects the probability of territory establishment in a species in which possession of a territory is crucial to reproductive success.

The failure to find badge signalling in the winter population of territorial male great tits at Ormiston Hall is therefore not surprising. Also, it is noteworthy that the weak, seasonal effect on the VSI-dominance correlation in males reflects a slightly greater dominance of larger-striped birds early in the winter when site attachment, site familiarity and familiarity with neighbours have had little time to develop amongst first-year birds. Also unsurprising is the contrast with the results of Harper *et al* (in press). In that study, great tits of both sexes were attracted to feeding sites outside their territorial systems (Harper pers. comm.). Here, many more interactions than at Ormiston may have been between birds which had no prior experience of each other and, due to the 'neutral' location, the outcome of interactions may have had no implications for agonistic behaviour when the birds returned to their home ranges. So, the unusual situation created by the location of the feeding sites may have meant that there was little importance to the outcome of aggressive interactions beyond the value of the immediately contested food resource. In this context, Harper and his co-workers were able to demonstrate badge signalling by providing food resources which were genuinely of trivial value.

Female great tits rarely participate in any aspect of territory establishment or defence (Hinde 1952; Perrins 1979; pers. obs.). Drent (1983) found no evidence for the importance of prior residence, site familiarity, prior agonistic experience or prior experience of the opponent in determining the social status of females. In this study, female dominance was correlated with prior territoriality (i.e. being paired with a territorial male in the previous breeding season) , but this relationship was largely due to a few females remaining paired to the same male on the same territory in successive years. This lack of involvement of females in the system of site-correlated dominance and territoriality of males suggests that the outcomes of individual social interactions between females may have fewer long-term implications than those between males. Consequently, the criterion of "low resource value relative to cost of escalation" that is critical to the evolution of badge signalling may be more likely to be met in female dyads, where each contest may depend on the immediate value of the contested resource and little more. Accordingly, this study recorded that approximately 10% more of female dyads had the larger- striped bird as dominant than would be expected by chance. Though statistically significant, the importance of badge signalling amongst females seems to be minor. However, the relationship holds whatever the value of the food resource to the birds and, unlike males, it is not related to any measure of familiarity between the two birds.

A second correlation of VSI asymmetry in female dyads may help to assess the importance of badge signalling. Table 5.11. shows that highly VSI-asymmetric female dyads tend to associate relatively rarely. Since these association indices are based on observation of birds visiting feeding sites where competitive social interaction is frequent, this relationship may reflect active avoidance of social encounter by females perceiving themselves as subordinate on the basis of a clear-cut VSI asymmetry. As also discussed in Chapter 4.5., this would mean that observed social interactions represent only the less asymmetric subset in relation to a particular attribute. The main effect of the attribute may be to cause active avoidance of interaction by the more asymmetric dyads. In more symmetrical dyads, which actually compete at the feeders, outcome may be determined at the more proximate level of information gained during the course of the interaction.

This hypothesis has been tested by comparing the VSI difference between the birds in every intrasexual interaction at a feeder in 1988/89, with the distribution of all possible intrasexual, pairwise VSI differences in the colour-ringed population (Table 5.12.). In other words, each interaction samples one pairwise difference from the overall distribution, and the aim is to see whether this sample, over all interactions, is biased with respect to the overall distribution. The results support the interpretation of Table 5.11. in that females which interact at feeders are symmetrical with respect to VSI, in comparison with all possible female - female dyads. The implication that small-striped females are avoiding interactions with much larger-striped females at feeders by perception of the asymmetry from a distance is strengthened. If active avoidance is taking place, this may mean that VSI is a more important determinant of dominance between female great tits than observations at feeders would suggest. This is because VSI, as a conspicuous, visual cue, is perceptible by birds at considerable distances so that the 'outcome' of an 'interaction' is a result of behaviour which occurs without the human observer perceiving any social interaction to have taken place.

By contrast, there is no consistent evidence that interactions between male great tits at feeders are a biased sample of the population, with respect to VSI difference between interactants. Indeed, at the Yew, interacting males are significantly more VSI-asymmetric than would be expected by chance. The interpretation in this case is that the failure to find correlations between VSI and dominance in male - male interactions *cannot* be ascribed to the resolution of interactions at a distance (i.e. before birds meet at a contested resource), in those dyads where VSI is sufficiently asymmetric to play a role in determining outcome. The general conclusion that there is a real difference between female - female and male - male interactions in the importance of ventral stripe size as a dominance correlate is thus strengthened.

In conclusion, badge signalling as outlined by Maynard Smith & Harper (1988) is insignificant amongst male great tits in this population but may be of some importance amongst females. The occurrence of badge signalling in a winter flocking species such as the great tit may depend crucially on the time and place in which it is studied in relation to the birds' territorial system (Harper *et al* in press versus this study versus the captivity studies of Jarvi & Bakken 1984 and Jarvi *et al*

1987b). In addition, Jarvi & Bakken (1984) and Jarvi *et al* (1987b) simply state that great tits winter in unstable flocks with the implication that individual recognition is unlikely to develop. Yet Saitou (1978, 1979a,b,c) has demonstrated quite rigid, stable, hierarchical flock structure in Japanese great tits *P. m. minor.* This study has already shown that a predictability suggestive of individual recognition develops in the dominant - subordinate relationship of frequently meeting birds (Fig. 4.1.). Similarly, Whitfield (1986, 1988) has found that head plumage variability in turnstone *Arenaria interpres* is more likely to facilitate distinction of neighbours from intruders amongst territorial birds than to act as a social status badge. Chapter 6 will consider the possibility of the development of individual recognition in the social system of wintering great tits in more detail.

Other studies have shown correlations between aggressiveness and androgen levels in birds, especially when social structure is in a state of flux (Baptista *et al* 1987; Hegner & Wingfield 1987), though some have produced inconclusive results (Holberton *et al* 1989; Schwabl *et al* 1988). Maynard Smith & Harper (1988) modelled the evolution of badge signalling by treating the badge as a costless signal of aggressiveness rather than of social status per se and androgen levels *are* known to influence conspicuous external features. For example, Gjesdal (1977) showed that both comb flap and breeding plumage development are stimulated by high androgen levels in male ptarmigan *Lagopus mutus.* Petrie (1988) showed that maximum frontal shield development coincided with peak aggression, body weight and androgen levels in moorhens *Gallinula chloropus.* Groothuis (pers. comm.) has found both that androgen levels are reduced and brown hood development is retarded in black-headed gulls *Larus ridibundus* reared in isolation, and Moller & Erritzoe (1988) and Lofts *et al* (1973) have shown positive inter-correlations between bill colouration, bib size, testis size and androgen levels in male house sparrows. Moller (1988) has further demonstrated that badge (bib) size in male house sparrows may be selected for by female choice since large-bibbed males are preferred as mates over others and also tend to obtain better territories and more secure nest sites through their social dominance.

Clearly, a range of selective factors may influence the evolution of variable plumage features in flocking birds, especially in species such as the great tit with only one complete moult per year. A good example is the house sparrow in which large badge size confers high social status during the winter, perhaps due to high androgen levels and aggressiveness (Moller 1987b; Moller & Erritzoe 1988). Further selection pressures are then applied in the spring when females prefer to mate with large-bibbed males, probably because of their possession of high quality territories (Moller 1988) and their abilities in mate and nest defence (Moller & Erritzoe 1988). A similar interplay of breeding season and non-breeding season selection pressures may also control the evolution of ventral stripe size in great tits (Norris in prep.).

Future work might include observational and experimental study on the effect of prior social experience and associated hormonal state on plumage development at post-juvenile and post-nuptial moults. Such studies might help to discover whether there is a simple effect of plumage on social status, as conventional badge signalling theory would suggest, or whether there is a causal loop in which accumulated social experience, through its physiological effects, can result in changes in precisely those plumage features which themselves affect social status. The work of Groothuis and Petrie suggests that these processes may be widespread. Moller's studies add the complication that what is a badge of status may by its nature also be a badge of nest/territory quality or guarding ability and thus be subject to sexual selection through female choice. If, in addition, plumage features are heritable as recent work on great tits suggests (Norris unpubl. ms.) badge size may be subject to direct natural and sexual selection. One thing is clear. The great tit should not be treated as a 'textbook example' of the evolution of social status signalling using costless plumage badges. There is little evidence that the ventral stripe of the great tit is a consistent correlate of social status and to state that differences in ventral stripe size have no associated cost remains a largely untested assumption.

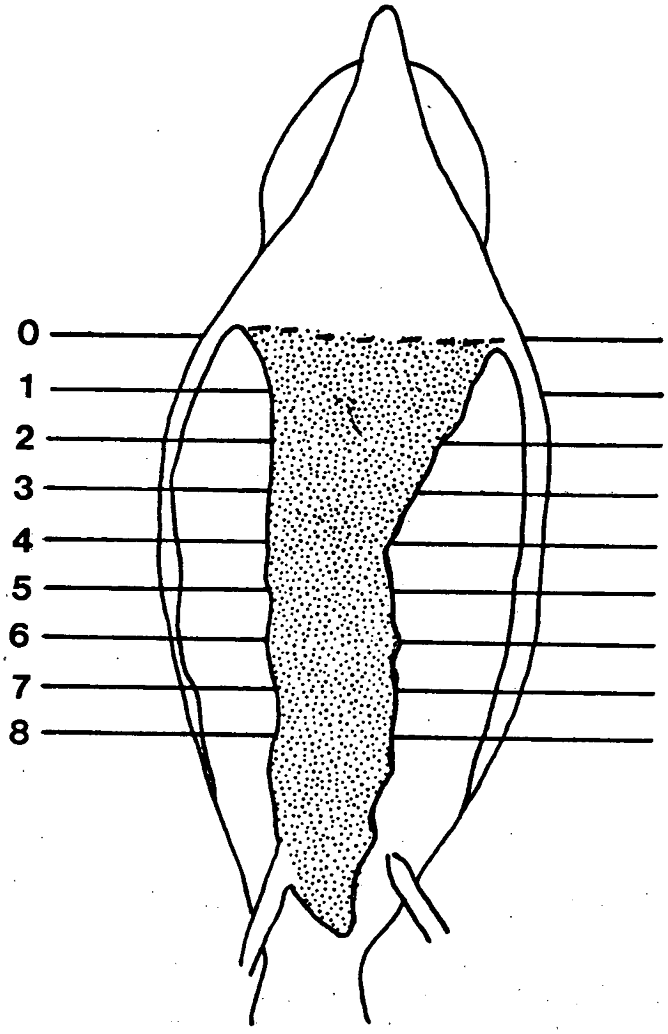


Fig. 5.1. Technique for measurement of Ventral Stripe Index (VSI). See text for full explanation.

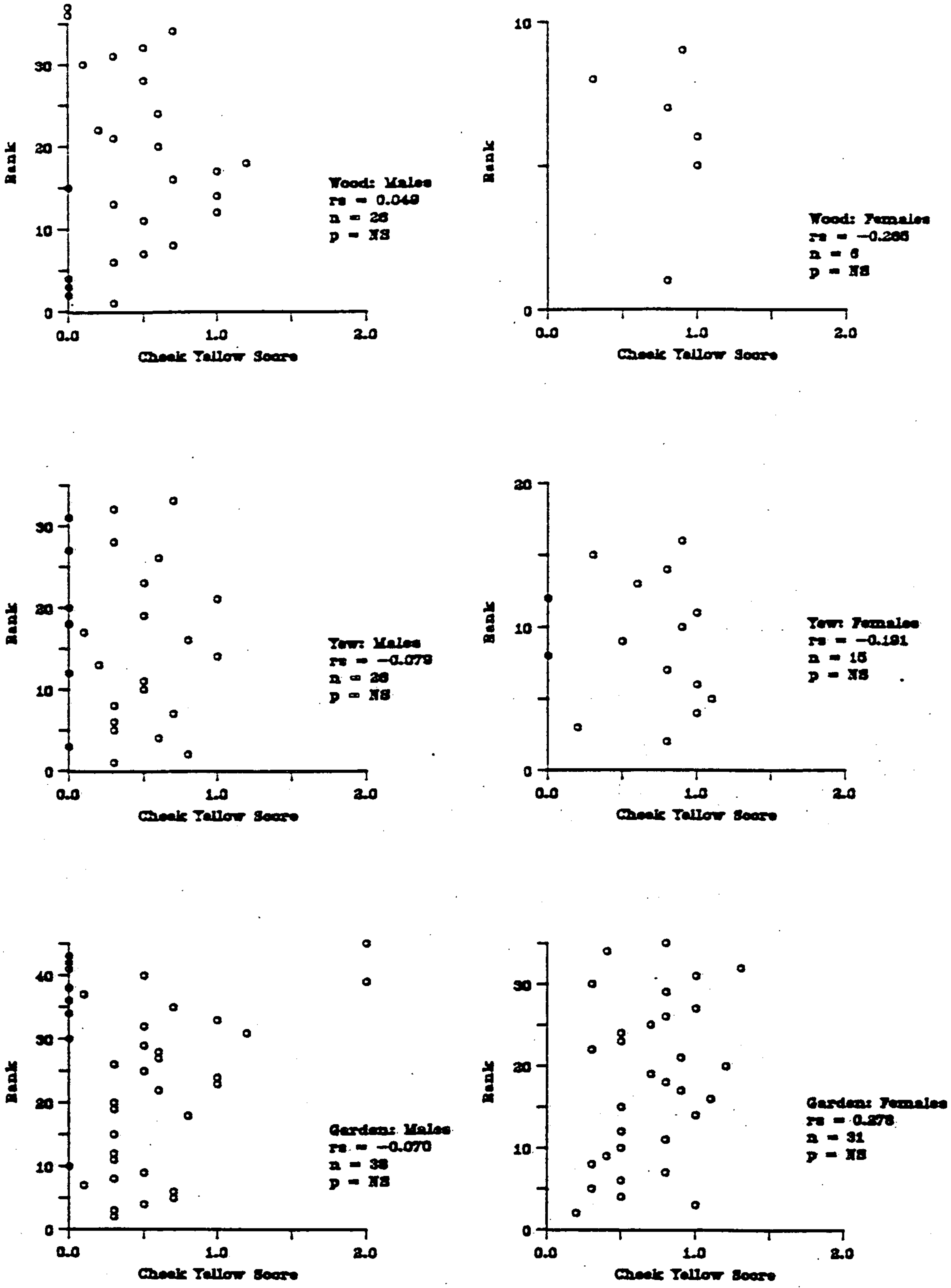


Fig. 5.2. Relationship between Cheek Yellow Score and rank (as derived from Appendix 6) for birds of both sexes, at each site during the 1988/89 winter.

		REPEATABILITY
MALES	i) Within-capture	$r=0.967$, $n=99$, $p<0.001$
	ii) Between-capture	$r=0.614$, $n=55$, $p<0.001$
FEMALES	i) Within-capture	$r=0.931$, $n=105$, $p<0.001$
	ii) Between-capture	$r=0.403$, $n=54$, $p<0.001$

TABLE 5.1. Repeatability of VSI measurements: i) between duplicate photographs at a single capture, ii) between mean VSIs at successive captures within a season.

SEASONAL CHANGES IN VSI

MALES (n=55)	VSI on (CD1) vs. CD1	$r=0.340$, $p=0.01$
	VSI on (CD2) vs. CD2	$r=0.190$, p=NS
	rate of change of VSI vs. CD1	$r_s=-0.379$, $p=0.005$
FEMALES (n=54)	VSI on (CD1) vs. CD1	$r=0.399$, $p<0.005$
	VSI on (CD2) vs. CD2	$r=0.203$, p=NS
	rate of change of VSI vs. CD1	$r_s=-0.467$, $p<0.001$

TABLE 5.2. Seasonal changes in VSI exhibited by birds caught more than once in a season. CD1 = day of first capture. CD2 = day of next capture (September 1 = 1). Rate of change of VSI expressed as the percentage of (VSI on CD1) by which VSI changes between the first and second capture days, divided by the inter-capture interval (CD2 - CD1).

		VSI		
	n	mean	SD	
AM	32	1074	132	t=0.30, p=0.77
FM	86	1065	161	
AF	40	690	139	t=1.30, p=0.20
FF	104	659	108	

TABLE 5.3. Mean VSI in first-year and adult birds of both sexes.

MALES	WING LENGTH(mm)	$r=0.038$, $n=118$, $p=NS$
	TARSUS LENGTH(mm)	$r=-0.200$, $n=115$, $p<0.05$
	WEIGHT(g)	$r=-0.004$, $n=118$, $p=NS$
FEMALES	WING LENGTH (mm)	$r=0.056$, $n=144$, $p=NS$
	TARSUS LENGTH(mm)	$r=-0.038$, $n=138$, $p=NS$
	WEIGHT(g)	$r=-0.003$, $n=143$, $p=NS$

TABLE 5.4. Relationships between VSI and three measures of body size in both sexes. All variables are expressed as mean values from all captures within a season. Weight data were previously corrected for time of day where appropriate.

CORRELATION MATRIX FOR PLUMAGE SCORES

	Crown Gloss	Stripe White	Cheek Yellow	VSI	
Crown Gloss	-	-0.345^{***}	-0.204^{*}	0.216^{*}	MALES
Stripe White	-0.471^{***}	-	0.161	-0.218^{*}	
Cheek Yellow	-0.194^{*}	0.041	-	0.014	
VSI	0.163^{*}	-0.083	-0.052	-	

FEMALES

Sex and Age Relationships of Crown Gloss, Stripe White and Cheek Yellow

Crown Gloss

MALES: u = 1.8, n = 140.

W = 17684, $p < 0.001$

FEMALES: u = 1.0, n = 183.

AM: u = 2.0, n = 44; FM: u = 1.7, n = 96. W = 3655, p = 0.01
AF: u = 1.0, n = 54; FF: u = 0.8, n = 129. W = 5840, p = 0.008

Stripe White

MALES: u = 0.5, n = 138.

W = 39431.5, $p < 0.001$.

FEMALES: u = 1.5, n = 181.

AM: u = 0.5, n = 43; FM: u = 0.5, n = 95. W = 2625, p = 0.09
AF: u = 1.4, n = 53; FF: u = 1.5, n = 128. W = 4253, p = 0.076

Cheek Yellow

MALES: u = 0.5, n = 140.

W = 33268.5, $p < 0.001$

FEMALES: u = 0.5, n = 183.

AM: u = 0.25, n = 44; FM: u = 0.5, n = 96. W = 2624, p = 0.03
AF: u = 0.5, n = 54; FM: u = 0.5, n = 129. W = 4798, p = 0.60

TABLE 5.5. Relationships between plumage variables. Values presented in correlation matrix are Spearman rank correlation coefficients. Differences between age and sex classes are analysed using the MINITAB Wilcoxon-Mann-Whitney test. AM = adult male, FM = first-year male, AF = adult female, FF = first-year female. u = median score.

		VSI ASYMMETRY				
		0-49	50-99	100-199	200+	POOLED(%)
MALES	1987/88	9/18	8/15	6/15	8/25	31/73(42.5)
	1988/89	27/53	25/52	44/92	52/111	148/308(48.1)
	TOTAL	36/71	33/67	50/107	60/136	179/381
	%	(50.7)	(49.3)	(46.7)	(44.1)	(47.0)
FEMALES	1987/88	6/11	7/13	14/25	9/16	36/65(55.4)
	1988/89	$32/48_1$	26/45	$32/47_2$	17/39	$107/179_5$(59.8)
	TOTAL	$38/59_3$	33/58	$46/72_4$	26/55	$143/244_6$
	%	(64.4)	(56.9)	(63.9)	(47.3)	(58.6)

1: X^2 = 5.35, df = 1, $p<0.05$.
2: X^2 = 6.17, df = 1, $p<0.05$.
3: X^2 = 4.92, df = 1, $p<0.05$.
4: X^2 = 5.57, df = 1, $p<0.05$.
5: X^2 = 6.85, df = 1, $p<0.01$.
6: X^2 = 7.23, df = 1, $p<0.01$.

TABLE 5.6. Proportion of dyads in which overall dominant also possessed a larger VSI. Analysis based on pooled total of all intra-sexual interactions in each year at all sites. Subscript figures mark significant differences from null expectation and refer to X^2 tests below. See text for analysis of between-sex and between-year differences.

MALES	FEEDER DATA	150/305 (49.2%)
	NON-FEEDER DATA	$21/61_1$ (34.4%)
	FEEDER: 'OWNER' WINS	53/112 (47.3%)
	FEEDER: 'INTRUDER' WINS	129/258 (50.0%)
FEMALES	ALL FEEDER DATA	$102/172_2$ (59.3%)
	ALL NON-FEEDER DATA	13/21 (61.9%)
	FEEDER: 'OWNER' WINS	$83/139_3$ (59.7%)
	FEEDER: 'INTRUDER' WINS	36/63 (57.1%)

1: $X^2 = 5.31$, df = 1, $p<0.05$.
2: $X^2 = 5.95$, df = 1, $p<0.05$.
3: $X^2 = 5.25$, df = 1, $p<0.05$.

Table 5.7. Effect of resource type and ownership on the proportion of dyads whose overall dominant also had the larger VSI. Interactions not occurring at a feeder are assumed to represent competition over territorial space.
Analysis restricted to 1988/89 data, all sites pooled.
Subscript figures indicate significant differences from null expectation and refer to X^2 tests presented below.

		n	r_s	p
MALES	VSI Difference (dominant - subordinate)	588	0.072	0.08
	VSI Asymmetry (absolute difference)	588	0.025	0.54
FEMALES	VSI Difference (dominant - subordinate)	291	-0.091	0.12
	VSI Asymmetry (absolute difference)	291	0.044	0.45

TABLE 5.8. Relationship between resource value, as estimated by interaction rate, and the VSI asymmetry between the interacting birds. Analysis restricted to 1988/89 garden data collected at the feeders.

MALES		n	mean date	SD	
Garden	+	262	75.9	49.3	t=2.60, p=0.0097
	-	335	86.5	49.9	
VSI Difference (dominant - subordinate)					$r_s = -0.113$, $p = 0.006$
VSI Asymmetry (absolute difference)					$r_s = 0.109$, $p = 0.008$
Wood	+	61	150.9	28.3	t=0.82, p=NS
	-	52	155.2	27.1	
VSI Difference (dominant - subordinate)					$r_s = -0.084$, $p = 0.37$
VSI Asymmetry (absoloute difference)					$r_s = -0.081$, $p = 0.39$
Yew	+	74	159.6	23.3	t=0.99, p=NS
	-	83	163.1	20.7	
VSI Difference (dominant - subordinate)					$r_s = -0.126$, $p = 0.12$
VSI Asymmetry (absolute difference)					$r_s = 0.004$, $p = 0.96$
FEMALES					
Garden	+	164	77.7	31.2	t=0.14, p=NS
	-	129	77.3	27.0	
VSI Difference (dominant - subordinate)					$r_s = 0.026$, $p = 0.66$
VSI Asymmetry (absolute difference)					$r_s = 0.084$, $p = 0.15$
Wood	+	18	134.4	35.4	t=1.82, p=NS
	-	14	153.9	24.9	
VSI Difference (dominant - subordinate)					$r_s = -0.186$, $p > 0.20$
VSI Asymmetry (absolute difference)					$r_s = 0.104$, $p > 0.50$
Yew	+	53	144.5	23.9	t=0.75, p=NS
	-	24	149.6	28.8	
VSI Difference (dominant - subordinate)					$r_s = 0.179$, $p = 0.12$
VSI Asymmetry (absolute difference)					$r_s = 0.448$, $p < 0.001$

TABLE 5.9. Mean date (October 1 = 1) of interactions in which the larger-striped bird was dominant (+) and those in which the smaller-striped bird was dominant (-). Sexes and sites are analysed separately using 1988/89 data. For each analysis, the significance of the difference in mean date of occurrence of (+) and (-) interactions is examined with a t-test. Also presented are correlations between date and VSI asymmetry for the same samples.

	Interaction Frequency (number of interactions observed in season)	
MALES		
	1	112/221 (50.7%)
	2	37/72 (51.4%)
	3	20/50 (40.0%)
	4-6	22/49 (44.9%)
	7+	12/24 (50.0%)
FEMALES		
	1	82/145 (56.6%)
	2-3	36/57 (63.2%)
	4-5	16/29 (55.2%)
	6+	10/15 (66.7%)

TABLE 5.10. Effect of interaction frequency on the proportion of dyads in which the bird with the larger VSI was the overall dominant. Data from all sites pooled to give overall outcomes. Dyads from both years pooled.

		n	r_s	p
MALES	VSI Difference (dominant - subordinate)	168	0.037	0.63
	VSI Asymmetry (absolute difference)	168	0.032	0.68
FEMALES	VSI Difference (dominant - subordinate)	114	-0.026	0.78
	VSI Asymmetry (absolute difference)	114	-0.253	0.007

TABLE 5.11. Relationship between VSI asymmetry and association index for those dyads recorded at the garden feeders in 1988/89. Dyads involving birds occupying a territory within 100m have been excluded from the analysis. See text for comparison of these results with those obtained by taking into account all possible dyads for which association index and VSI asymmetry were known.

Site	Sex		n	median VSI difference	Mann-Whitney-Wilcoxon test
GARDEN	Males	INT	495	137.0	$W = 1.386\text{x}10^{6}$
		TOTAL	5256	143.0	p = 0.29
	Females	INT	273	77.0	W = 964092
		TOTAL	8010	110.0	$p < 0.001$
YEW	Males	INT	115	179.0	W = 349339
		TOTAL	5256	143.0	p = 0.01
	Females	INT	32	75.5	W = 100211
		TOTAL	8010	110.0	p = 0.03
WOOD	Males	INT	157	156.0	W = 448228
		TOTAL	5256	143.0	p = 0.23
	Females	INT	77	69.0	W = 227639
		TOTAL	8010	110.0	$p < 0.001$

Table 5.12. The VSI difference in interacting dyads (INT) compared with the same measure over all possible dyads in the colour-ringed population (TOTAL) in 1988/89. Each interaction is taken as an independent datum, and sexes and sites are treated separately. Only interactions at feeders are included. Differences between the (INT) and (TOTAL) data sets are analysed using the MINITAB Mann-Whitney-Wilcoxon test. See text for further discussion.

CHAPTER 6.

POSTURAL DISPLAY: DIVERSITY AND FUNCTION.

6.1. INTRODUCTION

6.1.1. Postural Display in the Great Tit

Hinde (1952), Stokes (1962b) and Blurton Jones (1968) have described in detail the range of postural displays used by great tits in agonistic encounters. The following list of display elements is exhaustive but few of the elements are mutually exclusive. Many postures may be associated to form a 'compound' display or may occur within a single bout of postural display. With the exception of crest-raising and 'fluffing', none of the postures described below was ever seen when a bird was alone. Table 6.1. equates Blurton Jones', Hinde's and my own terminologies for the display components. The range of basic body postures is well illustrated in Hinde (1952, pp. 24, 46, 73) and Blurton Jones (1968, p. 78).

No Display (ND). A broad category including apparent resting whilst at the feeder, feeding and any other posture or locomotion not obviously directed at another bird at the feeder. In some videotape analyses, this category is subdivided into 'feeding' (F), 'not feeding and stationary' (S), 'approaching another bird' (HT), 'hopping away from another bird' (HA), 'facing towards another bird' (FT), 'facing away from another bird' (FA), and 'facing sideways to another bird' (FS). If an interaction was so quickly over that one bird was displaced without apparently reacting in any way other than immediate departure, ND was also recorded for the displaced bird.

Head Up (HU). The beak and head are pointed upwards at a variable angle with the neck also stretched upwards.

Vertical Flight (VF). Exactly the same posture as HU but with the bird flying towards, or hovering whilst facing, the opponent.

Head Down (HD). The body is held horizontally with the legs bent and the head pointing downwards at an angle of between 45^o and 90^o with the line of the neck and back. This posture is very distinct from that adopted by a bird looking down whilst feeding (Blurton Jones 1968, p. 80).

Horizontal Body (HB). As above, but with the head and bill held pointing forwards.

Erect Body (EB). The bird 'stands tall' with the tibiotarsal joint fully extended.

Wings Out (WO). The wings are spread to a very variable extent but usually point towards the ground. The carpal joint is lifted clear of the body feathers. Blurton Jones (1968) distinguished categories of WO according to the degree of wing spreading. This procedure has not been followed due to the great variability of the posture, even within a single display bout.

Tail Fanned (TF). Spreading of the rectrices, occasionally coupled with vertical flicking of the whole tail.

Open Bill (OB). The bill is held open when facing an opponent though no vocalization is involved. In some videotape analyses, 'cleaning bill' (CB) is also recorded.

Turning Body (TB). A side-to-side turning of the head, sometimes with a synchronous sideways pivoting of the whole body.

Supplant (SA). Displacement of a second bird simply by arrival at or near the place occupied by the latter, without any apparent agonistic display.

Attack (ATT). Rapid hopping or flight towards an opponent coupled with attempts to grab the other bird with the feet and/or peck hard with the closed bill. This is the only form of physical contact seen between interacting tits.

Chasing (CH). Chasing of one bird by another, whether on the ground, in trees or in flight. This behaviour is treated as diagnostic of an interaction over territorial space; "reproductive fighting" to use Hinde's (1952) terminology.

In some of the videotape analyses, the following variants of the way in which the plumage may be held were also recorded as postural elements.

Crest Raising (CR). Raising of the crown feathers to form a 'crest'. This behaviour is not as conspicuous in the great tit as Stokes (1962a) found it to be in the blue tit.

Crown Flattening (CF). Flattening of the crown feathers against the skull to give a sleeked, 'flat-topped' appearance to the head.

Nape Raising (NR). Raising of the nape feathers to give the impression that the bird is 'raising its hackles'.

Fluffing (FF). General fluffing out of the whole plumage, usually whilst stationary but never as extreme as the posture adopted by a roosting bird.

The use of these plumage elements is not analysed below, but their importance as elements of agonistic display is discussed below. It is hoped that data collected by this study will allow a functional analysis of 'feather postures' in great tits to be published at a later date.

This repertoire of postural display can be put into the context of passerine display in general, by reference to a review of display in reproductive contexts by Andrew (1961). Andrew suggested that in most passerine species, displays typical of contests with rivals during the breeding season (reproductive fighting) are a different subset of the overall repertoire from those used during 'ordinary' contests over food resources. In particular, displays based on HU ("bill raising" in Andrew's terminology) and HD ("bill lowering") were seen as characteristic of reproductive fighting, and those based on HB ("head forward") as typical of contests over food or other maintenance resources. HU was recorded in reproductive fighting from 34 species of 13 Families, but was rare as a female display being recorded from only the great tit, robin *Erithacus rubecula* and chaffinch *Fringilla coelebs*. Though also common in courtship behaviour, HU tends to occur only in one of the two contexts in a given species. The Paridae was found to be the only Family in which HU is found in reproductive fighting but not courtship. HB was found to be a common, perhaps universal, agonistic posture in passerines, often being associated with OB. In contrast to the dichotomy within agonistic display repertoires emphasized by Andrew, Hinde (1952) stressed the similarity of behaviour between 'reproductive' and 'maintenance' contests in great tits, and Marler (1956) suggested that the two-tendency, "attack-flee conflict" model of agonistic behaviour was sufficient to explain the origin of agonistic display repertoires, whatever the context.

Although Andrew discussed HU, HD and raising of the body feathers in relation to passerine courtship, his review did not provide any comparative information on other elements in the display repertoire of the great tit. However, a brief scan of studies of particular species shows that most of the postural elements of the great tit are common in many other passerines (Table 6.2.). Most of these authors suggest that HB is the highest 'intensity' agonistic display in terms of the levels of the supposed conflicting, internal tendencies to escalate or to escape (e.g. Dilger 1956). WO, TF and OB are associated with HB in many species. Some (e.g. Dilger 1960; Tordoff 1954) consider the occurrence of OB with HB to reflect the predominance of defensive ('stay') over offensive ('attack') tendencies, whilst others (e.g. Coutlee 1967; Marler 1956; Popp 1987a) consider the addition of OB to represent a particularly hostile display. The increase in the number of elements comprising a compound display from simple WO or HB to, for example, (WO/TF/HB/OB) is generally considered to reflect its increasing intensity. For example, the series HB to HB/OB to WO/HB/OB in the American goldfinch (Popp 1987a) reflects increasing effectiveness of the display in causing an opponent to leave, but also entails a greater risk of retaliatory attack by the opponent. Similarly, Popp (1987c) describes an unusual but very effective compound display in the purple finch

Carpodacus purpureus. "The bird stands vertically with its body extended to full height but pointing its bill downwards at the opponent." This suggests a combination of HU, HD and EB. In general, EB is rarely distinguished as a display element in its own right (but see Ellis 1966). TB seems to be quite rare but is recorded from chaffinches (Marler 1956) when escape tendencies predominate and as avoidance behaviour in the American goldfinch (Coutlee 1967; Popp 1987a).

Within the Paridae, detailed studies of agonistic behaviour have been carried out by Stokes (1962a) on the blue tit and (1962b) on blue, great, coal and marsh tits P. palustris and by Blurton Jones (1968) on the great tit.

Stokes' (1962a) study was a description of the agonistic displays of the blue tit and an analysis of both reactions of birds to the displays of their opponent, and the behaviour following display in the original actor. This analysis was carried out as a quantitative test of the conflict hypothesis (Chapter 1) that different agonistic display postures reflect different states of a conflict between opposing internal tendencies (e.g. escape, attack or stay), and therefore provide recipients of the display with more accurate information about the performer's future behaviour probabilities (Hinde 1955, 1956; Marler 1956; Moynihan 1955; Tinbergen 1952). For example, performance of display X may allow the recipient to identify that the relative probabilities of the performer's next act are, behaviour A: 0.7, behaviour B: 0.2, behaviour C: 0.1, whereas prior to display, the recipient could not distinguish between the relative likelihoods of these acts. In other words, each had a relative probability of 0.33 as far as the recipient was concerned. This hypothesis in turn depends on the idea that there should be selection pressures for external indicators of such conflicts (e.g. intention movements or displacement activities) to become ritualized as display postures communicating future behaviour probabilities ('intentions'). Stokes' (1962b) paper stemmed from the same theoretical background and was a comparative study of the agonistic display repertoires of four British tit species.

Stokes (1962a) described the occurrence of HB, WO, TF, OB, CR, NR and FF in blue tits. CR and FF were highly correlated with subsequent departure or escape in the bird showing the posture. With the exception of OB, the remaining elements were almost equally predictive of more direct aggression (attack) or simply staying at the site of the contested resource. OB itself was most highly associated with subsequent staying and least with subsequent attack. The probability of subsequent attack increased with the number of elements in the HB/WO/TF/NR group that were used simultaneously, but the addition of OB to such a display reduced the probability of attack in favour of 'staying'.

In his comparative study, Stokes (1962b) found that great, blue and marsh tits possessed almost identical display repertoires but failed to record the occurrence of the HU, HD and TB elements in the great tit. However, subsequent behaviour of both actor and reactor to the various display elements varied considerably between species. For example, EB, WO and HB were all more likely to predict subsequent attack by the displaying bird in blue tits than in great tits (see Blurton Jones 1968 for confirmation of this). Amongst marsh tits, no display predicted subsequent attack by the actor on more than 19% of occasions. Between birds, CR was thirteen times more likely to elicit departure and three times less likely to elicit attack in the reactor, between great tits than between blue tits. WO and HB were very likely to elicit escape and very unlikely to elicit retaliatory attack in the great tit, whereas the relative probabilities of these two responses were much more similar in the blue tit.

Blurton Jones' (1968) extensive study of the causation of agonistic display in the great tit was also carried out as a test of Tinbergen's conflict hypothesis. It included both observation of great tits competing in the wild and use of conflicting experimental 'attack' (a red pencil) and 'flee' (a light bulb flash) stimuli to study behavioural responses. His conclusions were that the entire range of postural display could be seen in conflict situations where overt aggression was blocked by an opposing or counter-attractive stimulus, and could also be evoked by conflicting experimental stimuli of the same kinds. HU, HD, HB and WO were all elicited when an attack-evoking stimulus was blocked by a conflicting or counter-attractive stimulus or a physical barrier. TB and CR were both produced by conflicting approach and avoidance stimuli but did not require the presence of a stimulus to attack. Within these broad categories, particular elements were associated with variation in the intensities of the opposing stimuli. For example, HU was associated with a particularly strong fleeing stimulus and WO with a strong attack stimulus. HB became more frequent when the presence of food added a third stimulus to 'stay in one place'. In the field observations, HD, HB and WO were strongly positively correlated with the probability of subsequent attack by the displaying bird but the study did not collect data on the responses of other great tits to displays.

The data presented in the studies of Stokes and Blurton Jones provide considerable evidence that displays occur when stimuli to behave in conflicting ways are present simultaneously, that those displays do provide *some* information (Caryl 1982a) about a bird's probable future behaviour, and that the reactor's responses do vary with the actor's display. For example, Andersson (1976) found that many displays of the great skua *Stercorarius skua* influenced the behaviour of the recipient in the way predicted by the information that they gave about subsequent action in the displaying bird.

6.1.2. The Function of Postural Display: The Theoretical Background.

Data of the kind discussed above was the basis of the 'traditional ethological view' (Caryl 1979) that ritualized displays evolved from non-signal movements occurring in conflict situations, under selection pressures for individuals to *convey information about their future behaviour probabilities or 'intentions',* and thus reduce the risk of engagement in overt aggression. This view, summarized by Cullen (1966), implied that variation in display reflected variation in the position of the balance between, and the intensity of conflicting tendencies, and that the displays themselves had undergone little emancipation from their original motivational causes. However, the advent of game theory models of animal contests, especially the 'War of Attrition' (Bishop & Cannings 1978; Maynard Smith 1974; Norman *et al* 1977), resulted in much re-examination of the selection pressures behind communication by ritualized display. In its simplest form, the War of Attrition model predicts evolutionarily stable contest behaviour in contests involving a single display where the two animals are either genuinely symmetrical or effectively symmetrical due to lack of information about each other. In such a contest, an animal's course of action is determined only by the value of the contested resource to itself, and the energy and time costs of persistence in display. The evolutionarily stable solution is for such an animal to select randomly from a negative exponential distribution of persistence times. If, by its display, an animal were to signal its persistence time (p_1) to its opponent then this information would immediately enable the opponent to decide between giving up if its own persistence time (p_2) $< p_1$, or persisting if $p_2 > p_1$. A population employing this strategy would not be evolutionarily stable since it would be open to invasion by animals which always signalled the highest possible persistence time, irrespective of actual intentions and thus won almost all their interactions without escalation, through bluff. This invasion would be possible because motivational information could be signalled equally well by any member of the population, and changes in the signal would incur negligible fitness cost. There is thus no cost of bluffing to counter its obvious selective advantage. As the inherent costs of a signal increase so does its evolutionary stability since the advantages of bluffing will be increasingly countered. In terms of relevance to the outcome of animal contests, signals of resource-holding power - RHP - (Parker 1974) fulfil the criteria of costly signals. Roaring rate of red deer *Cervus elaphus* stags (Clutton-Brock & Albon 1979) and croak pitch of toads *Bufo bufo* (Davies & Halliday 1978) are both cues used in contests to assess RHP asymmetries, and all are costly to signal by virtue of their intrinsic relationship with the animal's size. As an alternative to motivational information, games theory therefore predicts that exchange of information about costly attributes is more likely to be an evolutionarily stable function of agonistic display.

Clearly, the War of Attrition is a very simplistic parody of most animal contests. For example, it takes no account of the possibility of an escalating series of displays (but see Norman *et al* 1977) and does not consider contests where the animals are either overtly asymmetrical or are able to perceive asymmetries either through information acquired in previous encounters or during the current contest. However, the general prediction still holds that signalling of variables (e.g. intentions) which can be signalled equally well by any member of the population at negligible cost will not be evolutionarily stable due to the probability of invasion of bluff signallers. As Caryl (1979) points out, this prediction is clearly opposed to the 'traditional ethological interpretation' of the function of ritualized agonistic display. Caryl's (1979) re-analysis of the data of Andersson (1976), Dunham (1966) and Stokes (1962a) emphasizes the difference between displays such as CR and FF which predict subsequent departure with very high probability, and 'aggressive' displays which rarely predict subsequent attack with greater than 50% probability. The War of Attrition predicts neither transmission of 'attack' nor 'escape' information (van Rhijn 1980). However, it seems intuitively reasonable that transmission of information that does not benefit the signaller (e.g signalling readiness to leave a contested resource) is unlikely to be bluffed, whereas bluff signalling (e.g. of future attack) which may put the signaller at an advantage would be selectively favoured (Caryl 1982b). A possible exception to this might be bluff submissive signalling prior to an attempt at kleptoparasitism, in order to allow the stealer to approach the victim. I have observed CR and FF in captive great tits, immediately prior to attempts to steal food from flockmates.

The recognition that different selection pressures might act on cost-independent signals, depending on the information they contained was a first step towards closing the apparent gap between theories of animal communication stemming from the conflict hypothesis, and those stemming from game theory (see Hinde 1981 and Caryl 1982a for contrasting views on the differences between the two approaches). Other arguments and data exist which suggest that the signalling of non-costly attributes may be evolutionarily stable in certain circumstances. Van Rhijn & Vodegel (1980) argue that in contexts where pairs of animals encounter each other repeatedly, each animal gains increasingly complete information about the other's agonistic behaviour and fighting ability (i.e. individual recognition develops). In this situation, where asymmetries are known to both animals, bluff is less likely to be successful and the signalling of otherwise bluffable variables such as intentions, may become evolutionarily stable. Empirical evidence for this was provided by Bossema & Burgler's (1980) work on small groups of captive jays *Garrulus glandarius*. They found that information about the probability of escalation was encoded in the manner in which a bird looked at its opponent, and that the recipient's reaction varied accordingly. Turner & Huntingford (1986) found that the contest behaviour of male Mozambique mouthbrooder fish *Oreochromis mossambicus* provided information which could be used to predict eventual outcome, with contest intensity decreasing as size asymmetry increased. These findings suggest that intention signalling may become more likely where asymmetries which would determine the outcome of an escalated contest are overt. Finally, Maynard Smith & Harper (1988) and Harper *et al* (in press) have developed and empirically supported a model defining the evolutionary conditions for cost-independent signalling of social status through plumage variation in winter flocking birds (see Chapter 5).

In essence, all these examples boil down to the argument that *any* variable which may be an 'outcome-relevant' asymmetry between competing animals *can* be signalled, but that the more independent of cost and open to bluff the signalling process is, the greater will be the constraints on its evolutionary stability. As Turner & Huntingford (1986) point out, "The requirement to conceal intentions is probably best regarded as one of many selection pressures likely to be acting on an individual engaged in a contest, and not as an absolute, inviolable rule".

In summary, the evolution of signals of submission and surrender of a contested resource to the opponent are expected to be evolutionarily stable since bluffing is very unlikely to be advantageous. This type of signalling might be expected in very highly asymmetric contests as a means of reducing the risk of injury to the weaker opponent. In contrast, the evolution of signals which exchange information between animals engaged in continued competition, as a means of reducing the risk of overt aggression, is determined by four fitness- related quantities.

i) the cost of escalation (c_e).

ii) the value of the resource (v).

iii) the cost of signalling as a function of the level to which the attribute concerned is signalled (c_s). If $c_s = 0$, then any individual can

signal at any intensity without incurring any variation in fitness cost.
iv) the cost of bluffing (c_b) over and above c_s.

As v/c_e increases, the greater c_s and c_b must be to nullify the selective advantage of bluffing. Conversely, as v/c_e decreases, the more likely it is that less costly signals will become evolutionarily stable due to the high relative risks of escalation and the relatively trivial value of the resource. In this situation there are two alternative scenarios. In the first, bluff is selectively favoured and invades the signalling system but the signals continue to be recognized by recipients due to animals' unwillingness to escalate. In this situation, the original motivational information carried by the signal is lost to bluff and the signal becomes no more than "I want this resource" (Maynard Smith 1982b). In the second scenario, bluff entails an intrinsic cost (c_b), for example as a result of bluffers running a higher risk of injury in escalated contests with animals of genuinely high fighting ability (e.g. Maynard Smith & Harper 1988). In this situation, the invasion of cost-independent signalling system by bluff is less inevitable and the system may be evolutionarily stable.

Studies employing this 'cost-benefit' approach to the evolution of agonistic displays (e.g. Enquist 1985; Enquist *et al* 1985; Popp 1987a) have already found that the range of displays in a species' repertoire may be related to variation in resource value (v), cost of the display in terms of risk of retaliatory escalation (c_b) and its effectiveness in displacing opponents. For example, the displays of the fulmar *Fulmarus glacialis* in competition over fish can be ordered into an increasingly effective but increasingly risky series which are used at successively higher levels of resource value (Enquist *et al* 1985).

Finally, two other variables may be relevant (Maynard Smith 1982b). Firstly, the outcome of contests for resources may not be "all-or-nothing". An example of this is in some types of competition for territorial space. Here, 'bargaining' is a necessary part of agonistic communication and variability in display repertoires may reflect this need (Maynard Smith 1979, 1982a,b). Secondly, bluffing may lose its selective advantage in populations where individual recognition is prevalent and opponents possess relatively complete knowledge of each other's abilities prior to any encounter (Bossema & Burgler 1980; van Rhijn 1980; van Rhijn & Vodegel 1980).

6.1.3. Introduction to the Study

Data from Chapters 4 and 5, and from existing work (Drent 1983) suggest that information concerning the following attributes may be relevant to the outcome of agonistic encounters between great tits.

i) Prior residence/prior territoriality and associated familiarity with the same area.

ii) Immediate, site-specific, agonistic tendencies ('aggressiveness') based on recent, local agonistic experience.

iii) RHP (size), in females only.

iv) Immediate agonistic tendencies based on a proximate internal stimulus such as hunger.

A range of postural displays occur during these encounters and the main aim of this study is to see to what extent this display can be explained in terms of transmission of information about these attributes. In contests between females we already know that a proportion of the information predicting outcome is conveyed by a more fixed, non-behavioural aspect of phenotype, the size of the ventral stripe.

Excepting size, the attributes listed above seem not to be intrinsically costly attributes of their possessor. If they are communicated by postural display, then they could be signalled equally well, at any intensity, by any bird, if we assume that the performance of a postural display is a negligibly costly act. In other words, we would be concerned with the possibility of cost-independent signalling systems and their evolutionary constraints, as discussed above. This assumption is not trivial. For example, in the case of variables (i) and (ii), above, prior residence or a high level of local 'aggressiveness' will both be consequent on success in numerous, risky agonistic encounters. Physiology and agonistic behaviour are known to be causally linked. For example, Bronson *et al* (1973) showed variation in adreno-cortical activity of mice, depending on agonistic success or failure, and Ramenofsky (1984) and Hegner & Wingfield (1987) have shown increased levels of plasma testosterone in agonistic interactions between mutually unfamiliar quail *Coturnix coturnix* and house sparrows *Passer domesticus*. If hormone levels, in turn, play a role in determining which display elements are performed by the interacting birds, then although the display act itself may be of negligible cost, the physiological state causing it may be a direct consequence of costs incurred during prior social experience. Known cases of the influence of hormonal state on the use of agonistic display by birds are rare, but include Adkins & Pniewski's (1978) study of the effect of steroids on reproductive displays in male quail, and Searcy & Wingfield's (1980) demonstration of the effects of androgens in increasing the intensity of aggressive display in red-winged blackbirds *Agelaius phoeniceus*.

In addition, the importance of mutual familiarity of individuals in this population remains to be established and the distinction between competition for food and competition over territorial space introduces the difference between 'all-or-nothing' resources (time at a feeder) and divisible resources (territorial space).

Maynard Smith & Riechert (1984) harmonized the conflict hypothesis and game theory approaches to the study of agonistic behaviour by modelling the selective pressures on various behavioural options (ultimate causes) in competing spiders *Agelenopsis aperta*, according to their overall fitness payoff, using criteria such as RHP, resource value and cost of escalation. However, this fitness payoff is modelled as being realized (proximate causes) via a classical 'two-tendency conflict' model of 'aggression' and 'fear'. Increasing potential fitness benefits are translated into an increased aggressive tendency, and increased potential fitness costs into an increased fear tendency. If the two balance at a high level, high intensity displays result with low intensity displays occurring at a low level of balance. Increasing asymmetry between the fitness costs and benefits (i.e. an increased net, positive or negative payoff) increases the chance of resolution of the contest through attack or withdrawal. The authors emphasize that both the proximate and ultimate explanations of agonistic behaviour are necessary. "The proximate mechanism is merely the means by which the fitness effect (ultimate cause) dictated by natural selection is realized" (p.565). In effect, it would be possible to label the two conflicting 'causal factor strengths' (Mc Farland & Sibly 1975) at any point on this causal chain. "Aggression" and "Fear" are proximate labels. "Estimation of own fighting ability and willingness to continue" and "Estimation of opponent's fighting ability and willingness to continue" (Maynard Smith & Riechert 1984) would be intermediate. "Estimated fitness gain" and "Estimated fitness cost" are ultimate causal factor labels.

Given that the ultimate function of ritualized display is to optimize fitness gain by reducing the cost of competition over contested resources, the aim of this study is to see which proximate labels great tits use when the exchange of information about 'causal factor strengths' is used as a mechanism for achieving this.

The chapter is organized as follows:

i) The Distribution of Postural Display

Analysis of associations between display elements both within and between birds during single interactions. The effects of season, resource type and the sex of the interacting birds on the display repertoire used will also be considered. A comparison of display repertoires between intraspecific encounters and those with blue and coal tits is important because some display functions may only be relevant in intraspecific contexts (e.g. asymmetries in territorial experience) and the use of a display between species may argue against such functions.

ii) Risk and Effectiveness of Postural Display

Following the approach of Enquist *et al* (1985) and Popp (1987a,c), this section will examine the possibility that the effectiveness of apparently cost- independent postural displays in ensuring access to resources is related to the risk of escalation of a contest, and that displays differing in their risk and effectiveness may vary in their usage depending on resource value.

iii) Postural Display and Individual Attributes

Are there correlations between display usage and those asymmetries between birds which have been found to be relevant to the outcome of agonistic encounters ?

6.2. THE DISTRIBUTION OF AGONISTIC BEHAVIOUR ELEMENTS

6.2.1. Methods

The data used in this section come from the following sources.

i) Observation of intraspecific interactions at feeders during all three winters at the Garden (all years), Yew (1987/88) and Wood (1987/88) sites.

ii) Observation of intraspecific, 'non-feeder' interactions during all three winters at the Garden (all years), Yew (1987/88) and Wood (1987/88) sites.

iii) Observation of interspecific interactions with blue and coal tits at feeders during all three winters, at the Garden (all years), Yew (1987/88) and Wood (1987/88) sites.

iv) Transcription of 76 hours of videotape, recording activity at a feeding table in the Garden, during the 1986/87 winter.

In the first three data sets, display behaviour elements were recorded on a binary, 'occurred' (1) or 'did not occur' (0) basis for each great tit in a dyadic encounter. At feeders, an interaction was defined as starting when a second bird flew to join a great tit already at the feeder, and was considered as ending when either one or both birds left the feeder, or both birds remained on the feeder without apparently influencing each other's behaviour (i.e. both ND). Non-feeder interactions are more subjectively defined since they are not tied to a specific location or resource item. Any case where chasing, supplanting, display or attack occurred between two great tits, away from a feeder, was included in this data set. Whereas all feeder interactions during an observation session were recorded, some non-feeder interactions were almost certainly missed simply because my attention was directed at a feeder. It is possible, therefore, that the recorded sample is biased towards interactions conspicuous enough to attract an observer's attention. These data sets record the frequencies of occurrence of display elements and their associations both within, and between, competing birds. The only sequential information available relates mainly to the outcome of the interaction (i.e. leave or stay) and the preceding behaviour of both birds. In addition, attack (ATT) always terminates an interaction so that a recorded association between ATT and other elements actually represents a transition from those elements to attack.

In the final data set, the use of slow and frame-by-frame playback allowed a more detailed analysis of the course of interactions. This was facilitated by the greater area of food available to birds at the feeding table (154cm^2 as opposed to 72cm^2 at hanging feeder) which tended to increase the length of interactions by increasing the 'individual space' between the competing birds. In particular, many encounters were clearly divided into bouts separated by periods of non-interaction. For analysis of intra- and inter-individual behavioural associations, therefore, the binary scoring system was applied to each bout independently. Clearly, this analysis also increases the amount of sequential information available in the data set.

In contrast to the associations between individual birds studied in Chapter 4, associations between behavioural elements are likely to be *under-* estimated since one or more elements may be missed by an observer recording a brief bout of display, especially if compound displays are being performed. The Half-Weight Index (Cairns & Schwager 1987; Ficken *et al* 1981) has minimal bias in situations where a lack of independence between the observation of entities A and B reflects a bias towards scoring them when they occur separately. Consequently, this index was used to measure the associations between pairs of behavioural elements recorded from the four sources listed above. In cases (i) and (iv), both intra- and inter-individual associations were analysed. In cases (ii) and (iii), only intra-individual associations were considered. The Half- Weight Index is given by $T_t/(0.5(n_a + n_b))$, where T_t is the number of observations of elements A and B together, n_a is the total number of observations of A and n_b the total number of observations of B. Wherever polyadic associations occur (e.g. the compound display WO/TF/HB), these are broken down into their component dyads for analysis. In the above case, T_t would be incremented by 1 for each of the WO/TF, TF/HB and WO/HB dyads. Similarly, in the case of WO/TF given by individual A and HB/OB given by individual B, T_t would be incremented for each of the inter-individual associations WO/HB, WO/OB, TF/HB and TF/OB. It is important to realize that some information is lost by calculating an association index. For example, if there were 1000 occurrences of element A and 10 of element B, and the number of associated occurrences (A/B) was 9, then there is 90% association from the point of view of B but only 0.9% from the point of view of A. The Half-Weight Index produces a composite index of 1.78%. In other words, the index is limited by the disparity in sample size between the two elements. In this extreme case, the maximum if all 10 occurrences of B were with A is 1.98%. Possible causes of sampling bias between elements in observational data sets are discussed later.

The Half-Weight Index allows the conversion of raw data into a similarity matrix of pairwise associations between elements. However, some form of cluster analysis is necessary to visualize the overall patterns of association. The simplest technique is single-link cluster analysis (SLCA) (Morgan *et al* 1976) which produces a nested, strictly hierarchical set of clusters, without overlap (usually portrayed as a dendrogram). However, the process has two weaknesses. Firstly, the forcing of the similarity matrix into a hierarchical form may distort the true patterns of association. Secondly, the property of 'chaining' (Morgan *et al* 1976) causes a considerable loss of information between data and dendrogram. For example, if WO and TF were associated at a very high level (90%), and HB were associated with the WO/TF cluster at 40%, SLCA does not say anything about which of WO and TF, HB is most closely associated with. In effect, clusters at a high level become 'black boxes' on to which elements at lower levels of association are chained. The methods of B(k) cluster analysis (Jardine & Sibson 1971) have been chosen for this study, in preference to others, since they specifically overcome the problems of hierarchical distortion and chaining. They do this by allowing the existence of overlapping clusters, thereby revealing finer patterns of association that are hidden by the 'opaque' SLCA clusters. For any B(k) method, k-1 elements are allowed in an overlap between clusters. In this study, a B(2) method was used since at high levels of k, the extensive cluster overlaps may hinder rather than help the interpretation of associations. The detailed methodology of B(k) cluster analysis is described by Cole & Wishart (1970) and Jardine & Sibson (1971). The analyses in this chapter use the Cole-Wishart algorithm in the CLUSTAN package (Wishart 1978) and are all based on the transformation of raw data into similarity matrices using the Half-Weight Index.

6.2.2. Results

6.2.2.1. Patterns of Performance of Agonistic Behaviour Elements

Table 6.3. presents the frequency of occurrence of each element across the four sex categories of 'actor' and 'recipient' (male > male, male > female, female > male, and female > female) in interactions at feeders. This Table pools data from all sites and years (sources (i) and (iv), above). The raw data, tabulated by year and month is presented in Appendix 9. It is clear from inspection of the M>F and F>M columns that display by females, directed to males, is a rare phenomenon since most intersexual interactions involve simple supplanting of the female by the male. The distribution of elements across the remaining three categories is compared with random expectation, according to the number of available opportunities for an element to occur (i.e. for M>M and F>F there are 2n opportunities and for MF, n male opportunities, where n = the total number of interactions in that category). Only the frequency of OB shows no association with the sexes of the interacting birds. For the remaining elements, the percentage of the overall X^2 value contributed by each category is plotted in Fig. 6.1., being assigned a positive value if the observed deviation is above expectation and a negative value if it is below expectation. All display elements except HU are found disproportionately frequently in all-female encounters, but are relatively rare in displays directed by males to females. HU is particularly characteristic of males. Surprisingly, attacks are more frequent than expected between females. The distribution of SA and ND is largely a function of the very high proportion of intersexual interactions that are resolved almost immediately, by supplants.

Table 6.4. and Fig. 6.2. perform exactly the same analysis for interactions away from a feeder. In this case, only occurrences of HU, WO and TB, of the display elements, are significantly associated with the sex of the interacting birds. HU and TB are performed far more often by males than by females. WO and attacks are again disproportionately frequent in female - female interactions. Chasing is much more characteristic of males than of females, and VF is only seen between males. Supplants are relatively rare between males but more

common than expected between females and in intersexual interactions.

These data are put into context by Figs. 6.3a and 6.3b, and Tables 6.5a–c. Fig. 6.3a. shows the change in the distribution of interactions between feeder and non-feeder contexts over the course of the winter for each sex category. The proportion of interactions occurring away from a food source is minimal between October and December, and then increases to peak in March, coinciding with the process of territory establishment. The raw data are given in Appendices 9 & 10. Over the whole winter, contests away from food are more frequent between males than between females or between the sexes. These findings lend weight to the earlier hypothesis that interactions occurring away from any apparent material resource reflect competition over territorial space. By April, most local pairs are firmly established on breeding territories and the frequency of non-feeder interactions begins to decline again.

Fig. 6.3b. illustrates the seasonal changes in frequency of use of each behaviour element in feeder interactions, expressed as the percentage of opportunities for performance on which the element was used. HU and TB both become more common over the course of the winter in the three sex categories (male > male, male > female, female > female), as territoriality develops. None of the other elements show clear, seasonal trends, although WO, TF and ATT increase markedly in frequency in all-female interactions during April. The total number of opportunities in each sex category, in each month is given at the end of the Table and implies that some of the anomalous results for female - female interactions in April may be an artefact of small sample size, rather than a real seasonal effect.

Table 6.5a. shows the difference in frequency of performance of agonistic behaviour elements between feeder and non-feeder contexts, for all four sex categories of actor and recipient. Most elements occur in both contexts. However, HU, HD, HB and TB are all more frequently seen in non- feeder, territorial interactions, and WO, TF and ATT all tend to occur more frequently in interactions at food, at least in intrasexual cases. OB was never recorded in a territorial interaction. VF and CH were omitted from this analysis as they occurred exclusively in territorial interactions. ND was omitted because although 'non-interactive', ND/ND encounters were recorded at feeders, at least one bird had to perform some more overt action for an interaction away from feeders to be recognized. Consequently, the ND data sets are not comparable between the two contexts.

Table 6.5b. compares the distribution of interactions across the three sex categories of interactant with a chance expectation derived from the numbers of colour-ringed birds of each sex present during each winter. This analysis includes interactions between unringed birds and it is assumed that relative proportions of unringed males and females are not significantly different from those of the colour-marked birds upon which the calculation of the expected values is based. In all three years, there are many more male - male and fewer female - female interactions than expected. Between males this difference increased from 108% of expectation in 1986/87 to 118% in 1987/88 and 144% in 1988/89. Conversely, the number of all-female interactions fell from 89% of expectation in 1986/87 to 87% in 1987/88 and 75% in 1988/89.

Table 6.5c. performs the same type of analysis but this time pools all three years' data before comparing the number of all-male and all-female interactions with chance expectation across three categories of residence status (prior resident - prior resident, prior resident - newcomer, and newcomer - newcomer). In both sexes, interactions between birds ringed in a previous winter occur at 10% or less of their expected frequency, whilst those between newcomers (first-year birds, or adults not present in a previous winter) are more than twice as frequent as expected. Interactions between the two residence classes occur at 60-70% of their expected frequency in both sexes.

6.2.2.2. Associations between Agonistic Behaviour Elements

So far, analyses have treated all behaviour elements independently for the purposes of examining their frequencies of occurrence. In reality, only SA and ND must occur independently of other elements, by their definition. Most display elements rarely occur alone and attacks and chasing may also be accompanied by postural display. The following analyses describe the associations between elements in the intraspecific displays of the great tit. These associations may be compound displays, comprising several elements simultaneously, or a sequence of elements in a single bout of display. Secondly, there may be inter-individual associations between the display behaviours of interacting birds. An intra-individual association is said to exist between any two or more elements if they occur once or more in the behavioural record of a bird during one interaction. The difference between sequential and compound occurrence of elements and the number of times they are performed within an interaction is not considered at this stage. The same method is applied to scoring an inter-individual association between two or more elements in an interaction. For the analysis of videotape data, the same method is also applied but if an interaction is divided into bouts, then each bout is scored independently. The sexes of the interacting birds are not taken into account at this stage, in order to ensure adequate sample sizes. Tables 6.6. - 6.10. present the raw data and a similarity matrix for each of the following data sets.

Context	**Type of Association**	**Table**
Observation/Feeder	Intra-individual	6.6
Videotape/Food	Intra-individual	6.7
Observation/Territorial	Intra-individual	6.8
Observation/Food	Inter-individual	6.9
Videotape/Food	Inter-individual	6.10

Figs. 6.4. - 6.8. present the results of the B2 cluster analysis of these similarity matrices. Bars connect behaviour elements to form clusters which reflect association between the component elements. The width of the bar represents the strength of clustering (1cm = complete association) but the length has no significance. Exact strengths of association are annotated to each bar (1 = complete association, 0 = never associated). Clusters at lower levels of association may be formed by grouping of higher level clusters. The formation of these lower level clusters is represented by bars which connect elements indirectly, via the bars of the component, higher level clusters. For

example, bar 'X' in Fig. 6.4. connects the higher level clusters HB/OB and WO/TF/TB to form a WO/TF/TB/HB/OB cluster at a 0.209 level of association.

Figs. 6.4. and 6.5. show the dominance of two clusters, WO/TF and HU/TB, each of which is usually performed as a compound display. These two clusters are linked through the association of WO/TF with TB. EB also clusters with WO/TF. The only other strong association is between HB and OB (another compound display). This display is associated with the WO/TF/EB/TB cluster at a low level. HD is too rare to be associated with other elements but cross reference to Tables 6.6. and 6.7. shows that its few occurrences are strongly associated with WO, TF and TB. Attacks are too weakly associated with postural display in general, to appear in the Figures but Tables 6.6. and 6.7. show that only the WO/TF display is associated with attacking at a level that is considerably above zero. In territorial interactions (Fig. 6.6.), the dominance of the HU/TB and WO/TF displays persists and HU/TB is far more commonly performed than WO/TF (Table 6.5a). OB is never seen but HB is strongly associated with the WO/TF display. The WO/TF/HB and HU/TB clusters are linked by an association between TF and TB, and by a common association with HD. HU is the only element to be strongly associated with the two solely territorial elements, VF and CH. Attacks are too rare in territorial interactions to be figured.

Inter-individual associations (Figs. 6.7. and 6.8.) are characteristically weaker than those within individuals but WO/TF and HU/TB remain the strongest clusters. The pattern of associations between *different* elements does not differ greatly from that found in the intra-individual analyses. However, it is noticeable that several elements are more associated with the occurrence of *themselves* in the opposing bird than with the occurrence of many of the other elements.

Associations between behavioural elements in interactions with blue and coal tits are analysed in exactly the same way as above, in Table 6.11. and Fig. 6.9. All data for this analysis come from observation of interactions at feeders and interactions with blue tits and those with coal tits are pooled. It is clear from Table 6.11. that interspecific displays are dominated by WO, TF, HB and OB, with HU, EB and TB being rarely seen in comparison with their frequency in intraspecific encounters. HD was only recorded eight times and is omitted from the analysis. Attacks are also much more frequently directed at blue and coal tits than at other great tits. Table 6.12. compares the frequency of performance of each element in interspecific encounters with that in intraspecific encounters at feeders. Fig. 6.9. shows that WO/TF is a strongly associated compound display, as in intraspecific encounters. The HB/OB compound display is also common and is associated with WO/TF at a lower level to give a WO/TF/HB/OB compound display. Attacks are more strongly associated with the WO/TF/OB cluster than in intraspecific encounters. EB and TB form a strong cluster linked to HB, but reference to Table 6.11. shows that they are quite rarely seen in interspecific display. HU is so rarely seen in display to other species that it does not cluster with any other element.

6.2.3. Discussion

All these analyses of the distribution of postural display may suffer from inherent biases in the original data sets. The more subtle displays such as EB and OB may have been missed on some occasions and these omissions may have contributed to the apparent rarity of these elements. In addition, certain sets of elements (e.g. WO/TF, HU/TB, HB/OB) are more likely to show high association indices simply because they involve different parts of the body and can thus be associated either simultaneously or sequentially in a bout of display. Others (e.g. HU/HD/HB) can only occur sequentially and the probability that they will be scored together in a display bout is correspondingly reduced. With these provisos, the main conclusions from this section are summarized below.

i) With the exception of HU, postural display and attacks at feeders are more frequent between females than between males. This perhaps reflects the greater number of asymmetries relevant to the outcome of female - female interactions. This, in turn, may make it more difficult for the eventually subordinate bird to assess those asymmetries at an early stage and either avoid a competitive interaction altogether, or submit immediately, thus allowing what we see as a supplant. The importance of the subordinate as the individual whose behaviour eventually determines the outcome of a contest is also discussed by Rowell (1974).

ii) HU is much more frequently performed by males than by females and is especially prevalent as a HU/TB compound display given by males in competition over territorial space. In both sexes, HU and TB increase in frequency over the course of the winter, strengthening this view (Hinde 1952) that the HU display is closely associated with territorial competition. VF seems to be no more than the HU display performed whilst in flight and is only ever seen in territorial competition between males. Although rare, HD is also more frequent in territorial interactions. In contrast, WO, TF, OB and ATT are all more typical of competition over food sources. HB and EB show little association with resource context.

iii) Cluster analyses reveal WO/TF, HU/TB and, to a lesser extent, HB/OB as the main two-element compound displays in the repertoire of the great tit. However, many more combinations of elements do occur as compound displays at lower frequencies (e.g. WO/TF/OB, HU/TF, WO/TF/TB). EB occurs at low frequency with most other elements. Only the WO/TF display shows any marked association with attack, implying that this display reflects a higher level of escalation of competition than do the other postural elements.

iv) Inter-individual associations between displays in interactions at food reveal a marked tendency for the two birds to perform *the same* elements during an interaction. This may reflect the use of displays as means of mutual assessment of factors (e.g. body size) relevant to outcome. Alternatively, at a more proximate level, co-occurrence of display elements may simply reflect symmetry in the immediate agonistic tendencies of the competing birds. In cases where an asymmetry exists, mutual display is simply not observed due to the immediate submission of one of the birds.

v) In interactions with other tit species, the HU/TB display is very rare, further strengthening the argument that it functions in a purely intraspecific context - competition for territorial space. WO/TF and HB/OB remain common compound displays. Attacks are more frequent than in intraspecific interactions and remain more strongly associated with WO/TF than with other elements.

vi) At feeders, interactions between males are more frequent than would be expected by chance and those between females less frequent. In contrast, Chapter 3 found that capture rates of great tits at feeders were consistently female-biased and that females tended to come to feeders earlier in the day than males. The difference may reflect a tendency for females to visit feeders solitarily to avoid being immediately supplanted by a male. Consequently, any male approaching the feeder would be more likely to interact with another male than with a female. However, this argument would also predict that male - female interactions frequencies would be lower than expected, yet this is not the case. An alternative hypothesis is that males, although spending less time at feeders, actively seek out competitive interactions during this time because of the importance of establishing local social dominance as a prerequisite for territory establishment, as suggested by Drent (1983). This argument is supported by the data in Table 6.5b. which show an increasingly disproportionate frequency of male - male interactions as the study progressed. This was also a time of increasing population size and, perhaps, increased competition for territorial space amongst the male population.

vii) At feeders, interactions between previously resident, adult great tits are very much rarer than chance expectation would predict but those between first-year birds and non-resident adults are disproportionately frequent. This asymmetry may partly reflect the tendency of resident adults to remain within their former breeding territories and exploit natural food sources (Saitou 1978), whereas inexperienced first-year birds are more dependent on artificial food sources (e.g. Lehikoinen 1986; Orell 1989). However, in the mild winter conditions of this study, this explanation has less force. An additional factor may again be that there is a causal link between social dominance and territory establishment which in turn causes high rates of interaction between newcomers whose reproductive success in the breeding season depends on achieving local social dominance and establishing a local territory.

6.3. RISK AND EFFECTIVENESS IN THE DISPLAY OF THE GREAT TIT

6.3.1. Introduction

The evolution of agonistic communication through a repertoire of displays whose performances are not intrinsically costly has been modelled by Enquist *et al* (1985). Evolutionarily stable communication through choice of display is only predicted if the following conditions are satisfied.

i) Different displays have different *consequential* costs in that they have different probabilities of provoking overt aggression from the opponent.

ii) As the cost of a display (risk) increases, so does its effectiveness in securing priority of access to the contested resource. In other words, as potential effectiveness increases, the greater the probability that the interaction will be escalated to the level at which it is only resolved by physical fighting.

iii) As the value of the resource to the animal increases, more risky, effective displays are chosen.

This model thus replaces the idea of intrinsic cost by that of 'consequent cost' as a mechanism ensuring the resistance of the signalling system to invasion by bluff. Enquist *et al* see cost as the risk of overt, retaliatory aggression by the opponent and that a displaying animal is therefore signalling the risk that it is prepared to take (i.e. its 'motivation') to win the interaction. In effect, the classical 'two-tendency' model is condensed into a single variable, 'acceptable risk', as the causal factor being signalled.

The studies of Enquist *et al* (1985) on the fulmar, Popp (1987a) on the American goldfinch, Popp (1987c) on the purple finch and Popp (1989) on both the latter species support all of the predictions listed above. In the American goldfinch, effectiveness and risk both increased from the 'Low Intensity Head Forward' (= HB) to the 'High Intensity Head Forward' (=HB/OB) to the 'Wingflap Display' (= HB/OB/WO). In the purple finch, effectiveness and risk increased through the same two head forward displays to the 'Bill Display'. In this species, overt aggression was simply the combination of the Bill Display with attempts to peck the opponent. This study tests the same predictions on the agonistic display elements of the great tit.

6.3.2. Methods

All intrasexual interactions recorded at feeders in the Garden during the three years are included in this study. Males and females are considered separately. Behaviour elements were scored on a 'one-zero' basis for each individual in each interaction, whether derived from observation or videotape. A performance of a behaviour element was considered 'effective' if the performer was eventually dominant in that interaction, gaining priority of access to the food. Risk was scored as the percentage of performances of an element after which the performer was attacked by its opponent. Behaviour elements were treated independently in calculating their effectiveness and risk. This ignores the existence of compound displays and sequential and inter-individual dependence between behaviour elements, as discussed in Chapter 6.2. However, the choice of a few of many display clusters to be used as independent units of display would be inevitably arbitrary and would have curtailed sample sizes so severely as to make statistical analysis very difficult. The chosen solution was to return to the originally defined set of elements and examine the distribution of each element with respect to each of the putative correlates independently, but to interpret the results by reference to the associations which are known to exist between elements.

6.3.3. Results

Table 6.13. gives the effectiveness and risk of each behaviour element for males and females. SA is omitted because, by definition, it is 100% effective and carries zero risk of attack. Effectiveness is plotted against risk for the same data set in Fig. 6.10., as a test of the first two predictions of Enquist's model. The results bear little resemblance to those of the studies discussed above. Excluding ND, all elements are at least 41% effective and none show an effectiveness of greater than 73%. Within this range, there is little relationship with risk, and it is noteworthy that most postural displays are not significantly more risky than giving no display at all (ND). If anything, the two sexes show opposite trends; risk increasing rapidly with effectiveness in females and decreasing with increasing effectiveness in males. In general, postural display is more risky for a female to perform than for a male, this being most marked for OB - the most risky female display, but carrying a zero risk of retaliatory attack between males. Attack stands out as the most risky behaviour in both sexes but is not more effective than most postural elements. These results are discussed in Chapter 6.5., in the light of the conclusions of the next section.

6.4. POSTURAL DISPLAY BY GREAT TITS: CORRELATIONS WITH INDIVIDUAL ATTRIBUTES, MUTUAL FAMILIARITY AND RESOURCE VALUE

6.4.1. Introduction

In this section, prior residence (both sexes), body weight (females) and VSI (females) are the individual attributes examined as potential correlates of display use in intrasexual interactions, based on the results of Chapter 4. Any variation of display use with mutual familiarity would imply an important role for individual recognition in influencing the qualitative nature of any information exchanged during the course of interactions (Bossema & Burgler 1980; van Rhijn & Vodegel 1980), and would shed light on the role of specific elements in the repertoire of the great tit. Two measures related to mutual familiarity are used. Given that around 98% of intrasexual interactions at the Garden involved at least one bird new to the site during that season (either first-year or adult) (Table 6.5c.), date can be viewed as a crude positive covariate of mutual familiarity between members of the winter population. Date also provides an index of the development of territoriality in the population as the winter progresses (Table 6.3a). Association indices for each dyad, as calculated in Chapter 4, provide a more accurate index of the degree of mutual familiarity between interacting birds.

The frequency of occurrence of each bird at the Garden (Chapter 4) is also examined as a correlate of display use to introduce the importance of distinguishing between familiarity with *site* and familiarity with *opponent* as variables influencing agonistic behaviour.

As in Chapters 4 & 5, resource value is approximated by the rate of interaction at the feeders on the day on which each interaction at a feeder was recorded. Again, 1986/87 and 1988/89 Garden data sets are pooled to examine the relationship between resource value and display use.

Where the difference between two interacting birds in their scores of a particular variable (e.g. VSI DIFFERENCE, FREQUENCY DIFFERENCE, WEIGHT DIFFERENCE) is itself used as a putative correlate of display use, this is always expressed as 'dominant score minus subordinate score' for that interaction.

6.4.2. Methods

The analyses use the following Garden data sets.

i) PRIOR RESIDENCE: all three years; all recorded interactions.

ii) BODY WEIGHT: all three years; all interactions recorded at feeders.

iii) VSI: 1987/88 and 1988/89; all interactions recorded at feeders.

iv) ASSOCIATION INDEX, DATE, FREQUENCY OF OCCURRENCE, INTERACTION RATE: 1986/87 and 1988/89; all interactions recorded at feeders.

For all analyses using date as a variable, this is measured from October 1 (= Day 1).

As in Chapter 6.3., behaviour elements are scored on a one-zero basis for each bird in each interaction and analyses are carried out independently for each element.

Each interaction in the data set is also treated as an independent event. That this is not the case has already been discussed (Chapter 4). In this case, however, the need to maintain adequate sample sizes again makes this treatment unavoidable, the important caveats being:

i) that the same dyads are sampled repeatedly and,

ii) that repeat interactions on the same day may suffer from dependency in time.

The distribution of elements across the prior residence classes of interacting birds is examined by means of chi-square tests in Tables 6.14. and 6.15. For each of the other variables introduced above, two analyses are carried out. In the first, the distributions of the values of the variable at which each element is performed are compared using a Kruskal- Wallis test to test the null hypothesis that the performance of a particular element is uncorrelated with the chosen variable. In cases where the test shows significant variation in these distributions across the 11 elements, the distributions for each element are compared with that for supplants, using the multiple comparison technique for examining individual pairs of medians (Siegel & Castellan 1988, pp. 213-215). This analysis allows variables which might be causal in turning a simple supplant into a more complex interaction involving display or attack to be identified. An example of one of these tests is given in Appendix 11 and the results for all variables are given in Table 6.16. (males) and 6.17. (females). In the second test, all supplants are excluded from the data set in order to test the null hypothesis that the level of the variable concerned is not correlated with the performance of one display element *as opposed to another.* The distribution of variable scores at which an element is performed is then compared with the distribution of scores in the remainder of the data set (i.e.

cases where the element *is not performed*) using a Mann-Whitney-Wilcoxon test. This test is carried out independently for all elements except ND. In each test, the critical p-value for the rejection of the null hypothesis is reduced according to the formula ($p_1 = 1-(1-p)^{1/k}$) (Sokal & Rohlf 1981) because of the use of serial multiple comparisons. In these cases, k=9 since nine tests are performed in series, so that $p_1 = 0.005$. An example of one of these series of tests is given in Appendix 12, and the results for all variables are given in Tables 6.18. (males) and 6.19. (females).

It is recognized that the independent analysis of all these potential correlates of display use cannot take into account the possible effect of interactions between the variables in influencing these correlations.

6.4.3. Results

Tables 6.14. (males) and 6.15. (females) show the distribution of elements in all contexts, across the four prior residence categories of interacting birds, as defined in Table 6.5c. As in that Table, the expected number of elements in a category is calculated by dividing the total number observed in the same ratio as the total number of 'bird-minutes' of observation / videotaping time of colour-ringed birds of that category. Between males, HU, HD, HB and CH are significantly more frequent between birds of differing prior residence status than between newcomers. EB and OB show the reverse association. Between females, HU and TB (a compound display) are given especially by prior residents to newcomers but apart from this there is very little evidence of association between prior residence and display use in females. In both analyses, interactions between prior resident adults were so rare that their contribution to the overall pattern of display use could not be investigated.

The important conclusions which can be drawn from Tables 6.16. - 6.19. are summarized below for each Table.

i) Table 6.16. (males)

In comparison with supplants, the WO/TF compound display occurs at lower levels of interaction rate ('resource value') and between birds which are less strongly associated or which occur less frequently at the Garden site. The HU/TB display also occurs at lower resource values and tends to be more frequent, later in the winter. Attacks also tend to occur later in the winter. Non-interactive encounters show no seasonal trend but also occur when resource value is low and between birds less frequently seen at the site. It is noteworthy that HB, EB and OB, most of whose occurrences are associated with one of the two main compound displays (HU/TB, WO/TF) show almost none of the same correlations as these displays.

ii) Table 6.17. (females)

As amongst males, the HU/TB display occurs later in the winter and at lower resource values than do supplants. Almost all other elements, including attacks and non-interactive encounters also tend to occur later in the winter than do supplants. HB is characteristic of lighter females, but the significant entries in the HD column should be treated with caution due to the very small sample sizes.

The low minimum sample sizes in this Table lie entirely in the 'VSI' and 'VSI Difference' analyses. Sample sizes for all other elements are within ten of those given in the 'maximum' row.

iii) Table 6.18. (males)

After the exclusion of supplants from the data set, EB and the WO/TF compound display all tend to occur earlier in the winter (highly significant) and between birds that are relatively unfamiliar with each other (marginally significant). The HU/TB compound display (especially the HU element) tends to occur later in the winter and when resource values are lower (highly significant), and between birds which are more familiar with each other and with the Garden site (marginally significant). Attacks are also characteristic of frequently occurring birds and the later winter, and there is a marginally significant tendency for HB to occur in interactions between more highly associated birds.

iv) Table 6.19. (females)

After removal of supplants from the data set, the distribution of display use with respect to the five variables held in common with Table 6.18. shows marked differences from the latter. The WO/TF compound display shows almost no evidence of association with any of the variables. HU is characteristic of heavier females later in the winter but these results bear little relationship to those for TB, perhaps because the strength of association of HU and TB as a compound display is much weaker in females than in males (pers. obs.). There is a weakly significant tendency for TB to be performed by more frequently occurring birds, between relatively highly associated birds, and at times of high resource value. Attacks also occur more often as resource value increases. HD and HB are more frequently performed by birds familiar with the site, and HD also tends to occur between highly associated birds but, as with Table 6.17., these results must be treated with caution due to the small sample sizes involved.

As in Table 6.17., the low minimum sample sizes reflect the 'VSI' and 'VSI Difference' analyses. Sample sizes for all other analyses are within ten of those given in the 'maximum' row.

6.5. GENERAL DISCUSSION

6.5.1. Introduction

Agonistic interactions occur when animals compete directly for priority of access to a resource. The net fitness payoff from such an interaction is a trade-off between the benefits of 'winning' the interaction and gaining access to the contested resource, and the costs (in time, energy and risk of injury) of the interaction. This cost-benefit equation becomes more complex if the fitness consequences of winning or losing a specific interaction have longer term implications than access to the immediately contested resource. Chapter 4 has already shown that social dominance during the non-breeding season has long-term implications for territory establishment and successful reproduction in great tits. Drent (1983) also believed that prior experience was an important influence on agonistic behaviour in this species, and this dependency has been discussed elsewhere (e.g. Flannelly & Blanchard 1981; Francis 1983; Popp 1988; Ratner 1961; Thines & Heuts 1968).

A variety of other 'causal factors' may also affect the cost-benefit balance for an individual in an interaction. The location of the interaction, the identity of the opponent, the resource being contested and differences in the size, age, sex, plumage and physiological state of the interacting individuals have all been discussed and many have been found to correlate with the outcome of competitive interactions between great tits.

As Maynard Smith & Riechert (1984) have proposed, it may be realistic to view the combined input from all these variables as determining the strength of two, conflicting, proximate 'causal factors' which could be labelled operationally as "aggressiveness" and "fear". It is the magnitude of, and difference between, these 'causal factor strengths' which then determines an animal's immediate behaviour. This asymmetry has often been labelled as the animal's "intentions". (Chapter 1). The resulting behaviour is just one of the 'causal factors' acting on the same conflicting tendencies in the opponent, whose eventual response in turn feeds back to play a role in determining the next act of the first animal.

The general function of ritualized, communicative behaviour (display) in agonistic interactions is the minimization of the time and energy costs and risk to the performer, by transmitting unambiguous 'information' about the strengths of the causal factors which would determine the outcome of an escalated contest (e.g. Huxley 1966). The word 'information' is set in quotation marks to emphasize that it does not necessarily imply accuracy or 'honesty'. In other words, manipulation of an opponent's future behaviour through bluff (e.g. Krebs & Dawkins 1984) may well be involved in some circumstances. Tinbergen (1952) proposed that many agonistic displays had their evolutionary origin in unritualized displacement activities and intention movements resulting from aggression-fear ("attack-flee") conflicts. Most accounts of agonistic display repertoires in birds (e.g. Blurton Jones 1968; Stokes 1962a,b) have extrapolated this evolutionary hypothesis to one of immediate causation. They suggest that the same state of a two-tendency conflict still causes the same behaviour patterns, which have become ritualized to signal these states to the opponent. With this emphasis, there has been relatively little attention paid to the hypothesis that the variation in the repertoire might reflect signalling a greater variety of the more indirect, discrete causal factors listed above. An exception is Nelson's (1984) study of the communication of agonistic intentions in the pigeon guillemot *Cepphus columba* where he concludes that "the results of this study emphasize the importance of contextual factors in the communication process." Prior residence is emphasized in this respect. Similarly, Hazlett (1982) found that varying the resource value represented by the size of empty gastropod shells being competed for by hermit crabs *Pagurus bernhardus*, caused changes in the proportion of the display repertoire that was used.

The differing constraints on the evolutionary stability of signalling various causal factors have already been discussed, and an important conclusion was that these constraints are most severe in cases where the level at which a variable is signalled is unrelated to the cost of the signalling act. In this situation, any animal can signal at any level with no concomitant variation in cost. 'Bluff' signalling is thus selectively favoured and the signalling system may degenerate due to the unreliability of the information transmitted by the display of the signaller and consequent selection pressures for reduced receptivity to the display in the recipient. The signalling of internal state or 'intentions' which was implied by early tests of the conflict hypothesis and specifically investigated by later work (e.g. Bossema & Burgler 1980; Caryl 1979; Enquist *et al* 1985; Nelson 1984; Turner & Huntingford 1986) may often fall into this 'bluffable' category of causal factor. The resulting effects of evolutionary constraints on the likely stability of internal state signalling across different contexts is just part of the reason why "signalling intentions is attracting the attention of behaviourists, cognitivists, evolutionary biologists and philosophers in a most exciting fashion" (Colgan 1989; and see Dennett (1983) and Ristau (1983) for philosophical treatments). However, the signalling of aggressive internal state seems to be one function which *ritualized* behaviour (i.e. displays) in agonistic interactions may be less likely to perform, for the following reasons.

i) The process of ritualization, by definition, implies some degree of emancipation of the displays from their original physiological and neuromuscular causes.

ii) Why should the signalling of internal state based on a balance between just two proximate causal factors require the wide range of display postures and vocalizations, employing many different motor responses, that is seen in many species?

iii) Internal state is a continuously distributed variable which one might expect to be signalled by a continuously graded display (e.g. Green & Marler 1979; Morton 1977; Nelson 1984; Smith 1972). The clear discontinuities between display elements in the great tit contrast with this hypothesis, although it should be reiterated that HU and WO are variable in extent (e.g. Blurton Jones 1968) and that all elements can vary in non-structural parameters such as the duration of performance.

iv) Theoretical and empirical consideration of the evolutionary constraints on the signalling of bluffable variables (Chapters 1 & 6.1.) has suggested that signalling systems of this type will only be evolutionarily stable if there is no selective advantage to bluffing. This would occur either if the costs of having one's bluff called were very high (e.g. Chapter 5) or if outcome-relevant asymmetries between the animals were obvious (van Rhijn 1980) or known to both (i.e. individual recognition occurred - Bossema & Burgler 1980; van Rhijn & Vodegel 1980). In the latter two cases, there are also no selective pressures for ritualization of behaviour as a means of "promoting more unambiguous signal function" and "improving the stimulation/release of behaviour in other individuals" (Huxley 1966). The conclusion is that ritualized behaviour (i.e. display) is more likely to evolve in situations where the cost of signalling varies with the level of the signalled variable (e.g. Clutton-Brock & Albons 1979; Davies & Halliday 1978). However, ritualized behaviour may also be a stable, cost-independent signal where costs of escalation are very high relative to the value of the contested resource. In contrast, the signalling of bluffable variables such as internal state, where it occurs, may not always be recognized as a display because of the absence of selective pressures for ritualization. Bossema & Burgler's (1980) study in which they found that future behaviour in agonistic interactions between jays *Garrulus glandarius* was accurately predicted simply by the way in which the birds looked at each other (monocularly vs. binocularly, and long vs. short distance) is an excellent example of this.

v) Both Moynihan (1970) and Andersson (1980) have argued that if ritualized signals of bluffable variables do evolve then we might expect to see, over evolutionary time, the successive replacement of long-established, 'bluff- ridden', unreliable displays by new, effective signalling systems which in turn become ritualized and subject to invasion by bluff. If this is the case, then 'bluff-resistant' signalling systems should be the more phylogenetically stable since they would not be subject to cyclical, frequency-dependent selection of this kind. The postural display repertoire of the great tit falls far short of exhausting the range of postures which can be found in passerine display (e.g. Cramp 1988) but comprises postures which are found widely across passerine taxa (e.g. Table 6.2.; Andrew 1961; Cramp 1988). The implication is that, for whatever reason, most great tit display is signalling variables which are not easily bluffed.

Chapters 4 & 5 found a number of variables (physical, environmental and experiential) which correlated with the outcome of agonistic interactions between great tits and are thus implicated as 'causal factors' playing a role in determining a bird's 'intentions'. In Chapter 6, these variables have been analysed as correlates of the use of postural display in both intraspecific and interspecific interactions. The results are discussed below in view of the above arguments and in contrast with Blurton Jones' (1968) study which restricted itself to considering internal state as the immediate cause of display and the signalling of that state as its function.

6.5.2. Conclusions

Of all the cues which might contribute to the outcome of an agonistic interaction, those which are immediately perceptible (in this case, sexual dimorphism and dichromatism, and intrasexual size and plumage differences) were suggested as being least likely to be signalled by display. Accordingly, Table 6.3. and Fig. 6.1. show that, in interactions at feeders, display is much more frequent in intrasexual than in intersexual interactions. Size and plumage differences were found to be negligibly correlated with the outcome of male - male interactions. Amongst females, where these correlations were stronger (Chapters 4 & 5), there is still very little evidence that size and plumage differences are significantly correlated with patterns of display use (Tables 6.17. & 6.19.). Initial evidence, then, suggests that display is most prevalent in contexts where interacting birds have no overt cues (e.g. sex differences) as to the likely outcome of interactions.

Chapters 4 & 5 found size, plumage characteristics and prior residence to be correlates of dominance in all-female dyads, but only the latter in all-male dyads. This implies that a greater degree of mutual assessment might be necessary between competing females. This hypothesis is supported by Tables 6.5.b & c and Appendices 8-10 which provide evidence that there may be less opportunity for the development of mutual familiarity between females than between males. Accordingly, all-female interactions are disproportionately rare, both at feeders (Table 6.5b.) and in non-feeder contexts (Appendices 9 & 10), and high levels of pairwise association between females are rarer than between males (Appendix 8). Similarly, feeder interactions between females are mostly between first-year birds whose experience of the site and each other is necessarily limited in comparison with that of adults (Table 6.5c.). In accordance with this data, Table 6.3. and Fig. 6.1. show that most postural display elements are disproportionately *frequent* in all-female interactions. In addition, postural display is, in general, more frequent between females where overall 'agonistic symmetry' (as measured by relative rank - Appendix 6) is greater, and attacks are even more strongly associated with highly symmetrical dyads (Table 6.20.). In contrast, these correlations do not hold for male-male interactions.

Closer examination of Fig. 6.1: shows that attacks and all postural elements except HU and OB occur disproportionately often between female great tits. HU is typically a display given by males and is rarely seen between females. The distribution of OB shows no relationship with the sex of the interacting birds. However, HU aside (this element will be considered separately), Table 6.15. shows little evidence of any relationship between prior residence and display usage amongst females. Similarly, Tables 6.17. & 6.19. fail to uncover any consistent correlates of the use of postural display by female great tits, with the exception that it tends to occur later in the winter than do supplants. The answer may simply be that postural displays *are* transmitting proximate information about the performer's aggressiveness, in exactly the way implied by Blurton Jones (1968), but that differences in the elements comprising a display reflect differences in the amount of information about the causal factors underlying that internal state that are being transmitted. For example, Table 6.19. shows that HD and HB tend to be performed by birds which are more familiar with the site of interaction, and with each other, whilst the very common WO/TF compound display, and OB, show no such correlations. Also in contrast to WO/TF and OB, TB tends to be performed by females which are more familiar than their opponent with the site of interaction, on days when interaction rate is higher, and between mutually familiar birds.

6.5.2.1. The information content of the great tit display repertoire: a hypothesis

On the basis of the above discussion, it could be hypothesized that WO, TF and OB are bluffable, 'threat' displays carrying no more information than "I want this resource". These are expected to be seen in contexts where mutual knowledge is limited or absent, and where the 'escalation cost - resource benefit' asymmetry is so large that the 'calling of bluffs' by escalation is unlikely. If this context applies to almost all female - female interactions relative to those between males, this would explain the universal distribution of these elements across all contexts of female - female interaction. The hypothesis is then extended by suggesting that elements such as HD, HB and TB represent the transmission of information about prior residence as a causal factor behind the level of aggressiveness reflected by the use of postural display. The greater specificity of the information provided by these elements might also make use of them by bluff signallers less advantageous for two reasons. Firstly, as discussed in Chapter 6.1.3., displays correlated with prior residence may be caused by physiological states which are cost-correlated in that they reflect the bird's success in recent agonistic experiences in that area. Secondly, such bluffs would tend to elicit escalation from a more specific subset of opponents. These would be the genuinely dominant, local resident birds with the greatest potential to inflict damage on the bluff signaller in an escalated contest.

The validity of this hypothesis can be assessed by setting it against the distribution of display in all-male interactions. In both feeder and non-feeder contexts, far more interactions than would be expected by chance are between males (Table 6.5b, Appendices 9 & 10), and higher proportions of dyads have high pairwise association indices than between females (Appendix 8). Thus, between males, mutual familiarity probably develops much more quickly, and to a higher level, than between females. We would therefore expect WO, TF and OB to be more characteristic of infrequently occurring, mutually unfamiliar birds, and to occur earlier in the winter when levels of mutual experience within the male population are still low. Table 6.14. is somewhat ambiguous in its contribution to the above hypothesis. HD and HB both tend to occur when there is a gross prior residence asymmetry between competing birds, whereas OB almost always occurs between 'newcomer' (i.e. mostly first-year) birds. However, WO, TF and TB show no significant association with these broad categories of prior residence. Tables 6.16. and 6.18. are more conclusive. Table 6.16. shows WO/TF to be replaced by supplants as mutual familiarity increases, and also shows HB and TB to be more frequently seen, relative to supplants, later in the winter. Similarly, Table 6.18. shows that WO/TF tends to occur earlier in the winter and between mutually unfamiliar birds. By contrast, HB is seen between more mutually familiar birds and TB is characteristic of frequently occurring birds, later in the winter.

Overall, the results of Chapter 6 provide circumstantial evidence to support a hypothesis that the postural display repertoire of great tits can be divided into two categories of information content.

i) WO, TF, OB. Elements of simple 'threat', carrying no more information than the message, "I want this resource".

ii) HU, HD, HB, TB. Elements carrying information about prior residence and site attachment; the most important correlate of the outcome of intrasexual interactions.

EB is an element whose distribution is difficult to interpret. Possibly, body erectness is not a part of the ritualized repertoire, and is no more than an incidental consequence of a bird's posture at the onset of a bout of display.

At a more detailed level, the second category seems to be involved with the resolution of conflicts between long and short-term prior residence. For example, HU, HD, HB (males) and HU, TB (females) all tend to occur between birds having a large scale prior residence asymmetry (Tables 6.14. & 6.15.), and in most of these cases the newcomer is the performer of the display element almost, if not more often, than the prior resident adult. Yet, in Tables 6.16. - 6.19., the performance of these elements is consistently associated with the more frequently occurring of the two interacting birds. It seems that these elements are involved in the process of development of site attachment in newcomers and the resolution of conflicts that arise with birds having pre-existing attachments to the same area. HU is included in this category as an element which could be considered as going beyond the communication of 'prior residence' or 'site attachment' to the ultimate of signalling 'site ownership', as is manifest in the development of territoriality in male great tits as the winter progresses. HU is the only postural element with a clear bias towards performance by males (Table 6.3., Fig. 6.1.). It is the most frequently seen element in interactions away from material resources which are assumed to reflect territorial competition (Table 6.4., Fig. 6.2.), where its association with males is even more marked. It is also the only postural element that is markedly associated with chasing (Fig. 6.6.), a behaviour considered diagnostic of competition over space (Chapter 6.1.). Finally, HU, VF, TB and CH are the only elements seen commonly in boundary disputes between male great tits established on neighbouring territories (Hinde 1952, p.80; pers. obs.). In male great tits, HU is strongly associated with TB to form a compound display (Figs. 6.4. - 6.7.) but this association is much weaker in females, where HU is relatively rarely performed.

Tables 6.5a. and 6.12. provide final supporting evidence for the proposed hypothesis. Table 6.5a. is a broad comparison of the frequencies of use of elements across the two main resource types, pooling all sex categories of interaction. It shows a bias of category (ii) elements towards non-feeder (territorial) interactions involving conflicts of interest over priority of access to space. In contrast, category (i) elements are seen most frequently in competition over food where, except in extreme weather conditions, the outcome of any one interaction would probably have less significant fitness consequences than if it were over territorial space. In this situation, a bluffable threat display is most likely to be effective and least likely to result in escalation. Table 6.12. is a similar comparison of the frequencies of use of elements between intraspecific and interspecific contexts. It clearly shows that frequencies of performance are higher intraspecifically than interspecifically for most elements hypothesized to carry information about site attachment, although HB is an exception. This trend is as would be expected on the basis of the reasonable assumption that intraspecific priority of access to an area is a more important requirement for successful territory establishment than priority of access over less direct competitors such as blue and coal tits. Correspondingly, those elements carrying no information other than 'intent to win' or 'threat' are more frequent in interspecific contexts where eventual dominance is almost certain and effective escalation by the opponent is rare. In this situation, the selection pressures acting on bluff signalling are negligible since the physical asymmetry between the interacting birds is so large that outcome is almost certain. It is in the interests of the great tit to signal its intent to displace the blue or coal tit and thereby save the energetic costs and risks of attack, and it is in the interests of the latter to defer in response to the signal.

This 'two-category' hypothesis of the information content of the great tit display repertoire, based on the circumstantial evidence presented above, is tested more formally in the study of captive groups of great tits in Chapter 7.

6.5.2.2. Other remarks

The distribution of attacks has not yet been considered. The only postural displays to elicit it in a recipient at any appreciable frequency are the WO/TF display and OB (Tables 6.9. & 6.10.). This accords with the idea that these elements are more susceptible to bluff than others and are thus most likely to be ignored by the opponent and result in escalation. However, WO/TF and OB are also the most likely elements to lead to attack in the performing individual (Tables 6.6. & 6.7.) which suggests that they may themselves represent a higher level of escalation than category (ii) elements, perhaps being used when neither non- behavioural asymmetries nor category (ii) display has resolved the interaction.

Attacks tend to occur later in the winter than supplants in all-male interactions (Table 6.16.) and are especially characteristic of frequently occurring birds (Table 6.18.). This underlines the high value of 'resource' that is represented by site attachment in male great tits. Between females, attacks also occurred later in the winter than supplants (Table 6.17.), but attacking, as opposed to passivity or the performance of display, is associated with days of high interaction rate at the feeders, when the food itself is presumed to represent a high value resource. The implication is that the food itself often represents the primary 'goal resource' in interactions between females, whereas between males, no interaction, whether at a food source or not, should be assumed *not* to have long-term implications for site attachment and territoriality.

Chapter 6.3. found little evidence of any relationship between the effectiveness of display elements in displacing an opponent from a feeder, and the risk of eliciting attack from that opponent. This result contrasts with those of similar studies of other species (e.g. Enquist *et al* 1985; Popp 1987a,c, 1989). However, these studies are tests of the hypothesis that different displays represent different levels of risk the performer is 'willing to accept' in attempting to gain priority of access to the contested resource. This chapter, however, has led to the contrasting hypothesis that different great tit displays represent the signalling of *qualitatively* different information rather than *quantitatively* different levels of a single type of information. If the results of Chapter 7 support this idea, then the contrast between the conclusions of Chapter 6.3. and those of related studies will seem less surprising since this hypothesis implies that the effectiveness and risk associated with performance of a given display should not be predictable, except by reference to prescribed contexts.

6.5.2.3. Postural Display using the Plumage

Although data collected on the use of CF, NR, CR and FF in agonistic contexts have not been collated and analysed quantitatively, it is possible to make some informal remarks concerning the circumstances in which they are used and their possible functions.

i) Crest Raising

At the Ormiston feeders, I have seen this posture used by great, blue and coal tits, chaffinches *Fringilla coelebs*, greenfinches *Carduelis chloris*, robins *Erithacus rubecula* and dunnocks *Prunella modularis*. By great tits, it is usually performed independently of all other elements except FF and could be termed "submissive", since it is rarely, if ever, followed by an aggressive act on the part of its performer. Stokes (1962a,b) also listed CR as being much more strongly predictive of 'escape' in interacting tits than of any aggressive future behaviour. CR is also intriguing in that it is the only element which is regularly performed by a bird that is apparently alone at feeder, and is probably the most variable element, changing in extent almost continuously. Morris (1956) discussed the evolution of feather postures from pilomotor responses to the autonomic activity involved in thermoregulation, preparation for flight and the physiological responses associated with conflicting-stimulus situations. He proposed that in many species, generalized thermoregulatory ruffling of the feathers has become restricted to conspicuous areas of the body (e.g. the head) to serve a signal function, the extreme being the fixation of piloerection as a permanent crest, ruff, tuft or plume. Familiar examples of this include the grey heron *Ardea cinerea*, lapwing *Vanellus vanellus*, skylark *Alauda arvensis* and hoopoe *Upupa epops*. If crest raising by tits represents an evolutionary specialization of autonomic feather ruffling that has remained a behaviourally flexible signal rather than becoming morphologically fixed, then its occurrence in apparently non- interactive contexts is intriguing. It is unlikely to be a conspicuous enough signal to operate over long distances, yet appears sufficiently specialized that it could no longer perform its original thermoregulatory function. In view of Morris' (1956) comment that specialization of feather postures as signals has often involved addition of bright markings and colours to the restricted areas of piloerection, it is interesting that in the species with the most conspicuous crest raising, the blue tit, this area corresponds with the area of bright blue crown feathering.

ii) Fluffing

This is also a 'submissive' posture that is usually associated with retreat rather than aggression (Stokes 1962 a,b; Blurton Jones 1968; pers. obs.) and is often associated with crest raising. Generalized fluffing of the body feathers is a primary autonomic response associated with conservation of heat by inactive birds (Morris 1956), so it is not difficult to imagine its evolution as a signal of submissiveness (which may often equate with inactivity). For example, Morris (1954) noted the effect of fluffing by zebra finches *Poephila guttata* in inhibiting attacks from dominant birds, and Hinde (1953) recorded that subordinate chaffinches spent much time in a fluffed, inactive posture. Similarly, in social situations, a fluffed posture is far more commonly adopted by female great tits than by males (pers. obs.).

iii) Crest Flattening and Nape Raising

These two postures are almost always seen simultaneously. They were probably commonly associated with other 'aggressive' postural elements of great tits in this study, but this was only really appreciated in the aviary studies where extremely close views of interacting birds could be obtained. In this context, CF and NR were especially associated with HD and HB, as also recorded by Blurton Jones (1968). Stokes (1962a) also recorded CF and NR as being more predictive of 'attack' or 'staying' than with 'escape' in blue tits. Morris (1956) considered the primary function of feather sleeking and flattening as an autonomic pilomotor response readying a bird for flight, and ruffling (as opposed to fluffing) as a disordering of the plumage to allow heat loss during vigorous activity. The potential for the evolutionary ritualization of of these pilomotor patterns as signals of aggressive action is therefore clear. Again the suggestion is that specialization to signal function has been associated with restriction of piloerection to areas of the body at which the attention of the opponent is likely to be directed, namely the head.

The implications of the evolution of agonistic signals from autonomic motor responses for the evolution of agonistic communication in general, are discussed further in Chapter 8.

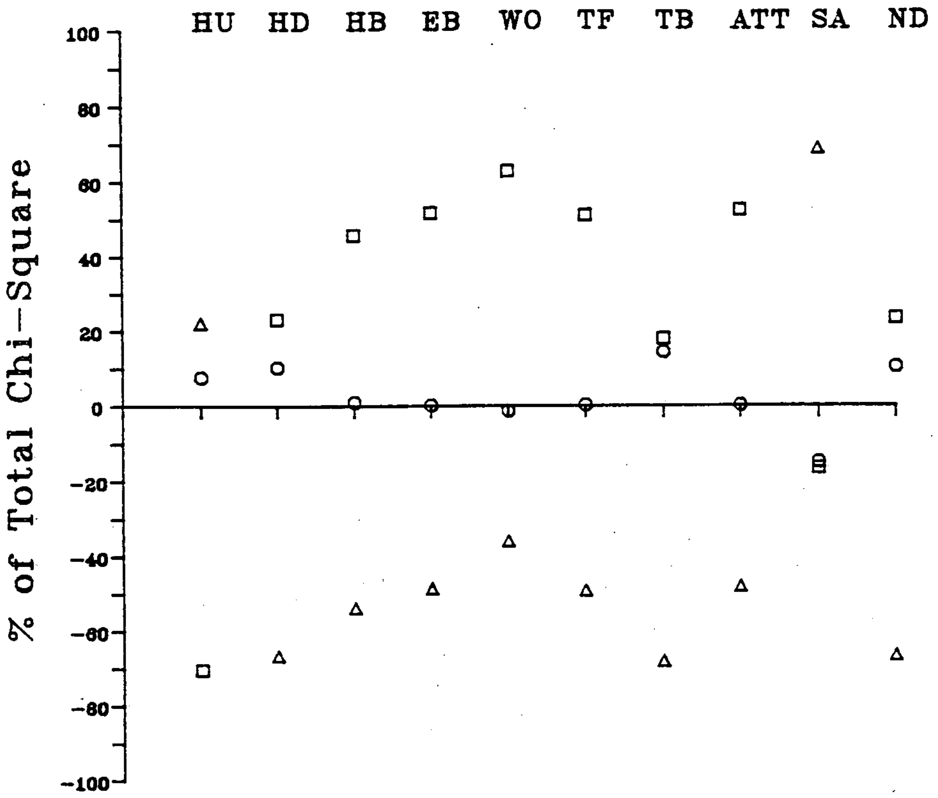


Fig. 6.1. Relationship between the frequency of performance of behaviour elements and the sex of birds interacting at feeders, based on data in Table 6.3. Y-axis = % of total X^2 value in Table 6.3. contributed by each sex category. Values above zero indicate a frequency above random expectation. Values below zero indicate a frequency below random expectation.
○ = male > male; △ = male > female; □ = female > female.
See text for further explanation.

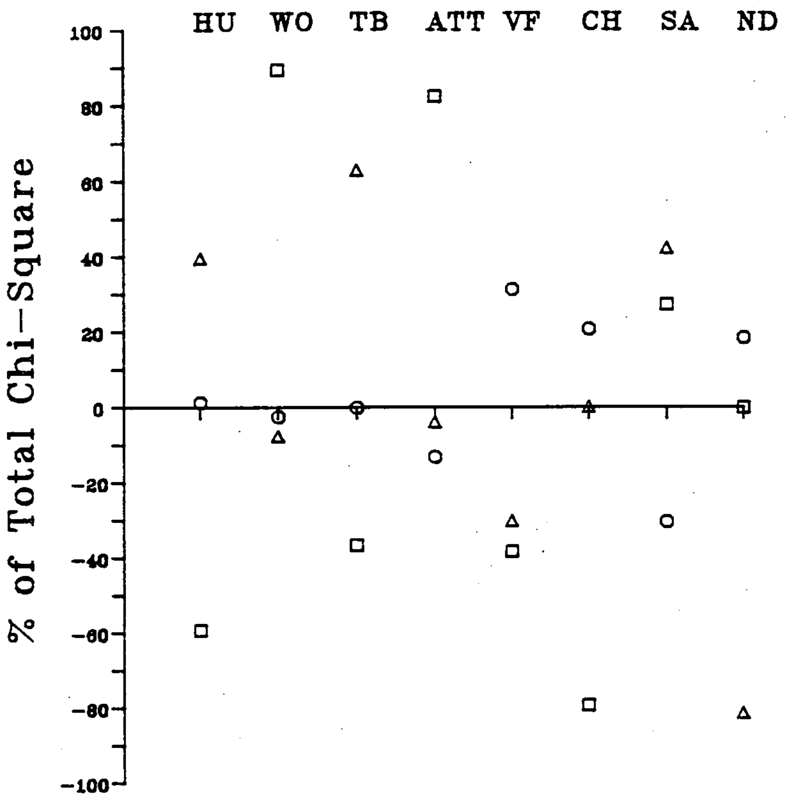


Fig. 6.2. Relationship between the frequency of performance of behaviour elements and the sex of birds interacting away from a food source, based on data in Table 6.4. Interpretation as for Fig. 6.1.

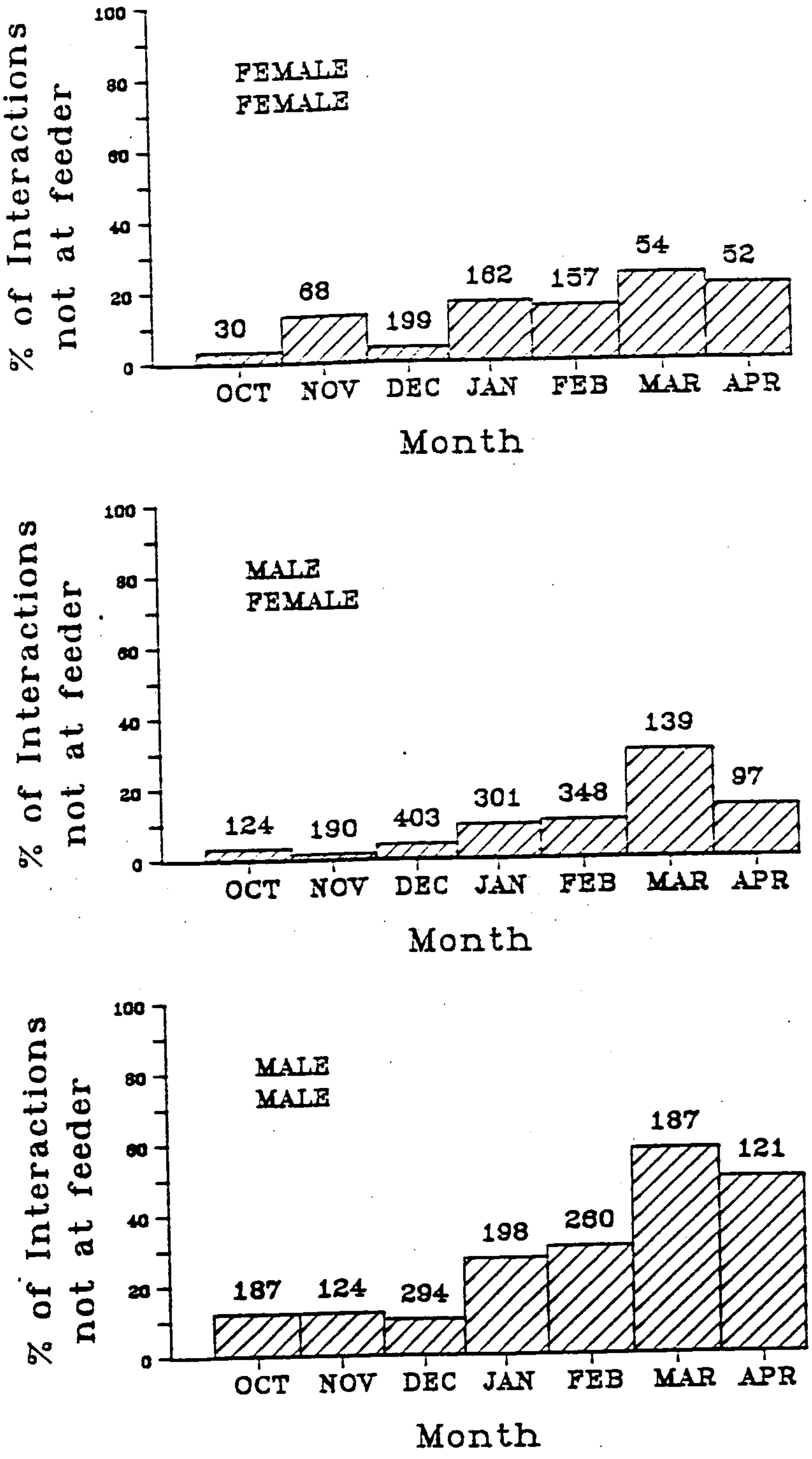


Fig. 6.3a. Seasonal changes in the proportion of all interactions that were recorded away from a food source, for all three sex categories. Data from all three winters pooled. Sample sizes for each month are appended.

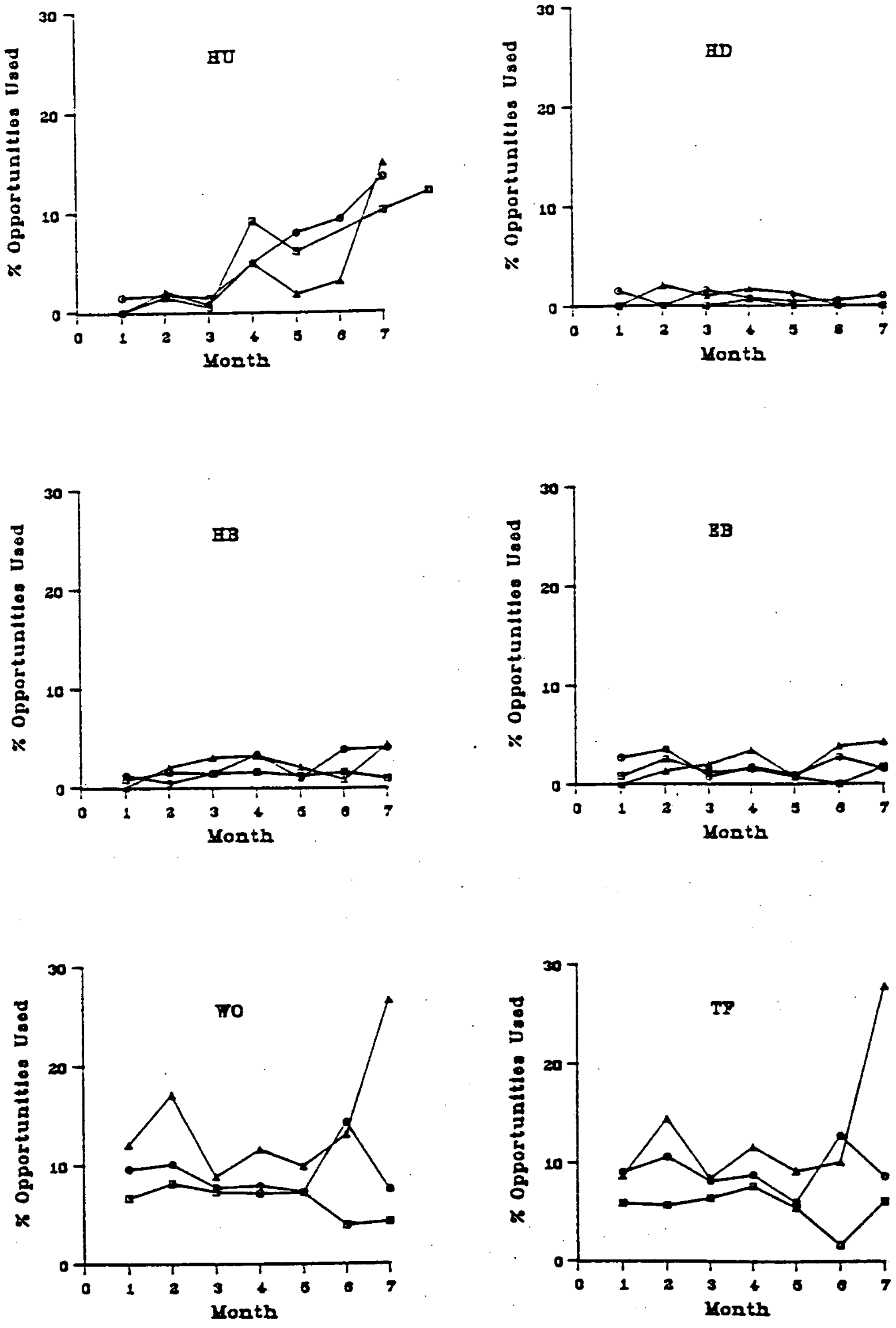
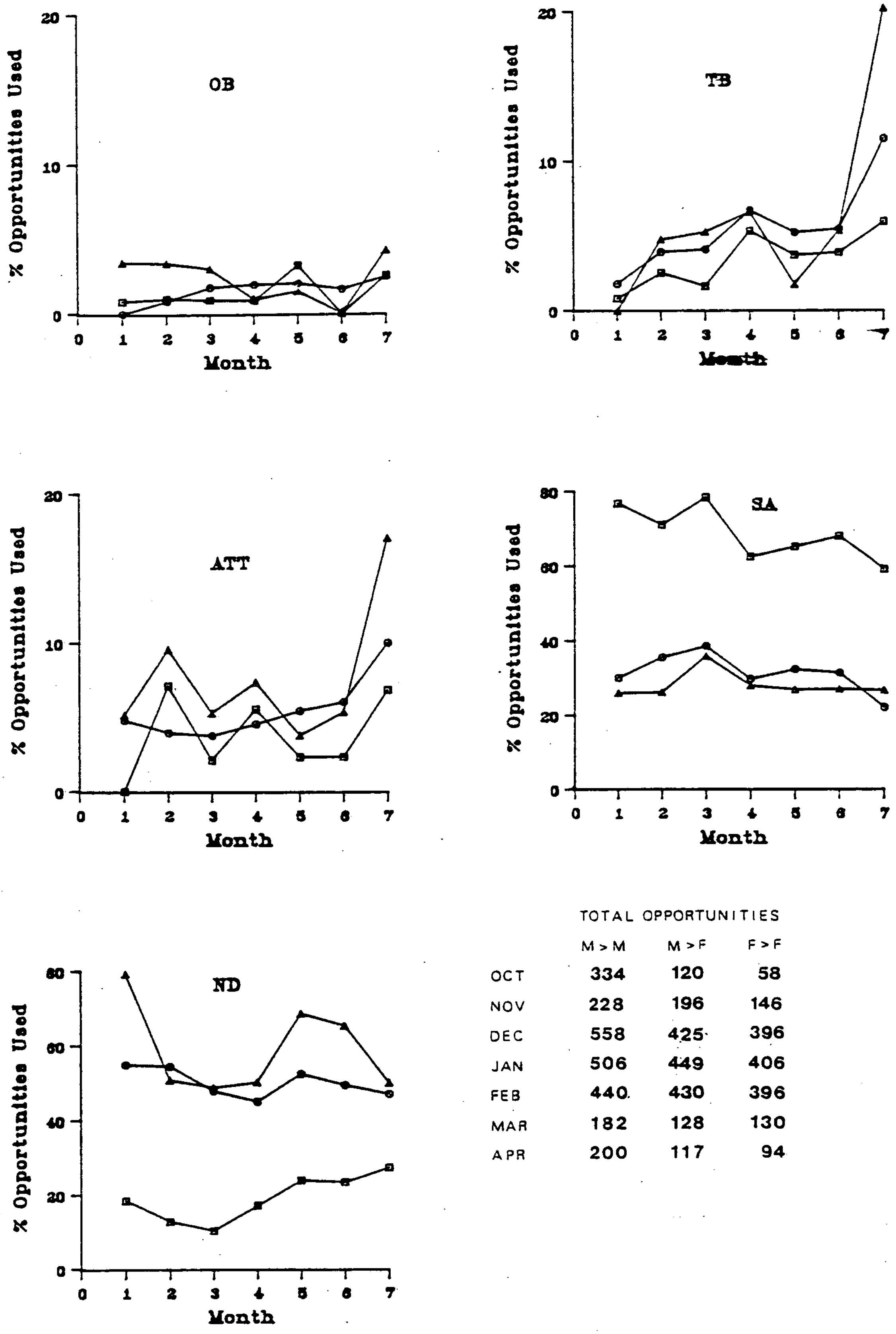


Fig. 6.3b. Seasonal changes in the frequency of use of behaviour elements (OCT = 1 ... APR = 7) expressed as the proportion of opportunities for performance on which an element was seen.
○ = male > male; □ = male > female; △ = female > female.
See text for further explanation.



TOTAL OPPORTUNITIES

	M > M	M > F	F > F
OCT	334	120	58
NOV	228	196	146
DEC	558	425	396
JAN	506	449	406
FEB	440	430	396
MAR	182	128	130
APR	200	117	94

Fig 6.3b. continued.

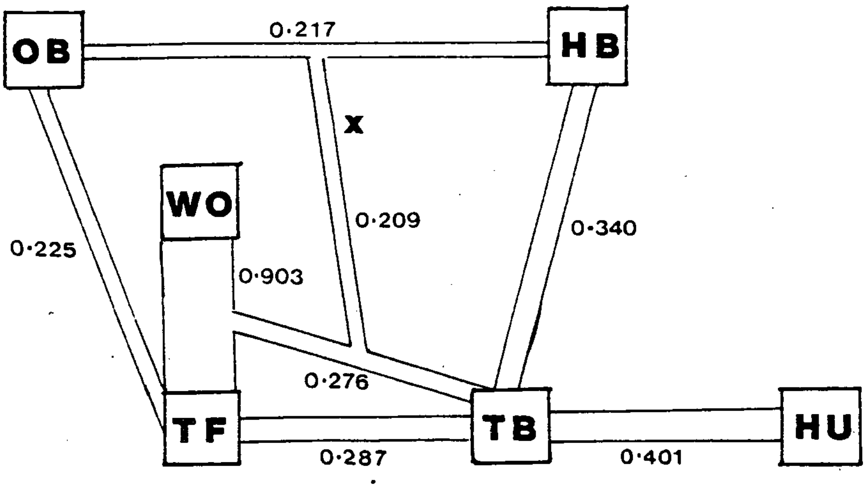


Fig. 6.4. B2 cluster analysis of the intra-individual similarity matrix in Table 6.6. Minimum level of association for inclusion = 0.200.

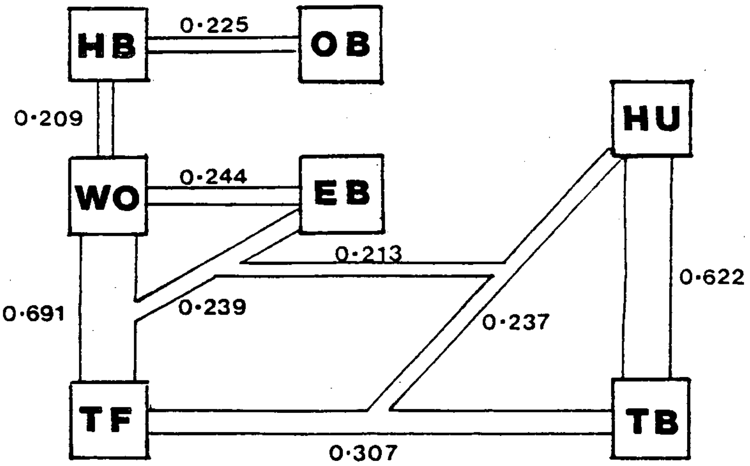


Fig. 6.5. B2 cluster analysis of the intra-individual similarity matrix in Table 6.7. Minimum level of association for inclusion = 0.200.

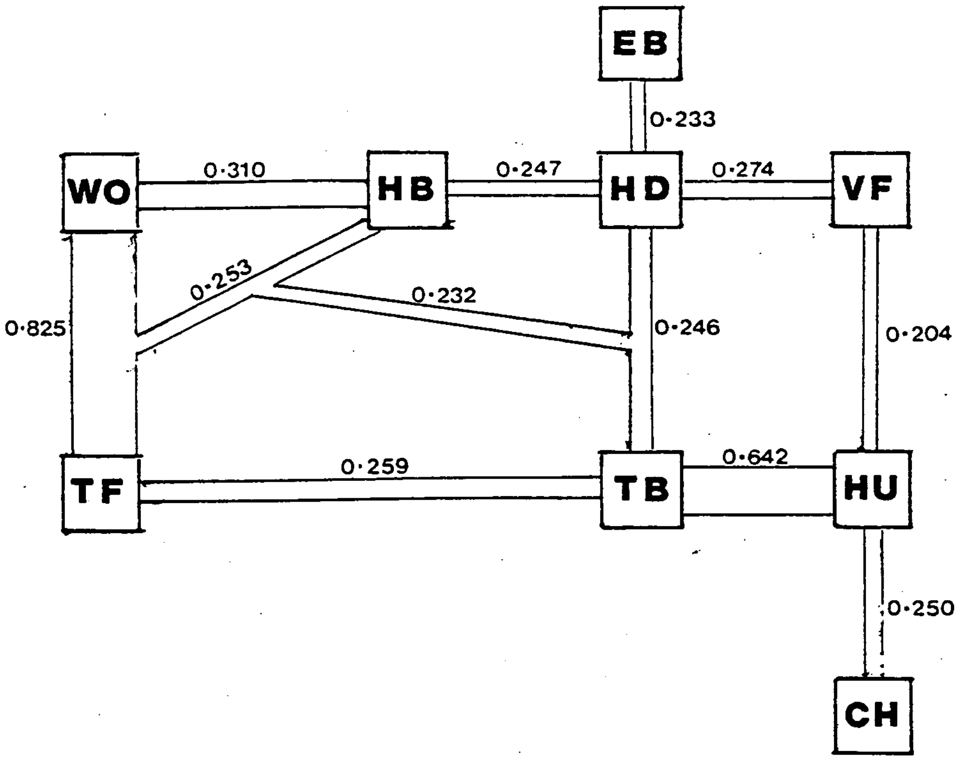


Fig. 6.6. B2 cluster analysis of the intra-individual similarity matrix in Table 6.8. Minimum level of association for inclusion = 0.200.

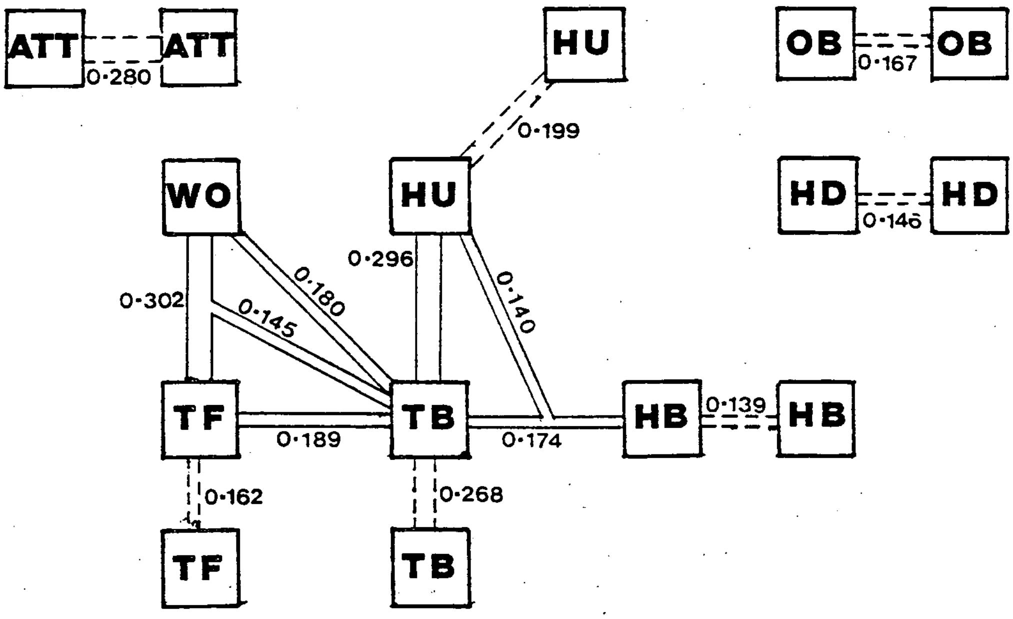


Fig. 6.7. B2 cluster analysis of the inter-individual similarity matrix in Table 6.9. Minimum level of association for inclusion = 0.140. Dashed bars depict inter-individual associations between occurrences of the same element.

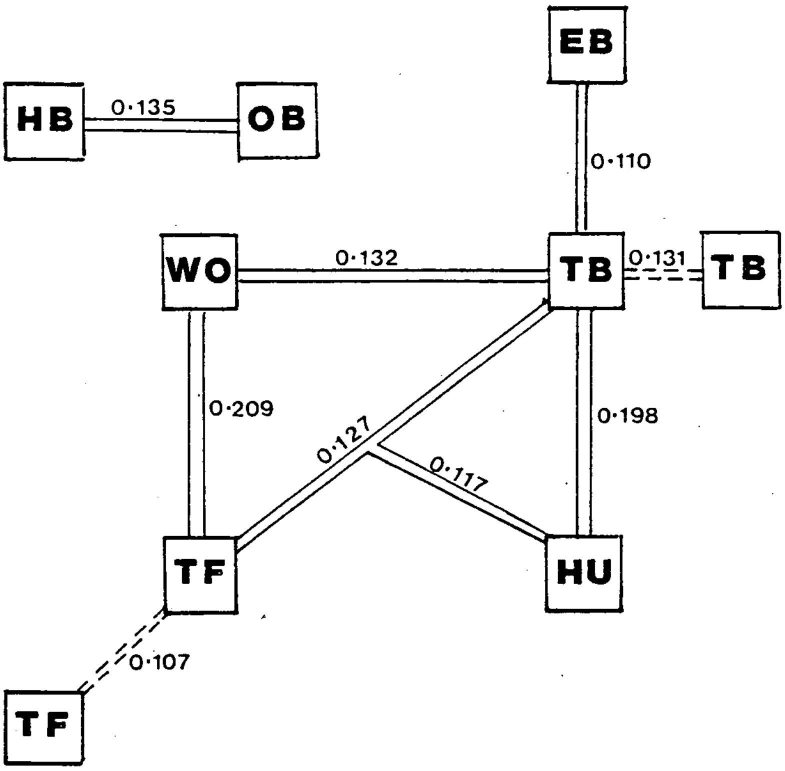


Fig. 6.8. B2 cluster analysis of the inter-individual similarity matrix in Table 6.10. Minimum level of association for inclusion = 0.100. Dashed bars depict inter-individual associations between occurrences of the same element.

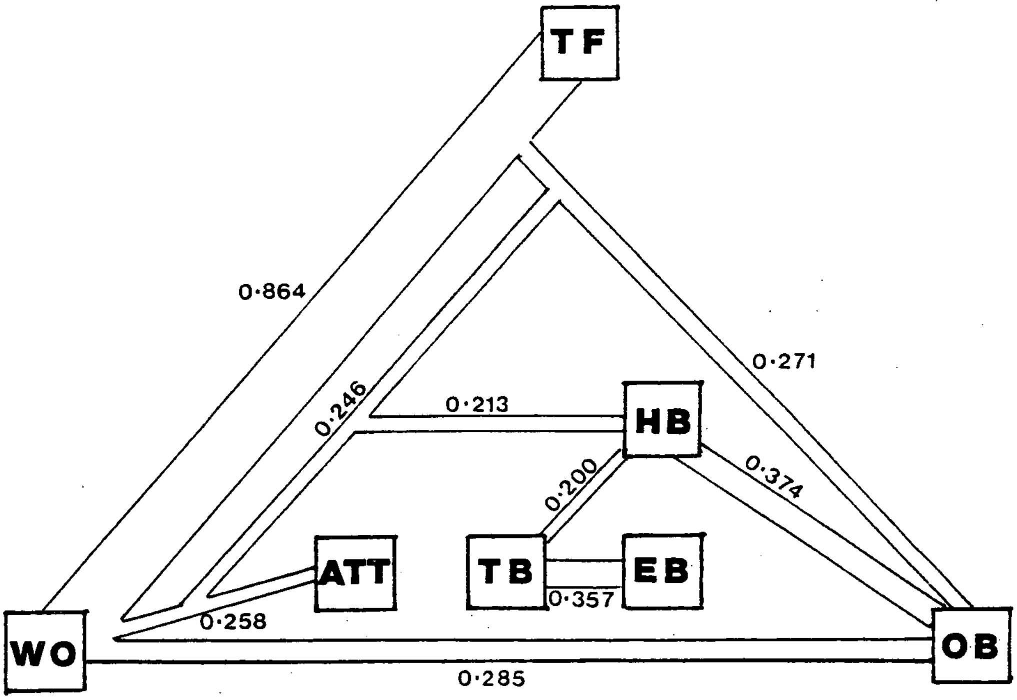


Fig. 6.9. B2 cluster analysis of the intra-individual similarity matrix in Table 6.11. Minimum level of association for inclusion = 0.200.

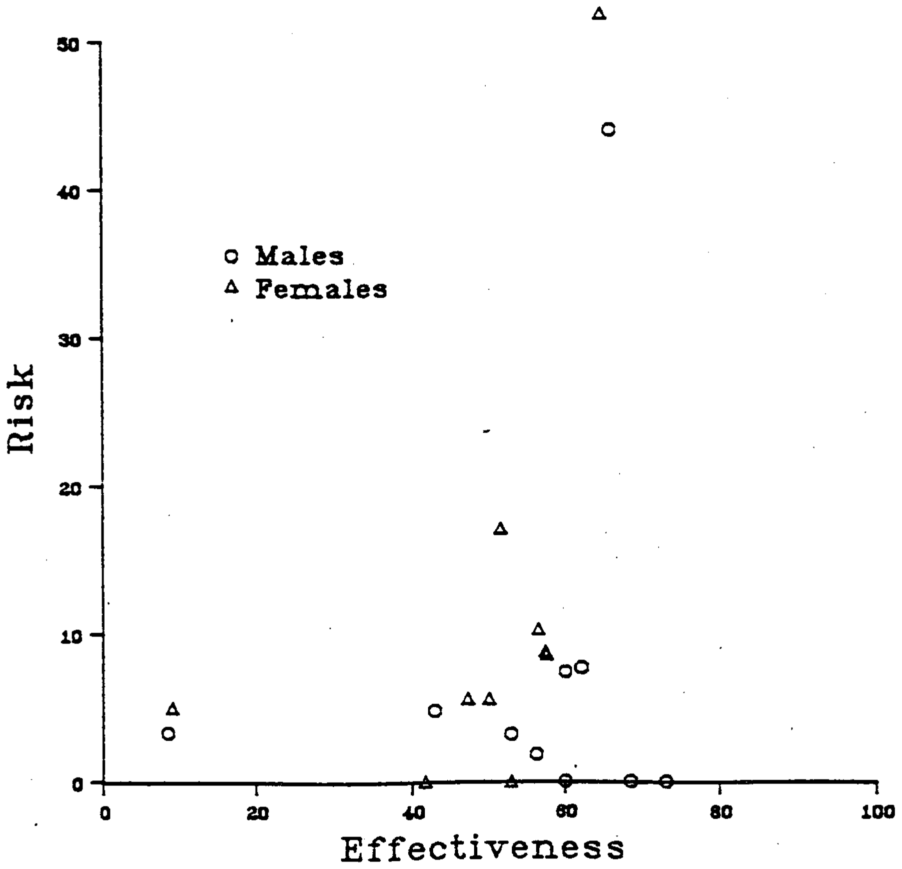


Fig. 6.10. Relationship between effectiveness and risk of behaviour elements in intrasexual interactions at a food source, based on data in Table 6.13. Effectiveness = percentage of performances which lead to priority of access to the food source. Risk = percentage of performances which result in the performer being attacked by its opponent. ○ male > male, △ female > female.

Blurton Jones (1968)	Hinde (1952)	This study
Head-up	Head-up	**Head Up (HU)**
Head-down	-	**Head Down (HD)**
Horizontal	Head-forward	**Horizontal Body (HB)**
Wings-out	Wings-raised	**Wings Out (WO)**
Tail-fanning	-	**Tail Fanned (TF)**
Crest-flattening	-	**Crest Flattening (CF)**
Crest-raising	-	**Crest Raising (CR)**
Attack	Combat	**Attack (ATT)**
Turns	Head Swaying	**Turning Body (TB)**
Fluffing	-	**Fluffing**
Supplanting	Supplanting attack	**Supplanting (SA)**
Body Erect	-	**Erect Body (EB)**
Bill Open	Beak Open	**Open Bill (OB)**
-	Upright Flight	**Vertical Flight (VF)**
-	Chases	**Chasing (CH)**

TABLE 6.1. A comparison of the terms used by Blurton Jones (1968), Hinde (1952) and this study, to describe the agonistic display elements of the great tit.

Reference	Species studied	Elements recorded
Andrew (1957)	*Emberiza* buntings	HU, HB, WO, OB.
Balph (1977)	Dark-eyed junco *Junco hyemalis*	HU, HB, EB, TF, TB, FF.
Coutlee (1967) Popp (1987a)	American Goldfinch *Carduelis tristis*	HU, HB, WO, OB, TB, VF, FF
Dilger (1956)	*Catharus* and *Hylocichla* thrushes	HU, HB, OB, CR, FF
Dilger (1960)	Redpoll *Carduelis flammea*	HU, HB, WO, OB, FF
Dunham (1966)	Rose-breasted grosbeak *Pheucticus ludovicianus*	HB, TF, OB, CR
Ellis (1966)	Starling *Sturnus vulgaris*	HB, EB, WO, TB
Marler (1956)	Chaffinch *Fringilla coelebs*	HU, HB, WO, TF, OB, TB, CR, FF
Martin (1970)	Varied Thrush *Ixoreus naevius*	HB, WO, TF
Samson (1977)	Cassin's Finch *Carpodacus cassini*	HB, WO, TF, OB
Thompson (1960)	House Finch *Carpodacus mexicanus*	HU, HB, WO, TF, OB
Tordoff (1954)	Crossbill *Loxia curvirostra*	HB, OB

TABLE 6.2. A selection of studies showing the range of other passerine species in which display elements similar to those of great tits occur.

Element	M > M	M > F	F > M	F > F	TOTAL	X^2	p
HU	121	99	22	51	293	10.29	<0.01
HD	23	3	1	18	45	12.71	<0.001
HB	49	25	5	41	120	6.34	<0.05
EB	42	23	5	36	106	4.91	<0.05
WO	211	128	26	195	560	26.05	<0.001
TF	209	111	22	181	523	27.67	<0.001
OB	39	28	13	33	113	1.64	NS
TB	128	65	22	88	303	8.99	<0.01
ATT	124	69	23	106	322	13.71	<0.001
SA	789	1280	39	474	2582	425.41	<0.001
ND	1217	333	1791	921	4262	379.80	<0.001
Total Interactions	1224	- 1865 -		813	3902		
Total Opportunities for Display	2448	1865	1865	1626	7804		
Excluding F > M	2448	1865	-	1626	5939		

TABLE 6.3. Distribution of occurrences of behaviour elements at feeders, according to the sex of the interacting birds. Data from observation and videotape over all sites and years pooled (see 6.2.). In data derived from videotape, individual bouts within an interaction are not distinguished. The deviation of each element's distribution from random expectation is examined for the M>M, M>F and F>F categories, using a chi-square test.

Element	M > M	M > F	F > M	F > F	TOTAL	X^2	p
HU	163	54	9	7	233	44.54	<0.001
HD	26	2	0	4	32	2.47	NS
HB	27	6	1	7	41	0.06	NS
EB	7	2	0	2	11	0.20	NS
WO	25	4	2	12	43	4.39	<0.05
TF	34	8	2	10	54	0.29	NS
OB	0	0	0	0	0	-	-
TB	94	31	8	14	147	11.86	<0.001
VF	41	0	0	0	41	18.60	<0.001
ATT	16	3	0	10	29	5.81	<0.05
CH	232	40	1	22	295	21.18	<0.001
SA*	70	40	2	44	156	39.89	<0.001
ND*	209	5	90	43	347	31.91	<0.001
Total Interactions	366	- 146 -		93	605		
Total Opportunities for Display	732	146	146	186	1210		
Excluding F>M	732	146	-	186	1064		

TABLE 6.4. Distribution of occurrences of behaviour elements in 'non-feeder' interactions, according to the sex of the interacting birds. Data from all sites and years pooled (see 6.2.). Asterisks indicate that the element was only scored in two of the three years. The deviation of each element's distribution from random expectation across the M>M, M>F and F>F categories is examined using a chi-square test.

	M>M	M>F	F>M	F>F	X^2 tests
HU	4.9/22.3	5.3/37.0	1.2/6.2	3.1/3.8	+ + + 0
HD	0.9/3.6	0.2/1.4	0.1/0.0	1.1/2.2	+ + 0 0
HB	2.0/3.7	1.3/4.1	0.3/0.7	2.5/3.8	+ + 0 0
EB	1.7/1.0	1.2/1.4	0.3/0	2.2/1.1	0 0 0 0
WO	8.6/3.4	6.9/2.7	1.4/1.4	12.0/6.5	- 0 0 -
TF	8.5/4.6	6.0/5.5	1.2/1.4	11.1/5.4	- 0 0 -
OB	1.6/0	1.5/0	0.7/0	2.0/0	- 0 0 -
TB	5.2/12.8	3.5/21.2	1.2/5.5	5.4/7.5	+ + + 0
ATT	5.1/2.2	3.5/2.1	1.2/0	6.5/5.4	- 0 0 0
VF	0/5.6	0/0	0/0	0/0	+ 0 0 0
SA	32.2/14.3	68.6/33.6	2.1/1.7	19.2/26.2	- - 0 0

TABLE 6.5a. Comparison of frequencies of use of agonistic behaviour elements in feeder (left of slash) and 'non-feeder' (right of slash) contexts, across all four sex categories of actor>recipient. Results based on data in Tables 6.3. and 6.4. Frequency of use expressed as % of total opportunities, on which an element was seen. Differences between contexts are analysed using chi-square tests with results condensed into the right-hand column. '+' = significantly more, '-' = significantly less frequent in non-feeder than in feeder interactions. '0' = no significant difference.

	Male - Male	Male - Female	Female - Female	Total
1986/87				
Observed	364	678	297	1339
Expected	335.6	669.5	333.9	
X^2	2.40	0.11	4.07	6.58^*
% of total X^2	36.5(+)	1.6(+)	61.9(-)	
1987/88				
Observed	178	314	147	639
Expected	150.4	319.5	169.1	
X^2	5.06	0.09	2.89	8.04^*
% of total X^2	62.9(+)	1.1(-)	35.9(-)	
1988/89				
Observed	682	873	369	1924
Expected	472.8	962	489.2	
X^2	92.56	8.23	29.53	130.32^{***}
% of total X^2	71.0(+)	6.3(-)	22.7(-)	

TABLE 6.5b. Distribution of interactions across the three sex categories of interactant, at feeders in each year. Chi-square tests show the significance of deviation from random expectation (* = $p<0.05$, *** = $p<0.001$). Expected values calculated from the total number of bird-minutes of observation/videotaping time for colour-ringed birds of each sex. The last row for each year gives the percentage contribution of each category to the total X^2 value, and the direction of the deviation from random expectation. See text for further explanation.

	PR - PR	PR - NC	NC - NC	Total
MALES				
Observed	21	416	833	1270
Expected	281.7	635	353.3	
X^2	241.3	75.5	651.3	968.1^{***}
% of total X^2	24.9(-)	7.8(-)	67.3(+)	
FEMALES				
Observed	17	297	527	841
Expected	160.9	420.5	259.6	
X^2	128.7	36.3	275.42	440.4^{***}
% of total X^2	29.2(-)	8.2(-)	62.5(+)	

TABLE 6.5c. Distribution of interactions across the three categories of prior residence, for each sex. All three years' data pooled. Interpretation as for Table 6.5b. PR = prior resident, i.e. bird present in a previous winter. NC = newcomer, i.e. first-year bird, or adult colour-ringed during the current winter. All prior residents must be adults and the great majority of newcomers are first-year birds. See text for further explanation.

RAW DATA

	HU	HD	HB	EB	WO	TF	OB	TB	ATT	Total
HU	-	0.0	4.3	8.5	24.8	28.4	2.1	46.1	0.7	141
HD	0.0	-	32.3	3.2	80.6	80.6	9.7	67.7	0.0	31
HB	7.3	12.2	-	0.0	48.8	50.0	22.0	54.9	1.2	82
EB	16.9	1.4	0.0	-	60.6	54.9	7.0	38.0	0.0	71
WO	7.6	5.4	8.7	9.3	-	87.2	12.3	19.3	8.7	462
TF	9.3	5.8	9.5	9.0	93.5	-	13.5	20.4	9.0	431
OB	3.6	3.6	21.4	5.9	67.9	69.0	-	19.0	4.8	84
TB	35.5	11.5	24.6	14.8	48.6	48.1	8.7	-	1.1	183
ATT	0.3	0.0	0.3	0.0	13.0	12.7	1.3	0.7	-	307

SIMILARITY MATRIX

	HU	HD	HB	EB	WO	TF	OB	TB
HD	0.0							
HB	5.4	17.7						
EB	11.3	2.0	0.0					
WO	11.6	10.1	14.7	16.1				
TF	14.0	10.8	16.0	15.5	90.3			
OB	2.7	5.2	21.7	6.5	20.9	22.5		
TB	40.1	19.6	34.0	9.7	27.6	28.7	12.0	
ATT	0.4	0.0	0.5	0.0	10.4	10.6	2.0	0.8

TABLE 6.6. Intra-individual associations between behavioural elements from observation of feeder interactions. Upper table gives percentage of total number of performances of each row element (right hand column) that occur with each column element. Lower table derives a similarity matrix from these data, using the Half-Weight method to calculate an association index for each pair of elements. See text for further explanation.

RAW DATA

	HU	HD	HB	EB	WO	TF	OB	TB	ATT	Total
HU	-	3.5	0.5	6.5	5.5	19.1	1.0	53.8	0.0	199
HD	35.0	-	15.0	10.0	40.0	30.0	5.0	30.0	0.0	20
HB	2.2	6.7	-	4.4	40.0	26.7	22.2	3.9	0.0	45
EB	35.1	5.4	5.4	-	54.1	51.4	2.7	51.4	0.0	37
WO	8.7	6.3	14.2	15.7	-	67.7	7.1	22.8	1.6	127
TF	31.1	4.9	9.8	15.6	70.5	-	3.3	33.6	1.6	122
OB	4.5	2.3	22.7	2.3	20.5	9.1	-	9.1	0.0	44
TB	73.8	4.1	2.8	13.1	20.0	28.3	2.8	-	0.0	145
ATT	0.0	0.0	0.0	0.0	6.9	6.9	0.0	0.0	-	29

SIMILARITY MATRIX

	HU	HD	HB	EB	WO	TF	OB	TB
HD	6.4							
HB	9.0	9.2						
EB	11.0	7.0	4.9					
WO	6.7	10.9	20.9	24.4				
TF	23.7	8.5	14.4	23.9	69.1			
OB	1.6	3.1	22.5	2.5	10.5	4.8		
TB	62.2	7.3	4.2	20.9	21.3	30.7	4.2	
ATT	0.0	0.0	0.0	0.0	2.6	2.6	0.0	0.0

TABLE 6.7. Intra-individual associations between behavioural elements in feeder interactions recorded on videotape. Interpretation as for Table 6.6.

RAW DATA

	HU	HD	HB	EB	WO	TF	TB	ATT	VF	CH	Total
HU	-	9.0	4.7	4.3	6.9	9.9	52.4	1.7	12.0	28.3	233
HD	65.6	-	28.1	15.6	18.8	12.5	68.8	3.1	31.3	12.5	32
HB	26.8	22.0	-	0.0	31.7	29.3	51.2	2.4	4.9	17.1	41
EB	90.9	45.5	0.0	-	45.5	54.5	90.9	0.0	36.4	63.6	11
WO	37.2	14.0	30.2	11.6	-	93.0	51.1	4.7	0.0	14.0	43
TF	42.6	7.4	22.2	11.1	74.1	-	48.1	1.9	0.0	16.7	54
TB	83.0	15.0	14.3	6.8	15.0	17.7	-	0.7	6.8	19.7	147
ATT	13.8	3.4	3.4	0.0	6.9	3.4	3.4	-	0.0	34.5	29
VF	68.3	24.4	4.9	9.8	0.0	0.0	24.4	0.0	-	73.2	41
CH	22.4	4.7	2.4	2.4	2.0	3.1	9.8	10.2	3.4	-	

SIMILARITY MATRIX

	HU	HD	HB	EB	WO	TF	TB	ATT	VF
HD	15.8								
HB	8.0	24.7							
EB	8.2	23.3	0.0						
WO	11.6	16.0	31.0	18.5					
TF	16.0	9.3	25.3	18.5	82.5				
TB	64.2	24.6	22.3	12.7	23.2	25.9			
ATT	3.4	3.3	2.9	0.0	5.6	2.4	1.1		
VF	20.4	27.4	4.9	15.4	0.0	0.0	10.6	0.0	
CH	25.0	8.6	4.2	4.6	3.6	5.2	13.1	6.2	17.9

TABLE 6.8. Intra-individual associations between behavioural elements observed in territorial interactions. Interpretation as for Table 6.6.

RAW DATA

	HU	HD	HB	EB	WO	TF	OB	TB	ATT	Total
HU	19.9	0.0	4.3	4.3	14.2	15.6	0.0	34.0	0.7	141
HD	0.0	16.1	19.4	0.0	51.6	58.1	9.7	48.4	0.0	31
HB	7.3	7.3	14.6	1.2	24.4	28.0	7.3	28.0	0.0	82
EB	8.5	0.0	1.4	11.3	21.1	21.1	4.2	8.5	0.0	71
WO	4.3	3.5	4.3	3.2	14.5	29.2	5.0	12.6	6.1	462
TF	5.1	4.2	5.3	3.5	31.3	16.2	5.3	13.5	5.8	431
OB	0.0	3.6	7.1	3.6	27.4	27.4	16.7	13.1	6.0	84
TB	26.2	8.2	12.6	3.3	31.7	31.7	6.0	26.8	1.6	183
ATT	0.3	0.0	0.0	0.0	9.1	8.1	1.6	1.0	28.0	307

SIMILARITY MATRIX

	HU	HD	HB	EB	WO	TF	OB	TB	ATT
HU	19.9								
HD	0.0	16.1							
HB	5.4	10.6	14.6						
EB	5.7	0.0	1.3	11.3					
WO	6.6	6.5	7.4	5.6	14.5				
TF	7.7	7.8	9.0	6.0	30.2	16.2			
OB	0.0	5.2	7.2	3.9	8.4	8.9	16.7		
TB	29.6	14.0	17.4	4.7	18.0	18.9	8.2	26.8	
ATT	0.4	0.0	0.0	0.0	7.3	6.8	2.6	1.2	28.0

TABLE 6.9. Inter-individual associations between behaviour elements in feeder interactions recorded by observation. Interpretation as for Table 6.6.

RAW DATA

	HU	HD	HB	EB	WO	TF	OB	TB	ATT	Total
HU	9.0	2.5	2.5	3.5	9.5	7.0	3.0	17.1	0.0	199
HD	25.0	0.0	5.0	5.0	15.0	10.0	0.0	10.0	0.0	20
HB	11.1	2.2	6.7	2.2	17.8	11.1	13.3	8.9	0.0	45
EB	18.9	2.7	2.7	5.4	16.2	13.5	5.4	27.0	0.0	37
WO	15.0	2.4	6.3	6.3	9.4	20.5	1.6	14.2	3.1	127
TF	11.5	1.6	4.1	4.1	21.3	10.7	2.5	13.9	3.3	122
OB	13.6	0.0	13.6	4.5	4.5	6.8	4.5	6.8	0.0	44
TB	23.4	1.4	2.8	6.9	12.4	11.7	2.1	13.1	0.0	145
ATT	0.0	0.0	0.0	0.0	13.8	13.8	0.0	0.0	3.4	29

SIMILARITY MATRIX

	HU	HD	HB	EB	WO	TF	OB	TB	ATT
HU	9.0								
HD	4.6	0.0							
HB	4.1	3.1	6.7						
EB	5.9	3.5	2.4	5.4					
WO	11.7	4.1	9.3	7.3	9.4				
TF	8.7	2.8	6.0	6.3	20.9	10.7			
OB	4.9	0.0	13.5	4.9	2.3	2.4	4.9		
TB	19.8	2.4	4.2	11.0	13.2	12.7	3.2	13.1	
ATT	0.0	0.0	0.0	0.0	5.1	5.3	0.0	0.0	3.4

TABLE 6.10. Inter-individual associations between behaviour elements in feeder interactions recorded on videotape. Interpretation as for Table 6.6.

RAW DATA

	HU	HB	EB	WO	TF	OB	TB	ATT	Total
HU	-	0.0	20.0	26.7	13.3	6.7	20.0	13.3	15
HB	0.0	-	1.0	56.2	49.0	47.9	13.9	0.5	194
EB	4.7	3.1	-	35.9	32.8	18.8	39.1	1.6	64
WO	0.5	12.6	2.7	-	78.2	19.2	3.5	24.7	863
TF	0.3	13.6	3.0	96.4	-	19.4	3.7	26.1	700
OB	0.3	30.7	4.0	54.8	44.9	-	5.3	3.0	303
TB	3.9	35.5	32.9	39.5	34.2	21.1	-	2.6	76
ATT	0.3	0.1	0.1	27.0	23.2	1.1	0.3	-	789

SIMILARITY MATRIX

	HU	HB	EB	WO	TF	OB	TB
HB	0.0						
EB	7.6	1.6					
WO	0.9	20.6	5.0				
TF	0.6	21.3	5.5	86.4			
OB	0.6	37.4	6.5	28.5	27.1		
TB	6.6	20.0	35.7	6.4	6.7	8.4	
ATT	0.5	0.2	0.2	25.8	24.6	1.6	0.5

TABLE 6.11. Intra-individual associations between behavioural elements of great tits. Data from observation of interspecific interactions with blue and coal tits, at feeders. Interpretation as for Table 6.6.

Element	Intraspecific n = 7804 opportunities	Interspecific n = 6178 opportunities	X^2
HU	293(3.75)	10(0.16)	209.9***
HD	45(0.58)	0(0.00)	35.7***
HB	120(1.54)	135(2.19)	8.1**
EB	106(1.36)	54(0.87)	7.2**
WO	560(7.18)	669(10.83)	57.4***
TF	523(6.70)	513(8.30)	12.9***
OB	113(1.45)	218(3.53)	64:6***
TB	303(3.88)	41(0.66)	149.2***
ATT	322(4.13)	667(10.80)	233.4***

TABLE 6.12. Comparison of frequencies of use of agonistic behaviour elements in intraspecific and interspecific contexts at feeders. Interspecific interactions are those with blue and coal tits. Results are based on data in Tables 6.3. and 6.11., but the interspecific data set is restricted to the pooled 1986/87 and 1987/88 data sets because only interspecific interactions involving display were recorded in 1988/89. Frequency of use is expressed as the number of occasions and percentage of total opportunities (in parentheses) on which an element was seen. For each element, the difference between the two contexts is analysed using a chi-square test. * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$.

Element	Effectiveness		Risk	
	Males	Females	Males	Females
HU	64/114(56.1%)	20/48(41.7%)	2/114(1.8%)	0
HD	13/19(68.4%)	9/18(50.0%)	0	1/18(5.6%)
HB	18/42(42.9%)	22/39(56.4%)	2/42(4.8%)	4/39(10.3%)
EB	27/37(73.0%)	19/36(52.8%)	0	0
WO	113/182(62.1%)	107/186(57.5%)	14/182(7.7%)	16/186(8.6%)
TF	114/190(60.0%)	98/171(57.3%)	14/190(7.4%)	15/171(8.8%)
OB	21/35(60.0%)	18/35(51.4%)	0	6/35(17.1%)
TB	66/125(52.8%)	42/89(47.2%)	4/125(3.2%)	5/89(5.6%)
ATT	69/105(65.7%)	60/93(64.5%)	46/105(43.8%)	48/93(51.6%)
ND	90/1089(8.3%)	68/767(8.9%)	36/1089(3.3%)	38/767(5.0%)

TABLE 6.13. Effectiveness and risk of agonistic behaviour elements in intrasexual interactions at feeders. Data from all three years pooled. Effectiveness = proportion of occurrences which led to priority of access to contested food. Risk = proportion of occurrences which led to attack by opponent. See text for further explanation.

Element	NC>NC	PR>PR	PR>NC	NC>PR	Total	X^2	p
HU/VF	147	4	44	53	248	7.81	<0.05
HD	14	0	14	12	40	20.34	<0.001
HB	29	0	16	12	57	8.59	<0.05
EB	32	0	4	1	37	6.56	<0.05
WO	111	3	30	21	165	1.58	NS
TF	117	2	30	19	168	2.74	NS
OB	25	0	1	0	26	(9.58)	<0.01
TB	111	2	32	32	177	1.70	NS
ATT	81	2	15	11	109	3.37	NS
CH	95	3	36	31	165	7.04	<0.05
SA	478	12	120	92	702	4.05	NS
ND	761	19	162	190	1132	2.27	NS
Total Interactions	821	21	386		1228		
Total Opportunities for Display	1642	42	386	386	2456		
Excluding PR>PR	1642	-	386	386	2414		

TABLE 6.14. Distribution of occurrences of behaviour elements, according to the 'prior residence' category of interacting males. Data from all contexts, sites and years pooled. In data derived from videotape, individual bouts within an interaction were not distinguished. The deviation of each element's distribution from expectation is examined for the NC>NC, PR>NC and NC>PR categories using a chi-square test. Categories defined as in Table 6.5c. X^2 values in parentheses are based on expected values of less than 5.

Element	NC>NC	PR>PR	PR>NC	NC>PR	Total	X^2	p
HU/VF	18	2	18	10	48	16.54	<0.001
HD	8	1	4	2	15	(1.11)	NS
HB	19	0	7	10	36	2.75	NS
EB	20	3	2	7	32	2.69	NS
WO	92	6	23	36	157	3.85	NS
TF	86	6	24	34	150	3.23	NS
OB	18	0	4	5	27	(0.17)	NS
TB	39	4	20	19	82	6.42	<0.05
ATT	62	0	9	13	84	3.88	NS
CH	11	0	4	2	17	(0.66)	NS
SA	242	4	67	68	381	0.01	NS
ND	459	12	126	118	715	0.59	NS
Total Interactions	442	13	246		701		
Total Opportunities for Display	884	26	246	246	1402		
Excluding PR>PR	884	-	246	246	1376		

TABLE 6.15. Distribution of occurrences of behaviour elements according to the 'prior residence' category of interacting females. Interpretation as for Table 6.14.

	HU	HD	HB	EB	WO	TF	OB	TB	ATT	ND/ND
Association Index	0	0	0	0	-	-	0	0	0	0
Date	+	0	+	0	0	0	0	+	+	0
Interaction Rate	-	0	0	0	-	-	0	-	0	-
Frequency	0	0	0	0	-	0	0	0	0	-
Frequency Difference	0	0	0	0	0	0	0	0	0	0
Minimum Sample	95	14	38	32	142	144	28	98	88	87
Maximum Sample	105	20	44	37	176	163	35	118	95	105

Minimum Sample for SA = 564
Maximum Sample for SA = 673

TABLE 6.16. Correlates of display use in interactions between male great tits. 0 indicates that occurrences of the element listed column-wise did not occur at a median level of the row variable which differed significantly from that at which supplants were performed. '+' indicates that the element was performed at a significantly higher level of the variable than were supplants, '-' at a significantly lower level. All results based on Kruskal-Wallis tests described in Chapter 6.4.2. and illustrated in Appendix 11. ND/ND refers to 'non-interactive' encounters in which neither bird performed any of the other elements. Sample size ranges over the five tests, for each element and for supplants, are also given. See text for further discussion.

	HU	HD	HB	EB	WO	TF	OB	TB	ATT	ND/ND
Weight	0	-	-	0	0	0	0	0	0	0
Weight Difference	0	0	0	0	0	0	0	0	0	0
VSI	0	0	0	0	0	0	0	0	0	0
VSI Difference	0	0	0	0	0	0	0	0	0	0
Association Index	0	+	0	0	0	0	0	0	0	0
Date	+	0	+	+	+	+	0	+	+	+
Interaction Rate	-	0	0	0	0	0	0	0	0	-
Frequency	0	0	0	0	0	0	0	0	0	0
Frequency Difference	0	0	0	0	0	0	0	0	0	0

	HU	HD	HB	EB	WO	TF	OB	TB	ATT	ND/ND
Minimum Sample	3	7	12	9	56	51	17	22	50	15
Maximum Sample	48	18	39	36	178	163	35	89	92	105

Minimum Sample for SA = 193
Maximum Sample for SA = 359

TABLE 6.17. Correlates of display use in interactions between female great tits. 0 indicates that occurrences of the element listed column-wise did not occur at a median level of the row variable which differed significantly from that at which supplants were performed. '+' indicates that the element was performed at a significantly higher level of the variable than were supplants, '-' at a significantly lower level. All results based on Kruskal-Wallis tests described in Chapter 6.4.2. and illustrated in Appendix 11. ND/ND refers to 'non-interactive' encounters in which neither bird performed any of the other elements. Sample size ranges over the nine tests, for each element and for supplants, are also given. See text for further discussion.

	HU	HD	HB	EB	WO	TF	OB	TB	ATT
Association Index	+	0	+	(-)	(-)	(-)	0	0	0
Date	++	0	0	--	--	--	0	(+)	+
Interaction Rate	--	0	0	0	0	0	0	0	0
Frequency	+	0	0	0	0	+	0	++	++
Frequency Difference	+	0	0	0	0	0	0	+	+
Minimum Sample	88	14	38	31	130	133	23	91	88
Maximum Sample	98	20	44	36	163	165	30	111	95

TABLE 6.18. Correlates of display use in interactions between male great tits, after exclusion of supplants from the data set. 0 indicates that occurrences of the element listed column-wise did not occur at scores of the row variable which differed significantly from those at which interactions *not* involving the element occurred. '+' indicates a significant positive difference, '-' a significant negative difference. Double symbols indicate that the difference was significant at $p<0.005$, single symbols at $p<0.05$, in parentheses at $p<0.07$. All results based on Mann-Whitney-Wilcoxon tests described in Chapter 6.4.2. and illustrated in Appendix 12. The range of sample sizes for each element over the five tests is given. See text for further discussion.

	HU	HD	HB	EB	WO	TF	OB	TB	ATT
Weight	++	-	-	0	0	0	0	0	0
Weight Difference	0	0	0	0	0	0	0	0	0
VSI	0	0	0	0	0	0	0	0	0
VSI Difference	0	0	0	0	0	0	0	0	0
Association Index	0	++	0	0	0	0	+	+	0
Date	+	-	0	0	0	0	-	0	0
Interaction Rate	0	0	0	0	0	+	0	+	++
Frequency	0	++	++	0	0	0	(+)	0	0
Frequency Difference	0	0	0	0	0	0	0	+	0
Minimum Sample	3	7	12	9	55	50	17	22	50
Maximum Sample	48	18	39	36	171	157	33	88	92

TABLE 6.19. Correlates of display use in interactions between female great tits, after exclusion of supplants from the data set. 0 indicates that occurrences of the element listed column-wise did not occur at scores of the row variable which differed significantly from those at which interactions *not* involving the element occurred. '+' indicates a significant positive difference, '-' a significant negative difference. Double symbols indicate that the difference was significant at p<0.005, single symbols at p<0.05, in parentheses at p<0.07. All results based on Mann-Whitney-Wilcoxon tests described in Chapter 5.4.2. and illustrated in Appendix 12. The range of sample sizes for each element over the nine tests is given. See text for further discussion.

MALE - MALE INTERACTIONS : PERFORMANCES BY DOMINANT BIRDS

Element	Sample	Median difference in relative rank
HU	53	-0.26
HD	7	-0.42
HB	17	-0.40
EB	23	-0.20
WO	81	-0.26
TF	84	-0.26
OB	15	-0.26
TB	54	-0.37
ATT	58	-0.31
SA	575	-0.29

Kruskal-Wallis H (adjusted for ties) = 7.00, df = 9, p = NS

MALE - MALE INTERACTIONS : PERFORMANCES BY SUBORDINATE BIRDS

Element	Sample	Median difference in relative rank
HU	22	0.13
HD	4	0.47
HB	10	0.27
EB	9	0.09
WO	45	0.26
TF	44	0.24
OB	11	0.34
TB	28	0.20
ATT	23	0.24
SA	742	0.29

Kruskal-Wallis H (adjusted for ties) = 9.17, df = 9, p = NS

TABLE 6.20. Comparison of the relative rank differences between interacting birds when different behaviour elements are performed. The analysis pools all intrasexual, Garden, feeder interactions where dominance and subordination could be assigned, from all three years. For each element, independently, the data set is split into two subsets: i) interactions in which the performer of the element proved to be dominant, and ii) interactions where the performer proved to be subordinate. The differences between the relative ranks of performers and recipients of each element are then compared using a Kruskal-Wallis test, for dominants and subordinates, respectively, of each sex. The same caveats regarding statistical independence as are discussed in Chapter 6.4.2. apply to these analyses. Continued overleaf.

FEMALE - FEMALE INTERACTIONS : PERFORMANCES BY DOMINANT BIRDS

Element	Sample	Median difference in relative rank
HU	14	-0.11
HD	8	-0.29
HB	20	-0.18
EB	14	-0.11
WO	78	-0.25
TF	71	-0.23
OB	16	-0.32
TB	32	-0.16
ATT	45	-0.06
SA	301	-0.34

Kruskal-Wallis H (adjusted for ties) = 28.63, df = 9, p<0.001

FEMALE - FEMALE INTERACTIONS : PERFORMANCES BY SUBORDINATE BIRDS

Element	Sample	Median difference in relative rank
HU	8	0.13
HD	3	0.14
HB	5	-0.09
EB	5	0.06
WO	33	0.16
TF	30	0.15
OB	10	0.25
TB	16	0.09
ATT	19	0.03
ND	426	0.29

Kruskal-Wallis H (adjusted for ties) = 37.14, df = 9, p = NS
(note small sample sizes)

CHAPTER 7.

POSTURAL DISPLAY AND THE DEVELOPMENT OF DOMINANCE RELATIONSHIPS IN GROUPS OF CAPTIVE GREAT TITS.

7.1. GENERAL INTRODUCTION

The idea of investigating the use of postural display and the development of social relationships within captive groups of great tits was initiated after the 1987/88 winter. This winter was so mild (Appendix 2), and interaction frequencies of great tits at the feeding stations were so low (Appendices 9 & 10) as to raise doubts about devoting the whole of the third winter of the study to field observation. In addition, some results beginning to emerge from data collected in the field suggested a number of hypotheses that would be amenable to testing on captive birds.

A total of 28 great tits (12-14 at any one time) were held in captivity throughout the periods 29/10/88 - 21/12/88, and 10/1/89 - 14/2/89 in order to test several hypotheses derived from the results of Chapters 4 and 6. These hypotheses are based on consideration of the following questions.

i) What differences are there between the wild population of great tits at Ormiston Hall, and a captive group of birds, in terms of the development of dyadic dominance relationships and the linearity of a rank hierarchy derived from those relationships?

ii) What differences exist between wild populations and captive groups, in terms of their use of postural display to resolve agonistic dyadic interactions?

Several fundamental differences between the wild and captive contexts may be important in this respect.

a) It is unlikely that there will be any effects of location on the dominance relationships of captive birds, simply because the aviary volume is too small for individual birds to show site attachment or overt territorial behaviour. Hardy (1965), Kikkawa (1961), Mc Bride *et al* (1969) and Masure & Allee (1934b) provide similar examples in other species.

b) There are no differential effects of prior residence for all birds that are released simultaneously into an aviary.

c) The mutual familiarity between birds in a captive group is controlled in the same way as (b) if all birds are captured at widely separated sites.

d) Once introduced to the aviary, the birds' mutual familiarity would be expected to increase much more rapidly than in a wild population since each bird is in sensory contact with *every* member of the 'population' for a much greater proportion of the daylight period than would be the case in the wild. If the aviary is provided with a single source of food and water, the high rate of interaction at these single sources will further enhance the rate at which mutual knowledge in the group increases.

e) Stress, both as an effect of the captive environment, and as a result of prolonged exposure to social contact with conspecifics, is likely to be much greater in a captive group than in a wild population. For example, in a review of the structure of primate societies, Gartlan (1968) reported that "field studies of primates previously studied only in captivity show without exception that in these latter circumstances hierarchies are both more pronounced and more rigid, and that aggression is more common".

7.2. GENERAL METHODS AND MATERIALS

7.2.1 Capture and Measurement of Birds

All birds used in the two experiments of this study were captured under licence from the Nature Conservancy Council (No. 5B:86:88) at one of three sites: Ormiston Hall, Blyth Bridge (55° 42′N 3° 23′W) and Loganbank (55° 51′N 3° 23′W). Birds were captured in mist nets and their ages and sexes were determined in the field according to the criteria described in Chapter 2. They were transported to the Zoology Department in cloth bags. There, each bird received either one (female) or two (male) colour rings of the same colour (orange (O), green (G), or black-white stripe (S)) on either the right (R) or left (L) leg, giving the following combinations which allowed individual recognition of birds in the aviary (SSR, SSL, GGR, GGL, OOR, OOL - male; SR, SL, GR, GL, OR, OL - female). Wing length (mm), mass (g), tarsus length (mm) and plumage scores of each bird were recorded using the techniques described in Chapters 2 (size measures) and 5 (plumage scores), before release into an aviary.

7.2.2. Aviaries

Three adjoining aviaries were available in a large, unheated, concrete - floored room with electric fan ventilation. This room is partitioned into three aviaries of 2.6m x 2.45m x 2.15m (height) by means of quarter-inch weldmesh secured to a wooden frame. All three aviaries are partitioned in the same way from a narrow service corridor running the full length of one side of the room. Each aviary has a 1.2m x 0.6m access door to this corridor and can be viewed from the corridor through two 0.8m x 0.6m perspex windows coated with one-way mirror film which makes the corridor invisible from the aviaries. A small hole was cut in the film in each aviary, to allow clear videotaping of bird activity from the service corridor using a tripod-mounted video camera. For these experiments, both inter-aviary partitions were screened with hardboard to ensure visual, if not auditory, isolation between aviaries. Each hardboard screen contained a 0.8m x 0.8m section covering a gap in the weldmesh. This section could be removed to provide a connecting flyway.

Each aviary contained six standard tit nestboxes and was provided with several small potted shrubs and numerous bamboo perches and wooden baffles which allowed birds to rest in visual isolation from at least some of their flockmates. The concrete floor was initially covered with a thin layer of garden peat but this practice was later abandoned due to the need to sweep out aviaries daily to ensure that food availability was restricted to a single, provided source. Each aviary was illuminated by four Osram 'Liteguard' 85W daylight tubes and the 24-hour light cycle was controlled by automatic time switches located in the service corridor. A plan view of the aviaries is shown in Fig. 7.1.

7.2.3. Husbandry

Captive great tits were maintained on a solid food mix described in Table 7.1. which has been used successfully by the Zoology Department for a variety of captive studies of wild birds (e.g. Clark 1983). A fresh supply of this food mix and a bowl of fresh water for drinking and bathing were provided daily.

Food was provided either in a 6cm diameter by 2cm depth tray on a small feeding table occupying the field of view of the video camera ('Restricted Food Access' - RFA) or, *ad libitum*, on a 100cm x 60cm litter tray on a stool in the centre of the aviary ('Open Food Access' - OFA). RFA was provided during the three hours after lights-on on days when interactions were to be recorded on videotape in Experiment 1, and during observation periods in Experiment 2. At all other times OFA was available with food in *ad libitum* quantities.

Aviaries were swept daily to remove scattered food and were more thoroughly cleaned every 7-14 days. During cleaning, birds were temporarily allowed to fly through to the adjacent aviary to minimize disturbance.

Aviary conditions and husbandry practices all had prior Home Office approval.

7.2.4. Data Collection

The occurrence and outcome of dyadic agonistic interactions were recorded in exactly the same way as described in Chapter 2 for field observations, using either direct observation and notebook-recording, or videotaping. In the first case, all interactions were recorded during an observation period, irrespective of their location within the aviary. In the second, only interactions at an RFA food source were recorded.

The recording of postural display was based on the same repertoire of elements as in Chapter 6 and all elements were recorded on a 'one-zero' basis for each individual in each interaction.

7.2.5. Release of birds

Wing length, mass, tarsus length and plumage scores for each bird were re-recorded at the end of the experimental period, before they were put into cloth bags and returned to their site of capture for release. Before release, each bird was ringed with B.T.O. ring and its colour-ring combination was changed in accordance with the scheme being used on the wild population (Chapter 2). Observations of these birds up to several months after release suggested that rehabilitation in the wild was in many cases successful.

7.3. EXPERIMENT 1: The Development of Dyadic Dominance Relationships and use of Postural Display in Captive Flocks of Great Tits

7.3.1. Introduction

In a captive group of great tits, the development of a peck-right structure in in dyadic dominance relationships and of linearity in the overall rank hierarchy may be favoured by some factors and opposed by others. If Gartlan's (1968) conclusions apply to captive groups of birds, then newly constituted flocks would be expected to show high rates of aggressive interaction due to stress associated with the sudden and dramatic change in the birds' environment and continuous exposure to social contact with conspecifics. This effect might be enhanced by the mutual unfamiliarity of the birds since several studies have noted that familiarity affects both the outcome and aggressiveness of interactions (e.g. Balph 1977; Candland *et al* 1968; Guhl 1968; Poole & Morgan 1975). Over a short time scale, these high initial interaction rates would be expected to lead to the rapid development of unilateral dyadic dominance relationships and a linear rank hierarchy, as an immediate positive feedback effect of recent agonistic experience on current agonistic behaviour (Chapter 4; Chase 1974, 1980, 1982, 1985; Drent 1983; Jackson 1988; Popp 1988). This rapid development of linearity in dominance hierarchies has been reported in chickens (Chase 1980, 1982, 1985) and rhesus macaques *Macaca mulatta* (Mendoza & Barchas 1983), but in other captivity studies the rate of development of linearity has been much slower (e.g. Chase & Rohwer 1987; Tordoff 1954).

This positive feedback effect is approximated in wild populations of great tits during the post-fledging period, when large numbers of mutually unfamiliar juvenile birds begin their histories of social interaction. Initially, the outcome of encounters may be determined by physical factors such as body weight (Garnett 1976, 1981), which may in turn be influenced by fledging date (Dhondt 1970, 1979; Kikkawa 1980b; Kluijver 1951). However, these initial asymmetries are thought to develop into unilateral dominance relationships through the reinforcement effect of previous wins or losses (Drent 1983). In the longer term, dominance relationships are accentuated by the establishment of dominant birds as local residents and a tendency for subordinate birds to be forced into dispersal to unoccupied areas or, at least, areas where they are not conditioned to be subordinate to a known set of opponents (Drent 1983). The result is a winter population in which dominance in intrasexual dyadic interactions is determined mainly by asymmetries in site familiarity and duration of prior residence and the local agonistic experience of competing birds. These asymmetries both maintain the site-related unidirectionality of dominance relationships in the wild and, ultimately, allow the establishment of breeding territories and reproduction by locally dominant individuals (Chapter 4). In an aviary population, all birds are constrained to occupy the same 'home range' and the consolidation of initial dominant - subordinate asymmetries through dispersal and the development of site-related dominance never occurs. Consequently, we might expect initial dominance relationships to become progressively *less* clear-cut as they continue to fluctuate under the continued influence of the positive feedback effects of recent experience and those periodic reversals attributable to other causes such as hunger, satiation, illness and errors in recognition of opponent. The pattern of food provision may also affect this process. For example, RFA conditions may be more likely to induce sufficiently intense competition for food that dominant - subordinate relationships do develop as a result of repeated encounter. But perhaps under these conditions subordinates are more likely to achieve reversals due to high levels of aggressive motivation created by hunger. By contrast, under OFA conditions predictable dominance relationships might never develop simply because of the absence of significant competition for priority of access to resources. It is very difficult to predict the effect of different regimes of resource provision on the development of dominance relationships and hierarchy linearity. However, if consistency is achieved over different regimes (e.g. RFA and OFA), this might indicate that the results are a response to more fundamental differences between field and aviary conditions rather than to specific aspects of the husbandry practice.

In a wild population, reduced stress effects, lower levels of aggression and lower interaction rates may make the initial development of unilateral dominance relationships and linearity in the rank hierarchy slower. However, as Fig. 4.1. showed, dominance relationships tend to become increasingly peck-right at any one site as they are reinforced by the development of prior residence asymmetries, site-related dominance and territoriality. As determinants of dominance, these asymmetries are then self- reinforcing. The prior resident will have a high probability of being dominant over the newcomer in each interaction and each interaction which has this expected outcome maintains or enhances the probability of the prior resident retaining its resident status. So, in wild populations dyadic relationships are expected to become *increasingly* unilateral with time at any one location, a process which is reflected by an increasingly linear rank hierarchy when these dyadic relationships are combined.

In Chapter 4, it has already been found that individual dominance relationships tend to become increasingly unilateral with time and repeated encounter (Fig. 4.1.). Also, rank hierarchies compiled from interactions at one site maintain a very high level of linearity despite being compiled from a data set of interactions accumulated over a six month period (October to March) (Appendix 6).

On the basis of the arguments presented above, the development of dominance relationships in a captive group of great tits is predicted to show the following features under RFA conditions.

a) There should be sequential dependency in the outcome of the interactions of any intrasexual dyad (A–B) so that for any given degree of unidirectionality 'wins' and 'losses' for individual A should not be randomly distributed, but should reflect alternating runs of success and failure.

b) The degree of unidirectionality in the dominant – subordinate relationship of each male and female intrasexual dyad should be roughly constant from day to day, but a cumulative score of outcomes for each dyad should show reduced asymmetry in comparison with wild populations as 'runs of success' for one member of a dyad periodically reverse to 'runs of failure'. As a consequence, compilation of the overall outcomes for each of the dyads to form an intrasexual dominance hierarchy should also show reduced linearity in comparison with hierarchies recorded in the Ormiston Hall population, although this may be partially countered by the greater numbers of individuals making up the latter.

c) Since intersexual dominance relationships (male is almost always dominant over female) are thought to be a result of permanent size differences between the sexes, their unidirectionality should remain constant in magnitude and consistent in direction from day to day, so that a cumulation of interaction outcomes over time should also show a consistent proportion of 'wins' by male birds.

Finally, from the conclusions of Chapter 6, the following predictions are made concerning the use of postural display in captive flocks.

a) WO, TF and OB, as bluffable threat displays, should only be seen in the period immediately following introduction of mutually unfamiliar birds to the aviary. If new birds are introduced to an established flock, the immediate prior residence asymmetry associated with unfamiliarity should result in the predominance of category (ii) displays (below). In intrasexual interactions, the frequency of performance of WO, TF and OB should wane thereafter as mutual knowledge increases. In the more overtly asymmetrical intersexual dyads, they may still be performed as signals of "intent to assert dominance" by males to females in the same way as they were seen in interspecific contexts in Chapter 6.

b) In Chapter 6, it was concluded that HU, HD, HB and TB "are involved in the process of development of site attachment and the resolution of conflicts that arise with birds having pre-existing attachments to the same area". In effect, all birds in one aviary, introduced simultaneously, have conflicting attachments to the same area. Although neither in this study nor others (e.g. Drent 1983) were individual great tits seen to successfully establish site-related dominance or territories within aviaries, these site attachment conflicts presumably remain and the use of the above elements would therefore be expected throughout the experimental period. An increase in their frequency of performance might be expected in response to increasing photoperiod and/or temperature (Silverin 1980; Suomalainen 1937) or the introduction of new birds to an established flock.

7.3.2. Methods

Twelve great tits were captured for this experiment; two first-year males and two first-year females from each of the three capture sites. Blyth Bridge and Ormiston Hall birds were captured on 29/10/88 and kept overnight in individual cages in visual isolation from each other. Loganbank birds were captured on 30/10/88 and all birds were kept for a second night in the same conditions. After ringing and measurement, all twelve birds were released simultaneously into aviary 1 on 31/10/88. The data collection regime for this flock until 23/11/88 is illustrated in Table 7.2. and the light - dark ratio was kept at 10.5 hours light : 13.5 hours dark throughout. In total, 43.6 hours of observation under RFA conditions and 21.9 hours under OFA conditions were carried out during this period and used in analysis.

On 30/11/88, one further first-year male and female were captured at Loganbank. After three hours recovery from the capture process and acclimatization to aviary conditions in aviary 2, they were released to join the captive flock in aviary 1. These 'newcomer' birds were distinguished from the 'prior resident' flock by red and white banded colour rings - BBR (male) and BR (female). During the period between

23/11/88 and 30/11/88, one female (SL) had died from natural causes, thus leaving an experimental flock of six prior resident males, five prior resident females, one newcomer male and one newcomer female. Unfortunately, BBR died during its first night in captivity, so BR was removed and released and the experimental introduction of two newcomers (BBL male and BL female) was repeated on 7/12/88. Again, one of the introduced birds (BL) died shortly after introduction, over the night of 8-9/12/88. On the assumption that stress associated with capture conditions and continuous exposure to unfamiliar conspecifics was at least partly responsible for these deaths, this experiment was not repeated, although the course of the surviving male's (BBL) integration into the 'resident' flock was followed until 20/12/88. Over the period 13/12/88 to 18/12/88, the light – dark ratio was gradually increased to 14.5 hours light : 9.5 hours dark to examine the effect of increasing 'daylength' (a crude simulation of approach to the breeding season) on the use of display by the captive flock. The data collection regime for the experimental period from 30/11/88 to 20/12/88 is also illustrated in Table 7.2. In total, 15.8 hours of observation under OFA conditions were carried out during this period and used in analysis. All birds were released on 21/12/88.

7.3.3. Results

7.3.3.1. The Development of Dominance Relationships

RFA conditions

After each day's observation of the flock under RFA conditions, the two samples of intrasexual interactions were added to the cumulative totals from preceding days and the dominance matrices were entered into the cardinal index program (Chapter 4). This allowed construction of both male and female dominance hierarchies and calculation of the following parameters.

i) Rank of each bird in the hierarchy.

ii) Cumulative total interactions.

iii) The proportion of interactions where outcome contradicted the overall rank positions of the birds ('reversals').

iv) The proportion of interactions won by the overall dominant in each dyad. For example, over dyads with scores of 5-2, 3-0 and 4-2, the overall dominants won (5+3+4)/(7+3+6) = 75% of interactions. This value ranges from 50% to 100% and gives an index of the ambiguity of dominance relationships, these becoming increasingly clear-cut ('peck-right') as the index approaches 100% (see Fig. 4.1. for use of this index on the wild population).

In the male hierarchy, there were five rank changes between 2/11 and 3/11, two between 3/11 and 6/11, 2 between 6/11 and 7/11, and 1 between 11/11 and 15/11. Thereafter, the rank order was completely stable in the order OOL (1), GGL (2), GGR (3), SSR (4), SSL (5), OOR (6). By 23/11, 987 interactions between males had been recorded of which the two lowest-ranked birds were only involved in 155, significantly fewer than the chance expectation of (987 x 2)/6 = 329, (X^2 = 82.9, df=1, p<0.001). Throughout the period 2/11 to 23/11, the proportion of interactions won by overall dyadic dominants remained constant at around 70%, as did the proportion of interactions whose outcome contradicted the rank order, at 30-40% (Fig. 7.2.). These results contrast with those in the wild (Appendix 6), where the proportion of interactions reversing overall rank order never exceeded 15% and the dominance relationships of frequently interacting males reached 85% asymmetry at any one site. Thus, in captivity, all-male dyads showed less clear-cut dominance relationships than are found in the wild, and the rank order cumulated over all interactions was less linear.

When sequences of male-male interactions under RFA conditions are examined, OOL and SSR (ranks 1 and 4, respectively) show no evidence of dependence between the outcomes of successive interactions, whereas GGL and GGR (ranks 2 and 3) have significantly fewer (and therefore longer) 'runs' of consistent 'winning' or 'losing' than expected by chance. This indicates sequential dependence in the form of 'winning begets winning' and 'losing begets losing' (Table 7.3.). The interactions of SSL and OOR could not be examined due to their rarity. Of course, if there is also sequential dependency in the identity of these birds' opponents then it may be simply that runs of winning are a consequence of runs of interactions with the same subordinate opponent, and vice versa for runs of losing. Table 7.4. takes this into account by examining the association between successive outcomes, according to the identities of the preceding and succeeding opponent. For the highest (OOL) and lowest-ranked (SSR) birds, the probability of winning their next interaction does not vary significantly with either the outcome of the previous interaction or the identity of the previous opponent in that interaction. In the case of GGR, the significant result is almost entirely a consequence (>99% of the total X^2) of runs of wins or losses against the same opponent. In the case of GGL, there is the same evidence of persistent defeat in successive encounters with one opponent (62% of total X^2), but successive runs of winning are more associated with changes of opponent (32% of total X^2) than with successive wins against the same bird (3% of total X^2). However, only in GGL is there any evidence that a win in one interaction is more likely after a preceding win than after a preceding loss, when the opponents in the two successive interactions are different.

In the female hierarchy, there were five rank changes between 2/11 and 3/11, three between 3/11 and 6/11, two between 6/11 and 7/11 and one each between 11/11 and 15/11, 17/11 and 18/11, and 21/11 and 22/11, thus implying greater long-term instability in female-female dominance relationships than between males. By 23/11, 149 interactions had been recorded. This corresponds with the relative rarity of all-female interactions in the wild (Tables 6.3. & 6.4.). The rank order was OL(1), OR(2), SL(3), GL(4), SR(5), GR(6). In contrast to the male hierarchy, it was the top dominant female that was involved in fewest interactions (35 of 149, as opposed to a null expectation of (149 x 2)/6 = 49.7, $X^2 = 3.72$, df = 1, $0.05 < p < 0.1$), whilst the two lowest ranking birds were involved in 101 interactions, almost exactly as would be expected by chance (149 x 4)/6 = 99.3). Over the period 2/11 to 23/11, the proportion of interactions won by overall dyadic dominants fell from over 90% on 2/11 to around 76% by 23/11. Correspondingly, the proportion of interactions whose outcome contradicted the rank order rose gradually to over 20% by 23/11 (Fig. 7.2.). Both these results suggest that dominance relationships between females were not becoming increasingly peck- right over the course of the experiment. This resulted in increasingly ambiguous cumulative dominant - subordinate scores for each dyad and decreasing linearity of the dominance hierarchy based on these scores. These results contrast with those for male-male interactions (above). The number of outcomes contradicting the overall rank order is high in comparison with those female hierarchies calculated from Ormiston data sets, where similar numbers of interactions were involved (Appendix 6). Similarly, the progressive decline in the asymmetry of dyadic dominance relationships contrasts with increasing asymmetry of frequently interacting dyads in the wild (Fig. 4.1.). As with the male hierarchy, it seems that dominance relationships in captivity remain less clear-cut and rank orders are correspondingly less linear than are seen in the wild.

Sequential dependency in the outcome of female-female interactions could not be examined due to their infrequent occurrence.

OFA conditions

When measured under OFA conditions (Fig. 7.2.), the development of dominance relationships and hierarchy linearity does not show any major differences from that described above, although male dominance relationships do show a slight tendency to become less clear-cut and there is declining hierarchy linearity, both changes which did not occur under RFA conditions. However, the final rank order of males under OFA conditions did differ significantly from that under RFA conditions. The most notable change was that SSL, a rare, subordinate visitor to the feeder under RFA conditions was at the top of the OFA hierarchy. OOL, GGL and GGR were ranked 2, 3 and 4, as under RFA conditions, but SSR ranked below OOR at the bottom of the hierarchy, despite OOR still being a rare interactant at the feeding tray even under OFA conditions.

Female dominance relationships perhaps show slight evidence of the reverse trend of those in males, under OFA conditions (Fig. 7.2.), but the most striking result is the absolute levels of dyadic dominant - subordinate asymmetry and hierarchy linearity are much lower throughout the experimental period, than under RFA conditions. With the exception of reversals amongst birds occupying ranks 4, 5 and 6, to give GR(4), GL(5), SR(6), there were no major differences between the final rank orders of females between RFA and OFA conditions. An important implication of these results is that although the difference between RFA and OFA feeding regimes influenced the *extent* to which dominance relationships became more ambiguous, there were no fundamental changes in the social structure of the flock that were contingent simply upon this aspect of husbandry practice. This is an important conclusion because the great majority of recorded interactions took place at the provided food source under OFA conditions, and all were at the food source under RFA conditions.

As in the wild, the male was the overall dominant in all intersexual dyads, and the proportion of all intersexual interactions won by males remained consistently above 90% throughout the experimental period, under both RFA and OFA conditions (Fig. 7.3.).

7.3.3.2. Use of Agonistic Behaviour Elements

In all analyses of the use of these elements, the four sex categories of performer and recipient have been pooled. This is partly because the distribution of display use across these categories was not seen to be significantly different from that found in the wild (Chapter 6.2.), but more importantly because sample sizes were small as display was relatively rarely used by captive birds in comparison with those watched at Ormiston Hall. For example, from 3902 interactions seen at the Garden feeders at Ormiston, 2385 occurrences of display elements (HU, HD, HB, EB, WO, TF, TB, ATT) were scored (Table 6.3.), a frequency of 0.61 per interaction. Under RFA conditions in this experiment (2/11 to 23/11), the rate was 170 occurrences from 2111 interactions (0.08 per interaction) and under OFA conditions (31/10 to 14/11), 82 occurrences from 968 interactions (0.08 per interaction).

Fig. 7.4. shows that, under RFA conditions, HU, HD, HB, EB, TB and

ATT occurred throughout the period 2/11 to 23/11 at a fairly constant rate. In contrast, WO, TF and OB were rarer and were barely seen at all after 9/11. Under OFA conditions (Fig. 7.5.), display in general was rare throughout the period 31/10 to 14/11, with the great majority of 'interactions' being either supplants or simple avoidance of an approaching bird by another. However, the two days on which new birds were introduced (30/11 and 7/12) are both marked by sudden increases in the frequency of use of most elements. The exception to this was OB which was only recorded once under OFA conditions. Of the 217 occurrences of display, attack or chasing between 30/11 and 12/12, 192 (91.2%) involved these elements directed by a member of the resident flock to one of the newcomers. Of the remaining 25, 18 were between two members of the resident flock. Displays by newly introduced birds were *extremely rare*. Similarly, introduced birds won very few of their interactions with resident birds of the same sex. BBR and BBL, between them, were dominant over resident males in only 22 of 294 interactions (7.5%). BR and BL were dominant in only 1 of 76 interactions with resident females (1.3%). Fig. 7.5. also shows that frequency of use of most postural displays, attacks and bouts of chasing declined rapidly within a few days of the introduction of BBL and BL on 7/12/88. Although this is partially attributable to the death of BL on 8/12, most interactions were between males and much of the decline is almost certainly due to the integration of BBL into the resident flock. The proportion of interactions in which BBL was involved supports this suggestion, declining from 52.8% of 369 interactions on 7/12 and 8/12 to 25.5% of 231 on 9/12 and 10/12 and 20.7% of 261 on 11/12 and 12/12.

After acclimatization of the flock to a 14.5h daylength over the period 13/12 to 18/12, the incidence of postural display and attack under OFA conditions remained very low (Table 7.5.), reflecting the integration of BBL into the established flock. However, the incidence of chasing bouts directed by males at birds of both sexes, increased markedly to 7.4 occurrences per hour from a rate of only 0.5 per hour during the period 31/10 to 14/11, when the birds had only a 10.5 hour photoperiod. This result provides experimental confirmation of the importance of daylength as a correlate of the increase in chasing and spatial intolerance that was seen in the wild population over the course of the winter.

7.4. EXPERIMENT 2: PRIOR RESIDENCE AND INDIVIDUAL RECOGNITION AS CAUSAL FACTORS IN POSTURAL DISPLAY

7.4.1. Introduction

Experiment 1 has demonstrated clearly that the introduction of new birds to an established flock induces a resurgence in the use of agonistic display and overt aggression by members of the flock, that behaviour being directed primarily at the newcomers. However, that experiment does not allow us to distinguish between the unfamiliarity of the opponent *per se*, and the recognition of that opponent as an intruder (i.e. a prior residence asymmetry) as causal factors in the elicitation of agonistic display. Experiment 2 is designed to give some insight into that distinction by testing the following hypotheses.

a) Category (ii) displays should be more prevalent when birds meet unfamiliar opponents within their home range (Experiment 1) than when the same birds meet on 'neutral' ground to which neither bird has a significant attachment.

b) The converse should be true of category (i) displays since at locations where neither bird has site attachment there is no asymmetry in this variable to mask the effects of mutual unfamiliarity on agonistic behaviour.

7.4.2. Methods

On 10/1/89, twelve first-year great tits (six male and six female), were captured at Loganbank and brought immediately to the Zoology Department. After measurement, each sex group was divided arbitrarily into two groups of three. One male and one female group were introduced simultaneously into aviary 1 (flock 1), and the other two groups into aviary 3 (flock 3). Before release into the aviary, birds of flock 1 were given the same left-leg colour ring combinations as used in Experiment 1 and the corresponding right-leg colour ring combinations were used on flock '3'.

Both flocks were allowed to establish themselves in aviary conditions for five days and were not disturbed except for the daily provision of *ad libitum* food, and water. The light cycle was maintained at 10.5h light to 13.5h dark throughout the experiment. Between 15/1 and 29/1, both flocks were observed to record a 'control' sample of the incidence of agonistic behaviour elements between flock members under OFA conditions in the home aviary. In total, each flock was observed for 270 minutes over six days and a total of 402 interactions were recorded, 192 in flock A and 210 in flock B. All observation sessions started ten minutes after the daily human intrusion to provide food and water. This regime provided a partial control for the disturbances (capture and translocation) which preceded the recording of interactions under the two experimental regimes (below). On each day during this period, one of the inter-aviary hatches was opened for one hour and the birds from one flock allowed to use aviary 2. This access was given alternately to the two flocks on successive days. This procedure allowed all twelve birds equal, but very limited, experience of aviary 2. The aim was that birds' behaviour in this aviary would not be affected by its being a completely novel environment, but that their experience of it would be sufficiently limited that site attachments would not have developed.

On a further twelve days between 19/1 and 11/2, the experimental regime was carried out. This involved introduction of two members of one flock to the other flock, followed by a ten-minute interval, and then sixty minutes recording of all interactions in the temporarily constituted flock under OFA conditions. The two introduced birds were then returned to their home flock. These were always a male and female of the same ring colour. Thus, each flock contained three such pairs (e.g. OOL/OL, SSL/SL, GGL/GL) and there were six potential introductions; each of three pairs from flock 1 to flock 3, and vice versa from flock 3 to flock 1. All six introductions were carried out twice. For any given pair, one introduction was to the other flock *in its home aviary* and the other was to the other flock *in aviary 2.* Since all birds had had equal but very limited experience of aviary 2 and were assumed to have negligible site attachment in that aviary, the latter introduction is termed 'neutral'. The former is termed 'asymmetric' since it was assumed that the home flock would have site attachments not possessed by the introduced birds.

Pairs of birds required for introduction or return to their home flock could be captured easily with a hand net without causing any more than a few minute disturbance to the flock as a whole. Captured birds were put in cloth bags and released into the appropriate aviary with minimum delay. A whole flock could be introduced to aviary 2 by opening the inter-aviary hatch from aviary 2, retiring, and then opening the door from the service corridor to the flock's home aviary. The sound of the door usually caused the entire flock to fly through the hatch immediately. The hatch could then be closed again from the home aviary.

The total of twelve experimental introductions and observation periods was carried out over the 24-day period on alternate days so that the birds did not receive human disturbance or experience of unfamiliar conspecifics on successive days. The order in which the introductions were carried out was arranged to maximize the interval between the two introductions of any one pair. Clearly, this was only a partial solution to the problem that with each experimental introduction, birds from the two flocks gained experience of each other, with only a limited time lag (one day) between these bouts of social contact. It was for this reason that the further experimental introductions that could have been made using the remaining pairwise combinations of male and female from each home flock were not undertaken.

7.4.3. Results

Table 7.6. supports the predictions of hypothesis (i). HU, HD, HB, EB and TB all increased in frequency of performance from 'control' to 'neutral' to 'asymmetric' contexts. However, with the exception of HU and TB, postural display of any kind was rare other than in 'asymmetric' contexts. WO, TF an OB were particularly rare, with the combined total of five occurrences over 21 hours of observation being insufficient to

make any interpretations with respect to hypothesis (b).

Table 7.7. shows that, for those elements where sample size was adequate (especially HU, HB and TB), display under 'neutral' and 'asymmetric' conditions was associated with interactions between a flock member and a newcomer and remained rare between flock members. Expected values for this Table were calculated by dividing the total number of performances of an element into the three categories (F>F, F>N and N>F), according to the number of dyads in each (see Table), given that the time available for observation of interactions in each category was equal.

7.5. GENERAL DISCUSSION

7.5.1. Dominance Relationships and Hierarchy Linearity

In general, the results of Experiment 1 provide empirical support for the hypotheses put forward in Chapter 7.3.1. In both male and female dominance hierarchies, and under either RFA or OFA conditions, reversals of the overall rank order are more frequent, and the linearity of the hierarchy less marked than in hierarchies recorded at feeding stations in the wild (Fig. 7.2.). This trend occurs despite the fact that the hierarchy size (six individuals) is much smaller than those recorded at Ormiston. This slow or incomplete development of peck-right relationships and hierarchy linearity in captivity has also been reported by Watson (1970) in house sparrows *Passer domesticus*, Chase & Rohwer (1987) in Harris' sparrows *Zonotrichia querula* and Senar (1985) in siskins *Carduelis spinus*.

The results in this experiment may be attributable to the lack of development of prior residence asymmetries and site-related dominance, which are the primary determinants of the consolidation of dyadic dominance relationships in the wild. However, in the absence of these asymmetries there is little evidence that more proximate influences such as recent agonistic experience and its physiological correlates are playing a significant role in determining current probabilities of winning or losing. What little evidence there is (Tables 7.3. & 7.4.) suggests that those runs of agonistic success or failure that do occur are largely a consequence of runs of interaction with the same opponent. In only one out of four birds whose interaction sequences were analysed was there a statistically significant tendency for the outcome of one interaction to correspond with that of the previous one when the opponents in the two interactions were different. Clearly, these results were weakened by the fact that the intervals between successive intrasexual interactions were very variable and that the possible influence of intervening interactions with females was ignored. Nevertheless, they are an interesting contrast with those of Popp (1988), who found that the outcome of previous interactions was a strong correlate of the probability that an American goldfinch *Carduelis tristis* would be dominant in a current interaction, when the identity of the two opponents was different.

An explanation may lie in basic differences between great tits and goldfinches in the ecology of their social groups. Thus, cardueline finches tend to show *year-round* flocking and stable flock membership (Senar & Metcalfe 1988), with an important function for flocking being reduction of predation risk and enhancement of the ability of individuals in the flock to exploit discovered food patches (see Elgar 1989 for a review). In this context, there is evidence to suggest that peck-dominance and weakened dominance asymmetries are adaptive means by which dominant birds ensure that subordinates do not leave the flock (Senar *et al* 1989). Similarly, dominant birds may often submit to subordinate birds which, perhaps through hunger (Popp 1987b), initiate agonistic interactions or perform aggressive displays (Senar *et al* 1989). Given this flexibility of agonistic response to the behaviour of known opponents, it is perhaps not surprising that the outcomes of contests between American goldfinches vary significantly with recent experience. In great tits, flocking may serve similar foraging and anti-predator functions as it does in other species (e.g. Krebs *et al* 1972). However, this flocking behaviour is limited by season, and at the end of the winter flocking period successful territory establishment and reproduction (at least in males), is dependent upon consistent, local social dominance over conspecifics and their eventual exclusion from the area. Consequently, in great tits, selection pressures for ensuring local social dominance may outweigh flock-based advantages of retaining subordinates by being behaviourally flexible and allowing occasional reversals of established dominant - subordinate relationships. As an evolutionary constraint, therefore, great tits might be expected to show less short-term flexibility in agonistic responses even when maintenance resources are unrestricted and the longer-term goals of social dominance (i.e. the establishment of site-related dominance and, ultimately, a territory) are not achievable. The result is that dominance relationships in an aviary fail to become peck-right due to the absence of asymmetries in prior residence and site attachment, but that those reversals that do occur do not tend to lead to 'runs' of success for the overall subordinate.

These contrasting expectations of the agonistic behaviour of great tits and carduelines both involve species with relatively stable flock membership and a high probability of repeated encounter and individual recognition. At the other extreme are species such as the red-billed weaver *Quelea quelea* (Shawcross 1982; Shawcross & Slater 1984) in which there is little evidence of flexible agonistic responses with respect to either recent experience or the identity of the opponent. This species forms very large, unstable flocks where the probability of repeated encounter with the same opponent is low and the effect on flock size of exclusion of a few subordinate individuals may be negligible. In these species, therefore, there may be no significant long-term consequences of the outcome of encounters and no selection pressures for individual recognition or the sensitivity current agonistic behaviour to recent experience. The consequence is that successive interactions are effectively independent with respect to these factors (Shawcross & Slater 1984).

The examples of great tits, American goldfinches and red-billed weavers simply serve to show the diversity of selection pressures influencing the development of dominance relationships in the wild. An understanding of the social ecology of the species may be essential to interpretations of social behaviour and the development of social relationships in captive groups.

By contrast with the discussion of intrasexual dominance relationships, in intersexual interactions the physical asymmetries between the sexes which maintain the dominance of males over females in the wild, are not precluded under aviary conditions. Correspondingly, the probability of dominance of a male over a female remained consistently above 90% (Fig. 7.3.).

7.5.2. Use of Postural Display

The results of both experiments 1 and 2 are very consistent with the hypotheses put forward in Chapters 7.3.1. and 7.4.1. Category (i) displays disappeared from the observed display repertoire soon after the setting up of a flock under aviary conditions (Fig. 7.4.), but were seen again when unfamiliar birds were introduced to the flock, as displays directed by the resident birds at the newcomers (Fig. 7.5.). By contrast, category (ii) displays occurred at a relatively constant rate throughout the initial phase of Experiment 1 (to 23/11/88), at least under RFA conditions (Fig. 7.4.). On the introduction of unfamiliar birds, the incidence of all category (ii) elements increased markedly (Fig. 7.5.). and, again, these were almost entirely directed by resident birds to newcomers in interactions initiated by the resident. Correspondingly, newcomers were subordinate to all resident birds of the same sex, a striking, if extreme, demonstration of the effect of prior residence on social status.

Although the surviving introduced male (BBL) failed to increase significantly its agonistic success over the days following introduction, it did become increasingly integrated into the resident flock, such that its frequency of involvement in agonistic interactions with residents decreased by over 50% within one week and the frequency of performance of agonistic display within the flock as a whole fell back to pre-introduction levels. A similar prior residence effect in a population of tits was found by Odum (1941) in an experiment involving translocation of black-capped chickadees *Parus atricapillus* to a feeding station in the home range of a different population. There the translocated birds were invariably relegated to very subordinate status, irrespective of their status in their home flock. Similar prior residence effects have been reported by Guhl & Allee (1944) in chickens, and Sabine (1959) in dark-eyed juncos *Junco hyemalis*.

In Experiment 2, the hypothesis that category (ii) elements should be more prevalent when unfamiliar birds are introduced to a flock in the latter's home range, rather than when the birds meet on 'neutral' ground, was strongly supported (Table 7.6.). The comparison between frequencies of agonistic display in an established flock ('control') and 'neutral' conditions demonstrates that any effect of the introduction of unfamiliar birds in eliciting agonistic display from flock members is almost nullified if the flock has been translocated from its 'home range' (the home aviary). The important conclusion is that mutual unfamiliarity between competing great tits may only be an important causal factor in the elicitation of agonistic display if it is correlated with the recognition of one of the birds as an *intruder*, by the other. Site attachment is again confirmed as the important underlying variable in explaining agonistic behaviour.

Category (i) elements were so rarely seen under any of the three data collection regimes in Experiment 2 that the second hypothesis could not be tested. However, the general rarity of these elements in aviary conditions contrasts with the wild population at Ormiston Hall, where WO and TF were the most commonly observed postural elements. A possible explanation is that the birds quickly became habituated to a reliable, non-limiting food source so that escalated competition over food, the context in which these elements were most frequently seen in the wild, never occurred. Those interactions which did involve display perhaps concerned conflicts of site attachment, even though they may have occurred at the food tray, so that category (ii) elements tended to be the only ones seen. The ideal test of this hypothesis would be to compare the use of postural display in a flock where food was provided continuously and *ad libitum*, with that in a flock where food was provided more sparingly, at random intervals and for varying lengths of time.

In comparison with the wild population of great tits at Ormiston Hall, postural display was, in general, rare under aviary conditions (Chapter 7.3.3.2.). Minimal display in established flocks was also recorded by Hartzler (1970) in black-capped chickadees and Coutlee (1967) in American goldfinches. Similarly, physiological studies of house sparrows and quail *Coturnix coturnix* (Hegner & Wingfield 1987; Ramenofsky 1984) have suggested that plasma hormone levels may correlate strongly with parameters of aggressive behaviour in situations of social flux such as the establishment of mutually unfamiliar individuals as a flock, but that these correlations often disappear in established social groups (e.g. Rohwer & Wingfield's 1981 study of established groups of Harris' sparrows) where individual recognition may be more influential in maintaining stabilized relationships (e.g. Chase 1982; Whitfield 1986).

The following results together provide evidence for the rapid development of individual recognition in flocks of captive great tits.

i) Postural display is much rarer within established captive flocks than in wild populations.

ii) The introduction of unfamiliar birds to an established flock causes a resurgence in the incidence of postural display.

iii) This renewed display activity is specifically directed by established flock members at introduced birds.

iv) With increasing time after such an introduction, the frequency of displaying declines to pre-introduction levels as does the frequency with which the newcomers are involved in agonistic interactions initiated by established flock members.

The implications of the ability of great tits to distinguish between individuals, for agonistic communication in wild populations is discussed further in Chapter 8.

LT: Litter Tray
FT: Food Table
F: Fan
W: Water

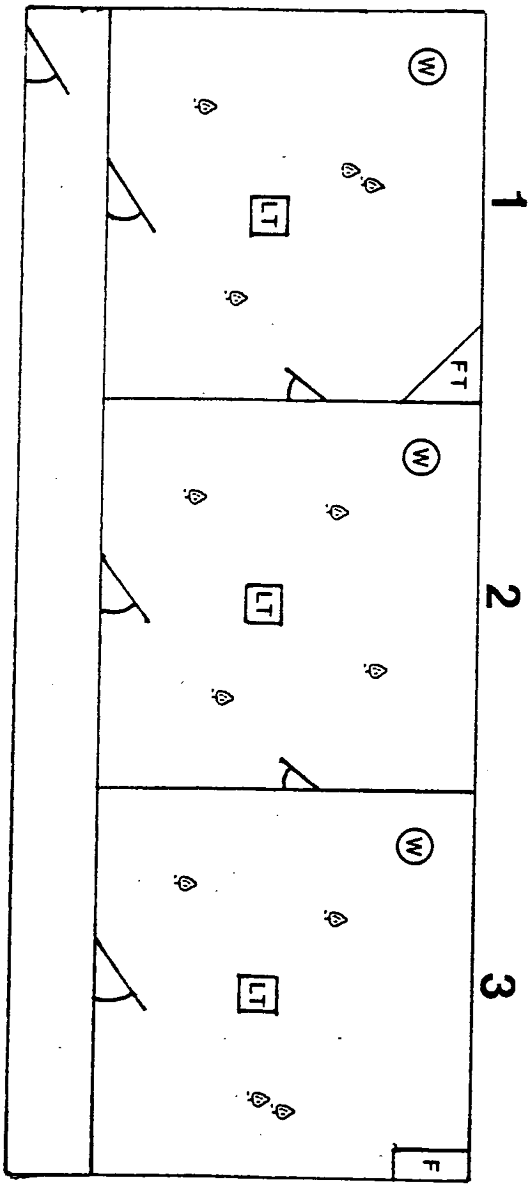
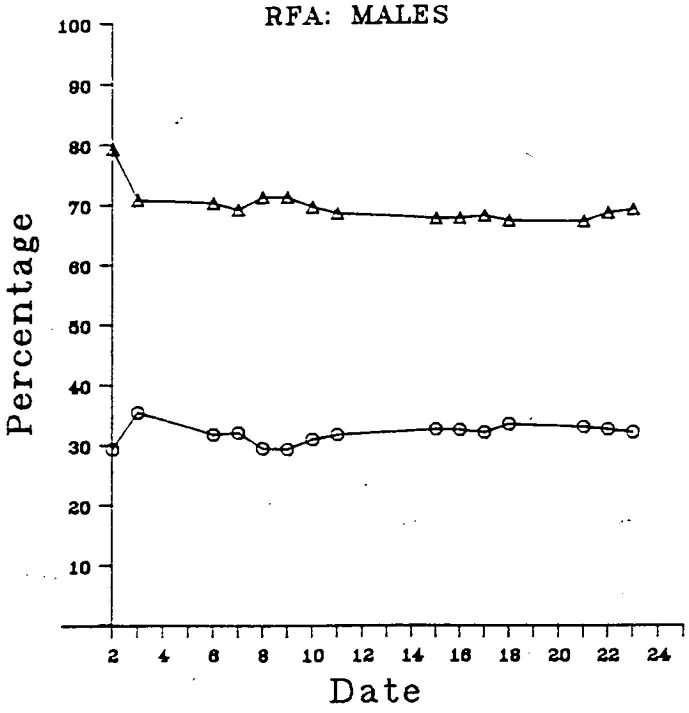
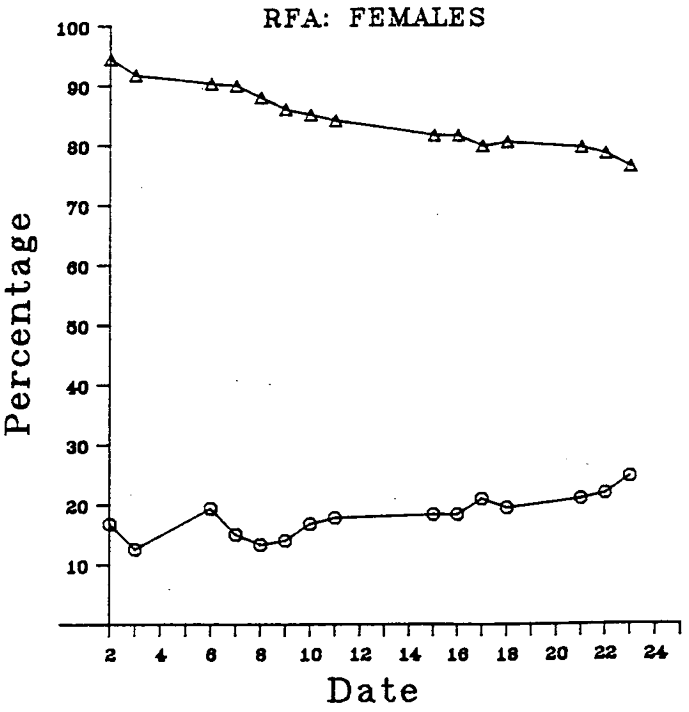


Fig. 7.1. Plan view of the aviaries.

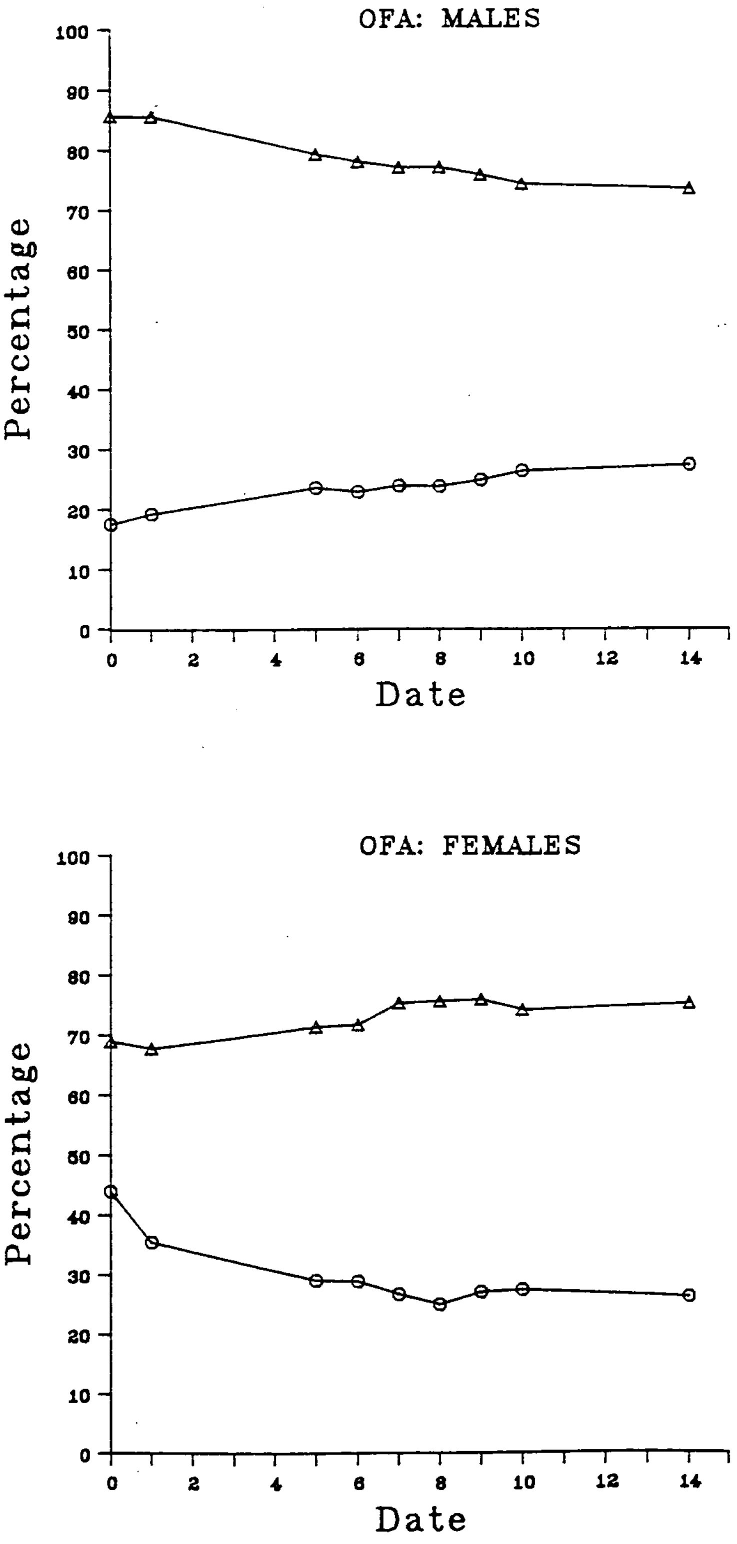


DAY	n
2	48
3	133
6	215
7	301
8	399
9	496
10	581
11	626
15	713
16	752
17	801
18	847
21	885
22	942
23	987



DAY	n
2	18
3	24
6	31
7	60
8	75
9	86
10	101
11	107
15	114
16	114
17	124
18	128
21	133
22	141
23	149

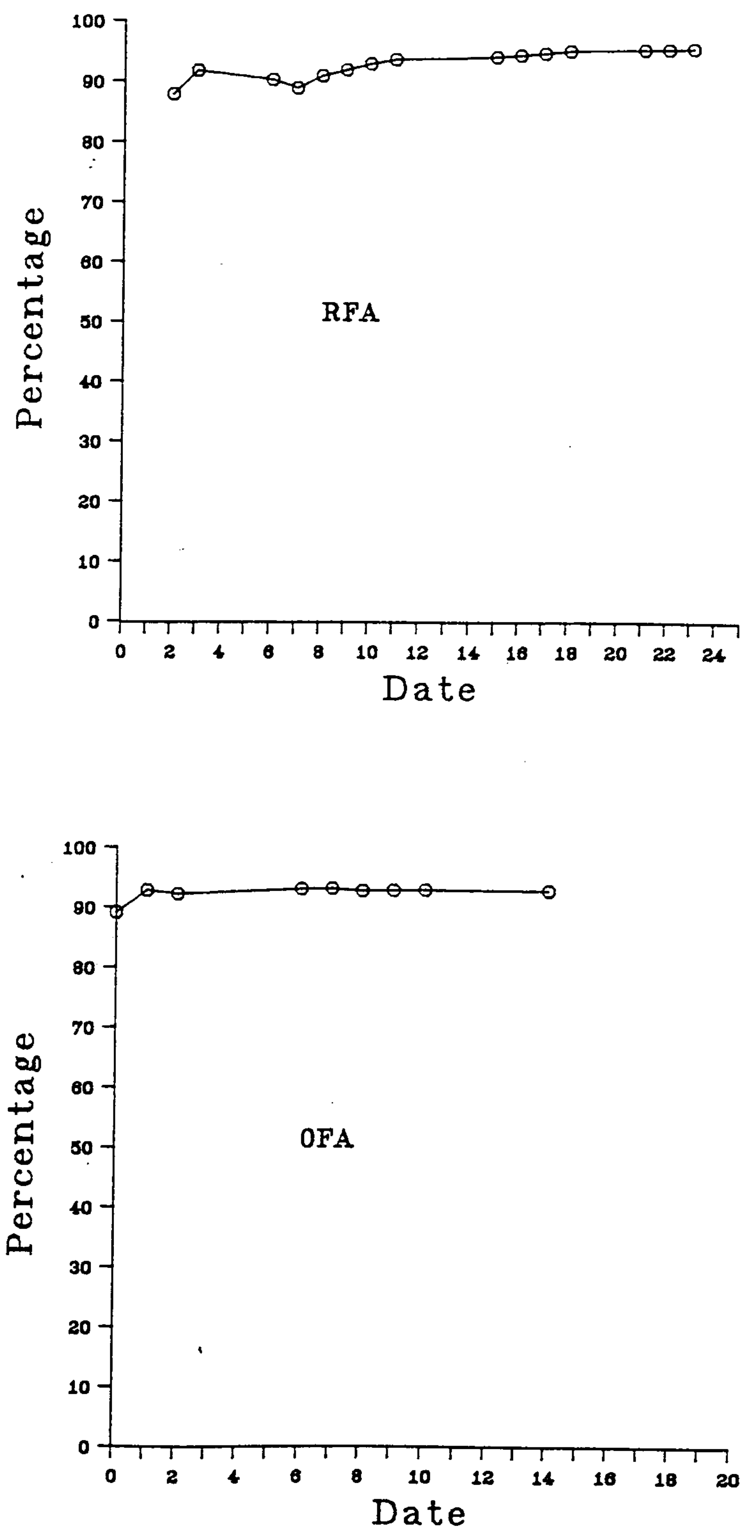
Fig. 7.2. Percentage of intrasexual interactions won by overall dyadic dominants (triangles) and percentage of outcomes that reverse the cardinal index rank order (circles), for both sexes, under RFA conditions. Data for the resident flock in Experiment 1 between 2/11 and 23/11/88. Cumulative sample of interactions on which each day's datum is based is given on the right.



DAY	n
0	132
1	173
5	299
6	335
7	372
8	415
9	473
10	511
14	536

DAY	n
0	16
1	34
5	59
6	63
7	72
8	77
9	86
10	92
14	96

Fig. 7.2. continued. Percentage of intrasexual interactions won by overall dyadic dominants (triangles) and percentage of outcomes that reverse the cardinal index rank order (circles), for both sexes under OFA conditions. Data for the resident flock in Experiment 1 between 31/10/88 (day 0) and 14/11/88. Cumulative sample of interactions on which each day's datum is based is given on the right.



DAY	n
2	49
3	96
6	151
7	284
8	396
9	492
10	572
11	640
15	707
16	745
17	787
18	844
21	900
22	938
23	975

DAY	n
0	49
1	90
5	165
6	190
7	218
8	246
9	288
10	317
14	336

Fig. 7.3. Percentage of intersexual interactions won by overall dyadic dominants under RFA (upper) and OFA (lower) conditions. Data for the resident flock in Experiment 1 between 31/10/88 (day 0) and 23/11/88. Cumulative sample of interactions on which each day's datum is based is given on the right.

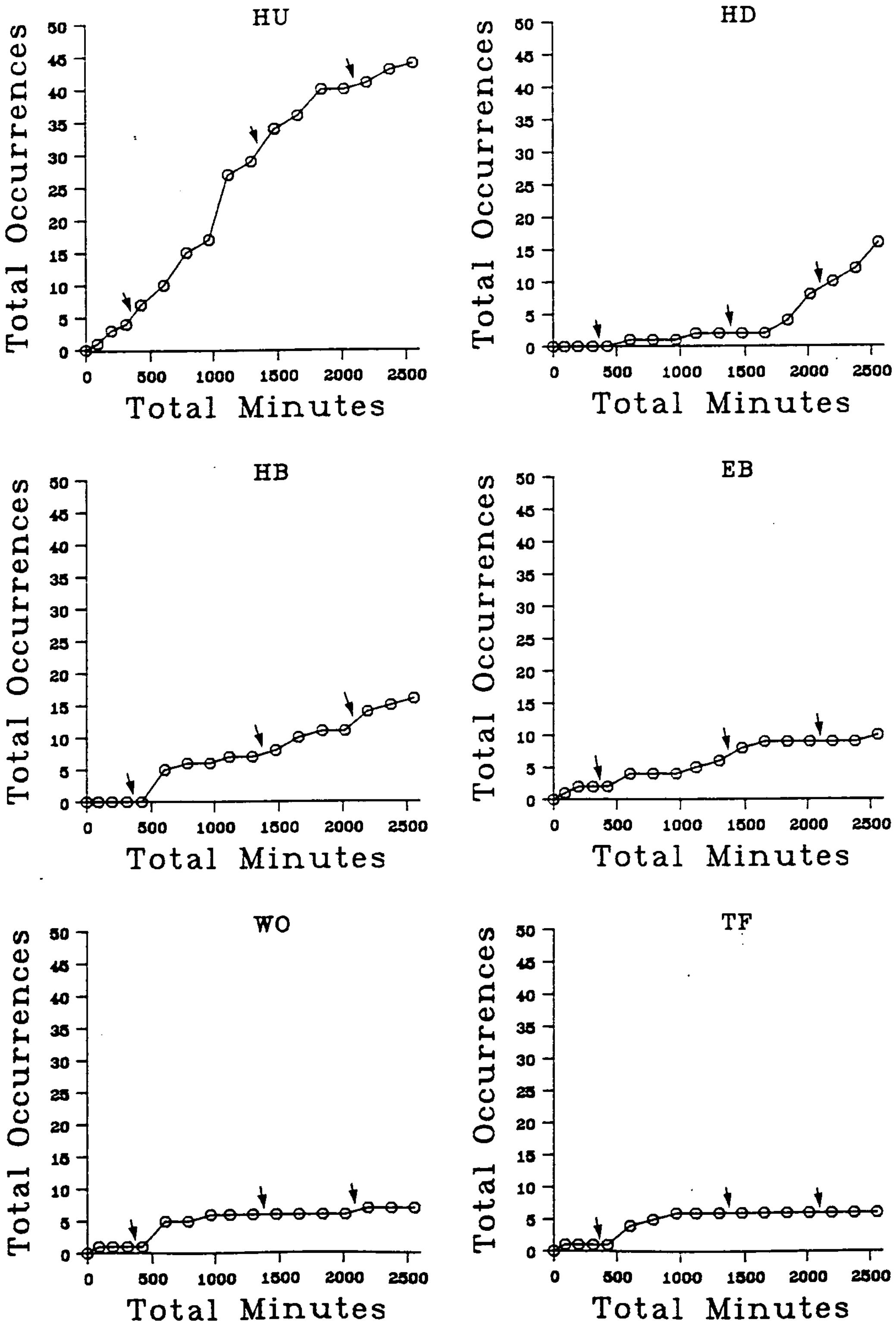


Fig. 7.4. Cumulative plot of number of occurrences of display elements versus observation time, under RFA conditions, for the resident flock in Experiment 1, between 2/11/88 and 23/11/88. All interactions pooled. Arrows mark lines connecting non-successive observation days.

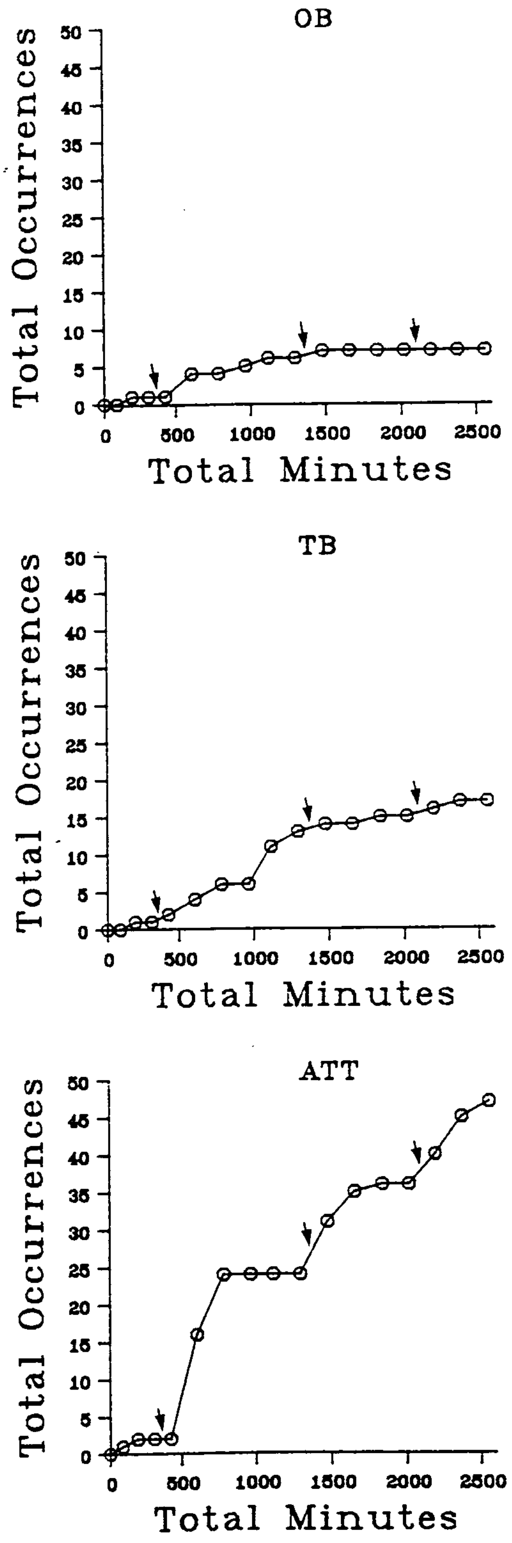


Fig. 7.4. continued.

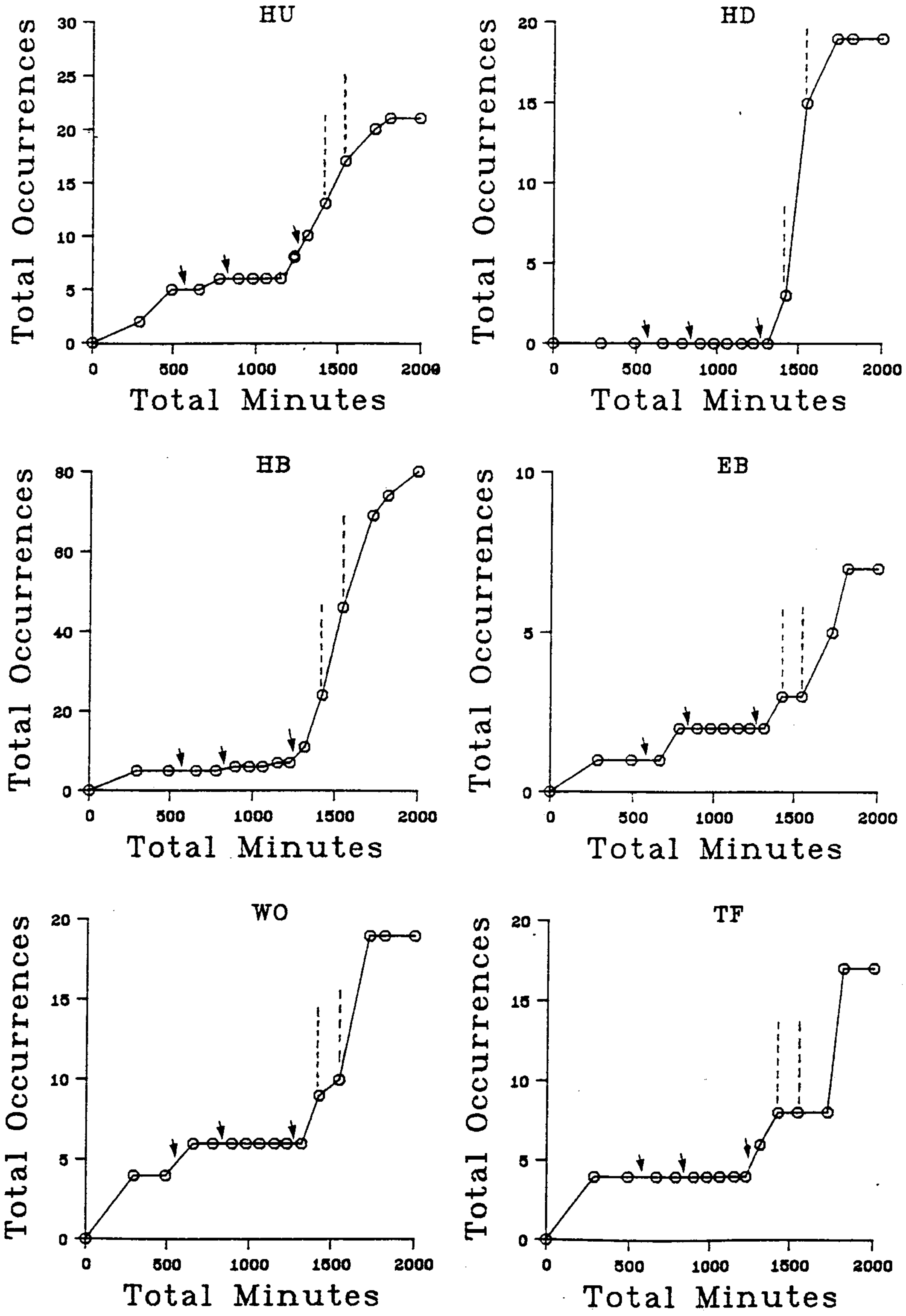


Fig. 7.5. Cumulative plot of total number of occurrences of each display element versus total observation time, under OFA conditions, for the flock in Experiment 1, between 31/10/88 and 12/12/88. All interactions pooled. Arrows mark lines connecting non-successive observation days. Vertical lines mark days on which birds were introduced to the resident flock (30/11/88 and 7/12/88).

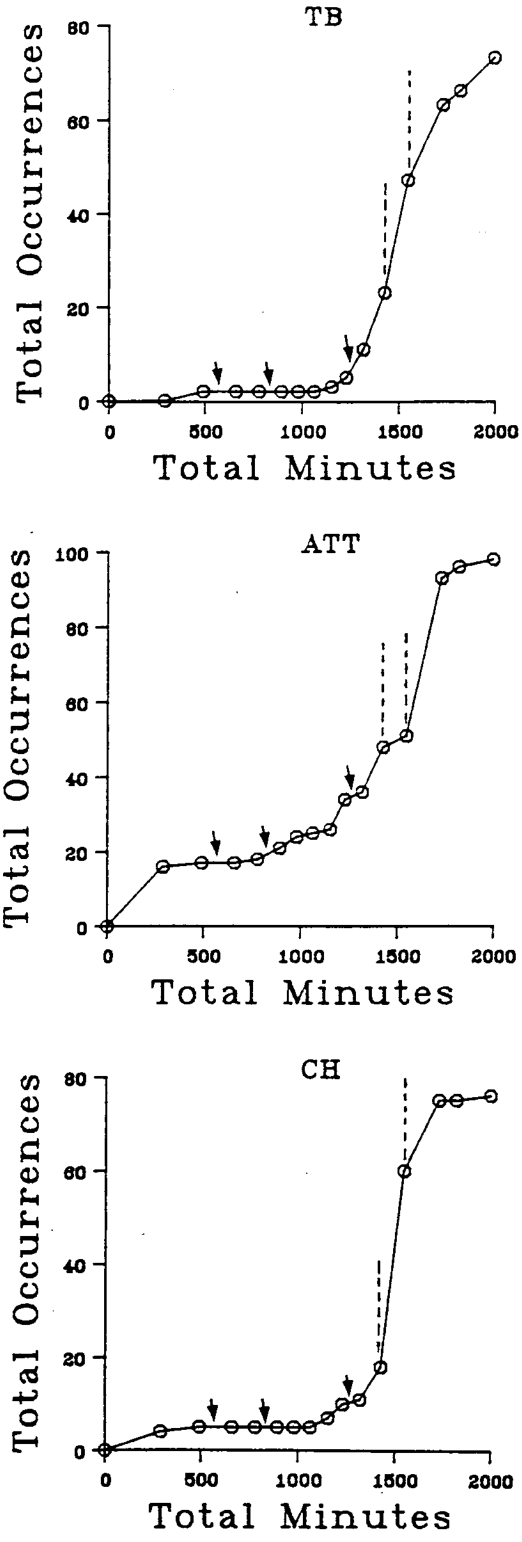


Fig. 7.5. continued.

Diet of Great Tits maintained in captivity

FOOD MASH

0.5 litres	Dry mixture*
1	Hard-boiled egg
1 tablespoon	Cod-liver oil
6 drops	Multi-vitamin solution
Water to moisten	

DRY MIXTURE*

6 parts	Ground dog biscuit
2 parts	Layers mash (poultry feed)
1 part	Wheatgerm
1 part	Ground dried meat
Handful	Mixed millet and sunflower seed

A few mealworms provided every few days to ensure the birds' continued familiarity with live prey.

TABLE 7.1. Recipe of food mix used to maintain great tits in captivity.

Dates	Data Collection Regime	Introduced Birds	Light:Dark Ratio
31/10/88 to 1/11/88	OFA	None	10.5h : 13.5h
2/11/88 to 10/11/88	RFA (am) OFA (pm)	None	10.5h : 13.5h
11/11/88	RFA (am)	None	10.5h : 13.5h
14/11/88	OFA (pm)	None	10.5h : 13.5h
15/11/88 to 18/11/88	RFA (am)	None	10.5h : 13.5h
21/11/88 to 23/11/88	RFA (am)	None	10.5h : 13.5h
30/11/88	OFA	BBR / BR	10.5h : 13.5h
7/12/88 to 8/12/88	OFA	BBL / BL	10.5h : 13.5h
9/12/88 to 12/12/88	OFA	BBL	10.5h : 13.5h
15/12/88 to 18/12/88	RFA (am)	BBL	14.5h : 9.5h
19/12/88	RFA (am) OFA (pm)	BBL	14.5h : 9.5h
20/12/88	OFA	BBL	14.5h : 9.5h
21/12/88	RELEASE		

TABLE 7.2. Data collection regime for Experiment 1.

	OOL	SSR	GGR	GGL
Observed Runs	111	116	236	179
Expected Runs	103.99	117.20	269.66	200.88
p (one-tailed)	0.115	0.435	0.002	0.014
n	366	237	564	402

TABLE 7.3. One-sample runs tests for randomness in the sequence of 'wins' and 'losses' in the intrasexual interactions of four males under RFA conditions in Experiment 1. Sequences of interactions for all data collection days from 2/11/88 to 23/11/88 inclusive were concatenated prior to analysis. Points of concatenation in the overall sequence are always treated as the end of a run to prevent the creation of spurious runs containing data from successive observation sessions.

MALE : OOL

PREVIOUS INTERACTION

			LOST	LOST	WON	WON
		Result:	LOST	LOST	WON	WON
		Opponent:	SAME	DIFF.	SAME	DIFF.
CURRENT INTERACTION	Lost	O	9	5	21	27
		E	5.42	5.42	25.24	25.92
		%	-	-	-	-
	Won	O	23	27	128	126
		E	26.58	26.58	123.8	127.1
		%	-	-	-	-

TOTAL X^2 = 3.80, DF = 3. p = NS

MALE : SSR

PREVIOUS INTERACTION

		Result:	LOST	LOST	WON	WON
		Opponent:	SAME	DIFF.	SAME	DIFF.
CURRENT INTERACTION	Lost	O	32	48	19	36
		E	31.33	43.86	25.06	34.75
		%	-	-	-	-
	Won	O	23	29	25	25
		E	23.67	33.14	18.94	26.25
		%	-	-	-	-

TOTAL X^2 = 4.45, DF = 3. p = NS

TABLE 7.4. Association between the outcome of each interaction and the outcome and opponent of the immediately preceding interaction. Analysis based on the same data set as Table 7.3. O = Observed, E = Expected. % = percentage of total X^2 value contributed by each cell in the contingency table. These values are not given where the total X^2 value shows no significant difference from the null hypothesis of no association. Continued overleaf.

MALE : GGR

PREVIOUS INTERACTION

CURRENT INTERACTION

	Result: Opponent:	LOST SAME	LOST DIFF.	WON SAME	WON DIFF.
Lost	O	126	100	39	76
	E	105.2	98.55	60.46	76.79
	%	13.83	0.07	25.61	0.03
Won	O	48	63	61	51
	E	68.80	64.45	39.54	50.21
	%	21.15	0.11	39.16	0.04

TOTAL $X^2 = 29.74$, DF = 3. $p < 0.001$

MALE : GGL

PREVIOUS INTERACTION

CURRENT INTERACTION

	Result: Opponent:	LOST SAME	LOST DIFF.	WON SAME	WON DIFF.
Lost	O	84	48	43	41
	E	67.16	51.04	46.21	51.58
	%	28.75	1.23	1.52	14.78
Won	O	41	47	43	55
	E	57.84	43.96	39.79	44.42
	%	33.38	1.43	1.76	17.16

TOTAL $X^2 = 14.69$, DF = 3. $p < 0.01$

Element	19/12/88	20/12/88 am	20/12/88 pm	Total
HU	0	1	3	4
HD	0	1	0	1
HB	2	4	5	11
EB	0	0	0	0
WO	0	0	0	0
TF	0	0	0	0
OB	0	1	0	1
TB	2	5	6	13
ATT	2	2	0	4
CH	23	35	9	67
Observation Time OFA	90 mins.	90 mins.	90mins.	270 mins.

TABLE 7.5. Number of occurrences of behaviour elements during 270 minutes of observation, in high light/dark ratio conditions. Flock had six days prior acclimatisation to the 14.5h light : 9.5h dark daily cycle. All interactions pooled.

Element	Control	'Neutral'	'Asymmetric'
HU	0.89 (8)	5.33 (32)	10.67 (64)
HD	0.11 (1)	0.17 (1)	1.33 (8)
HB	0.67 (6)	1.50 (9)	5.50 (33)
EB	0.22 (2)	0.33 (2)	1.83 (11)
WO	0	0.17 (1)	0
TF	0	0	0.33 (2)
OB	0	0	0.33 (2)
TB	0.78 (7)	3.33 (20)	8.83 (53)
ATT	0.89 (8)	0.50 (3)	1.17 (7)
CH	0	1.50 (9)	1.00 (6)
Observation Time	540 mins.	360 mins.	360 mins.

TABLE 7.6. Frequency of performance (per hour) of behaviour elements in Experiment 2, under control, 'neutral' and 'asymmetric' conditions. Raw data given in parentheses. All interactions pooled. See text for further explanation.

Element	F > F	N > F	F > N	N > N	Total	X^2	p
HU	29 (52.22)	23 (20.89)	42 (20.89)	2	96	31.87	<0.001
HD	4 (5.00)	2 (2.00)	3 (2.00)	0	9	0.70	NS
HB	6 (23.33)	12 (9.33)	24 (9.33)	0	42	36.67	<0.001
EB	3 (6.67)	1 (3.17)	8 (3.17)	1	13	10.89	<0.01
WO	1	0	0	0	1	-	-
TF	0	1	1	0	2	-	-
OB	1	1	0	0	2	-	-
TB	18 (40.00)	21 (16.00)	33 (16.00)	1	73	31.73	<0.001
ATT	3 (5.00)	0 (2.00)	6 (2.00)	1	10	10.80	<0.01
CH	5 (8.33)	0 (3.33)	10 (3.33)	0	15	17.99	<0.001
Number of dyads	15	----12----		1	28		

TABLE 7.7. Distribution of performances of behaviour elements across the four categories of 'flock member' (F) and 'newcomer' (N). All interactions from 'neutral' and 'asymmetric' experimental conditions are pooled. The distribution of each element across the F>F, N>F and F>N categories is compared with null expectation (see text) using a chi-square test. Expected values are given in parentheses. Note that several expected values are less than 5. Total X^2 and p-values for each test are given in the right-hand columns.

CHAPTER 8.

SUMMARY AND GENERAL DISCUSSION.

Interference competition over resources is an important facet of social organization in many taxa and also provides one of the most fruitful sources of data for investigating the evolution, functions and mechanisms of the communicative behaviour of animals (e.g. Huntingford & Turner 1987).

Communication during conflicts of interest over a resource (agonistic behaviour - Scott & Fredericson 1951), whether it be food, a mate or a nest site, often utilizes behaviour patterns which have become ritualized from non-signal function by exaggeration, stereotypy and repetition (Tinbergen 1952) to increase the efficiency with which an animal is able to influence the behaviour of another with which it is in sensory contact. These 'displays' have long attracted the attention of ethologists interested in explaining their evolution (e.g. Morris 1956; Tinbergen 1952), causation (e.g. Blurton Jones 1968) and function (e.g. Caryl 1979; Cullen 1966; Krebs & Dawkins 1984; Maynard Smith 1982b; Smith 1977; Stokes 1962a; Wiley 1983). However, the recent growth of behavioural ecology (Krebs & Davies 1987), and particularly its applications of game theory (Maynard Smith 1982a) and optimality theory (Krebs & McCleery 1984) have led functional studies of agonistic communication away from proximate processes such as information transfer and motivational change. Instead, the function of communicative behaviour is viewed in terms of ultimate fitness payoffs of alternative options, taking into account their dependence on the options adopted by other members of the population. As Enquist (1985) puts it, "it is treated as axiomatic that the ultimate purpose" (of agonistic communication) "is to win or defend a resource" (where a resource is anything which has the potential to contribute to reproductive success) "and not to communicate per se."

Clearly, any advance towards a functional understanding of the behaviour by which conflicts of interest between animals are resolved requires explanations at both proximate and ultimate levels (Tinbergen 1963). The ultimate function of agonistic behaviour can only be couched in terms of reproductive success and fitness gain. This may explain why animals compete over limiting resources, but it doesn't explain why one great tit is consistently dominant over another at a peanut feeder, or why certain types of agonistic behaviour are used as opposed to others. These explanations lie at the other end of the scale in changes in the internal state of the competing animals. These in turn depend on changes in both internal and external stimuli, the physical and behavioural properties of the opponent being pre-eminent amongst the latter. Maynard Smith & Riechert's (1984) study of the agonistic behaviour of a funnel-web spider is a rare example of a study which models the use of behavioural options on the basis of fitness gains and losses, but recognizes that these processes are mediated by internal (motivational) changes in competing animals that are responding to proximate cues such as body size.

As yet, 'ultimate function' approaches to agonistic behaviour (e.g. Archer 1988, Chs. 9–10) have addressed themselves to the question of which variables might be relevant in determining the outcome of individual interactions, and what might be the evolutionary constraints on their signalling (Chapters 1 & 6). However, only a few (e.g. Nelson 1984) have attempted to relate particular elements of the agonistic behaviour repertoire to communication about particular 'outcome-relevant' variables.

The great tit is a species whose agonistic behaviour is well described (Hinde 1952) and studied at the level of immediate causation (Blurton Jones 1968), and the display repertoire can be observed easily in birds competing over resources in the wild. Great tits are easily caught in mist-nets at bait, and colour-ringing provides an effective way of following the lives of particular individuals. Previous work (De Laet 1984; Drent 1983; Garnett 1976; Jarvi & Bakken 1984; Saitou 1978, 1979a,b,c) has suggested that a variety of physical and experiential factors may combine to determine the outcome of agonistic interactions between great tits, and that these outcomes may have important fitness consequences over and above those contingent on the value of the resource under immediate competition (Drent 1983). Finally, the demography of great tit populations ensures that a study population will contain individuals representing the full range of variation in these factors.

The great tit thus provided an ideal subject for a study designed to add to a functional understanding, at a proximate level, of the diversity of agonistic behaviour to be found within a single species.

CHAPTER 3 found that most aspects of the population ecology of the great tits at Ormiston Hall corresponded closely with those of populations studied elsewhere in Britain and Europe. What minor differences did exist were probably a consequence of the very mild winter weather conditions that were experienced in comparison with those in which most other studies of wintering parids have been undertaken. Thus, observed dispersal distances were very small and there was no evidence that winter conditions were a major agent of dispersal or mortality in the population. Similarly, body weight analyses showed no effect of current or preceding air temperature, a result only obtained in other studies when winter conditions were exceptionally mild by local standards (e.g. Haftorn 1976). Although not quantified, casual observations of flocking behaviour suggested that the permanency and coherence of tit flocks at Ormiston Hall was much lower than that in most other studies. Again, mild winter conditions and relatively abundant food may largely explain this discrepancy, a suggestion supported by the findings of one study of black-capped chickadees *Parus atricapillus* (Desrochers *et al* 1988).

An analysis of the correlates of dominance in dyadic interactions between great tits in **CHAPTER 4** yielded results comparable with those of other studies of social organization in this species (De Laet 1984; Drent 1983; Saitou 1978, 1979 a,b,c). Males were almost always dominant over females and, within the sexes, the primary dominance correlates were prior territoriality and length of prior residence. These correlations were stronger in males than in females. Body size was a negligible correlate of dominance between males, but there was a weak tendency for larger females to be dominant over smaller females within age classes.

Winter social status was found to be site-related in all age-sex classes, varying in some cases over distances of a few tens of metres. In adults, social status and frequency of occurrence (an index of proximity to the centre of the bird's home range) tended to be higher, the nearer the site of observation was to the area of the former breeding territory. In first-year birds, social status was positively correlated with frequency of occurrence at the site of observation. These results contrast with those of a study of site-related dominance in a European great tit population, in which social status only increased with proximity to the centre of the home range in adult males (De Laet 1984).

The distinction between spatially abrupt and spatially gradual ('site-correlated') changes in dominance relationships between birds is considered to be an important problem in understanding how birds perceive their spatial world in a social context. Are all spatial changes in individuals' relationships gradual outwith the seasonal establishment of breeding territories, or are bounded areas of social dominance a characteristic of the social organization of great tit populations throughout the year? The only data bearing on this point implied that at any one site, most intrasexual dyadic dominance relationships were highly asymmetrical and became almost peck-right between frequently meeting birds. If dominance relationships tended to change in a 'site-correlated' way then we might have expected a higher proportion of 'ambiguous' relationships with the overall dominant only winning 50-70% of all interactions. The suggestion is that site-related changes in the direction of dominant - subordinate asymmetries between two birds of the same sex reverse abruptly at definite boundaries or, at least, over very narrow zones of change. This interpretation has also been made, independently, for a winter population of black-capped chickadees (Desrochers & Hannon 1989) and has considerable implications for the ability of great tits to adjust their agonistic behaviour according to both the location and *individual identity* of their opponent.

Winter social status and frequency of occurrence are assumed to be mutually reinforcing, as was found by Drent (1983). They were positively correlated with both the probability that a male would successfully establish a local breeding territory in the following spring and with the proximity of that territory to the site of observation. In females, high local social status and site attachment were positively related to the probability of being the mate of a local territory holder.

However, the correlations were weaker and the possibility of pairing at any stage during the winter may mean that pairing status was actually the determinant of social status rather than *vice versa*.

This positive feedback loop between prior residence / prior territoriality, winter social status and future territorial status is an important finding. Dhondt & Schillemans (1983) have shown that establishment of breeding territories is crucial for successful reproduction. If territory establishment is, in turn, dependent on a high local social status during the preceding winter, then there may be long-term fitness consequences of success or failure in any given agonistic interaction that extend far beyond priority of access to the immediately contested resource. This may be particularly important in first-year males which are not established on former breeding territories. To suggest that females may be competing only for peanuts whereas males are competing for the chance of leaving offspring is perhaps extreme but does emphasize that there may be considerable individual variation in the importance ('resource value') attached to dominance in an agonistic interaction.

CHAPTER 5 was a specific study to assess the functional significance of the black ventral stripe in agonistic communication. This plumage feature is widely quoted as an example of the use of an arbitrary, cost-free 'badge' as a signal of social dominance within age-sex classes (e.g. Huntingford & Turner 1987), whose evolution is expected to be subject to severe constraints due to the susceptibility of cost-free signalling to evolutionary 'invasion' by bluff signalling strategies (e.g. Maynard Smith & Harper 1988). The most important conditions for the evolution of badge signalling are that the value of the contested resource be trivial relative to the cost of a physical fight, and that the competing individuals be sufficiently unfamiliar with each other as not to know each other's true fighting abilities. However, the social organization of great tit populations and the results of Chapter 4 would suggest both that individual recognition is likely to occur, and that it may be rare for the outcome of an intrasexual interaction to be 'trivial', especially between males. In addition, previous studies of status signalling in great tits have been flawed either in method (Jarvi

& Bakken 1984) or interpretation (Jarvi *et al* 1987b).

This study's conclusions were that stripe size is independent of body size and is a weak but significant positive correlate of dominance between females across most contexts of interaction. However, stripe size failed to correlate with the outcome of male - male interactions. The importance of stripe size in female - female interactions may have been under-estimated because the more stripe-asymmetric dyads were under-recorded at feeder sites, implying the perception of stripe size asymmetries at a distance and the avoidance of large-striped females by small-striped individuals of the same sex. These results correspond with proposed differences between the sexes in the resource value attached to contest outcomes. They also provide an interesting contrast with the results of Harper *et al* (in press) who found strong, positive correlations between stripe size and dominance in males at a feeder sites *outside* the territorial system of a breeding population. In this context, more of the dyads may have been between mutually unfamiliar birds drawn into bait from disparate home range areas. In addition, the likelihood of incipient territorial conflicts between competing males may also have been much reduced due to the occurrence of these interactions in habitats unsuitable for breeding.

The general conclusions are that ventral stripe size of great tits may have an agonistic signal function in certain contexts and between certain classes of individuals. However, more significant selection pressures on the evolution of plumage 'badges' may be brought to bear through sexual selection during the breeding season as a result of their involvement in mate choice processes (e.g. Norris pers. comm.), as has been found to be the case in other species (e.g. Moller 1988).

Future studies might profit by considering the physiological basis of variation in stripe size in great tits; for example by investigating the effects of prior agonistic experience and its hormonal correlates on changes that occur during moult.

After a review of the taxonomic diversity of passerine postural display elements and a consideration of the evolutionary constraints on the signalling of different variables, **CHAPTER 6** described the range of postural elements, and 'compound displays' made up of those elements, that are to be seen in great tits. This introduced a study whose aim was to associate elements of the display repertoire with those physical and experiential attributes of the birds that were found to be correlated with contest outcome (Chapters 4-5). Unfortunately, sample sizes were too small to allow the compound displays to be used as higher order units of agonistic behaviour. Instead, correlations of display use with outcome - relevant variables had to be made for each element independently, interpreting the results in the light of those associations that had been found to exist.

Although interactions between males were much more frequent than expected (see also Barkan *et al* 1986) at feeders, (perhaps due to the importance of dominance *per se* as a fitness correlate) and those between females much rarer, all display elements except HU were more frequent, per interaction, between females than between males. Most intersexual interactions were simple supplants. These results may be due to the greater number of variables relevant to the outcome of female - female interactions, thus requiring a greater degree of mutual assessment using display. Such an interpretation is supported by the fact that females showed a greater tendency to display or attack than to supplant, the closer the opponent was in social status to themselves. These correlations did not hold for males. In addition, mutual familiarity between females may have developed more slowly than between males, due to the lower frequency of interactions in the former. This would also imply a greater need for mutual assessment in interactions between females.

Correlates of display use suggested that the elements fell into two categories with respect to function. The results and their interpretation are too extensive to be summarized again here. However, WO, TF and OB (category (i)) were hypothesized to be elements of cost-independent, bluff-sensitive 'threat', carrying no more information to the opponent than "I want this resource". HU, HD, HB and TB (category (ii)) were hypothesized to convey information about prior residence and site attachment. Unlike the other elements in this category, HU was usually performed by males and was especially characteristic of conflicts between males over territorial space. EB may not be a true element of the ritualized repertoire.

If category (ii) elements do convey information about prior residence, then they may be cost-correlated in that they reflect the bird's previous success in numerous, costly (and risky) agonistic encounters. If prior agonistic experience is causally linked to the elicitation of these displays via a physiological mechanism such as hormone levels, then category (ii) displays may be seen as costly, bluff-resistant signalling systems, not subject to the same evolutionary constraints as the elements in category (i). Other studies exist (e.g. Ramenofsky 1984) which show the effect of hormone levels on aggressive behaviour, and a study of the physiological correlates of the elicitation of different display elements in the great tit would be an interesting undertaking. The hypothesis is also interesting in that it suggests that birds are effectively signalling *previously experienced costs* as a reliable, bluff-resistant indicator of ability and willingness to win, as opposed to bluffable signalling of *current* aggressiveness, as proposed by Enquist *et al* (1985) and Popp (1987a,c, 1989).

Stripe size and body size failed to correlate with the use of any display element, perhaps due to the fact that these are morphological characteristics that are potentially directly perceptible by competing birds and may not be under such strong selection pressure for amplification by ritualized display. In addition, these selection pressures may also be weakened by the fact that these variables are only relevant to the outcome of contests between certain classes of individuals (body size) and in certain contexts (stripe size).

The incidence of plumage postures in the great tit display repertoire was also discussed, although no rigorous analyses had been undertaken. The probable ritualization from autonomic, thermoregulatory and flight-readiness responses was discussed by Morris (1956). The tendency to use postures such as CR, CF, and NR by great tits in social situations indicates that they serve a signal function, just as restriction of the pilomotor responses to specific areas of the body suggests that ritualization has taken place and that they can no longer be performing their primary function. Crest-raising also occurs in 'non-signal' situations when birds are alone. This observation implies that this plumage posture may still be to some extent an autonomic response which has lost its original function but is still a direct response to underlying stimuli. However, another possibility is that, as a signal of submission, continuous crest-raising by subordinate birds might reduce the probability of receiving aggression from an arriving conspecific, thereby allowing the bird to divert time that would otherwise be spent in vigilance for dominant conspecifics, to foraging. The use of crest-raising by tits in relation to concurrent behaviour and social status is a subject worthy of further investigation.

In **CHAPTER 7**, it was shown that studies of display use by groups of captive great tits provided considerable experimental evidence to support the hypothesized two-way classification of the function of display elements, as set out in Chapter 6. Thus WO, TF and OB tended only to be performed in situations where birds were mutually unfamiliar and their incidence waned rapidly as a flock became established. By contrast, category (ii) displays were performed throughout the period of observation of a flock, as would be expected if aviary conditions reflected continuous site attachment conflicts which could not be resolved by dispersal and the development of site-related dominance. Marked increases in the use of category (ii) displays were seen when unfamiliar birds were introduced to an established flock. These displays were seen almost entirely in interactions between established birds and newcomers, as would be expected on the basis of the acute asymmetries in prior residence involved in those interactions. However, this effect was only seen if the introduction took place in the *home aviary* of the established flock. In a 'neutral' aviary, the effect of the introduction on the frequency of agonistic display was relatively minor, indicating that it was prior residence asymmetries and site attachment (i.e. the recognition of the newcomer as an 'intruder') that were primarily responsible for the elicitation of display directed at unfamiliar birds. Introduced birds remained low in rank but the incidence of escalated interactions involving them dropped to pre-introduction levels within a few days. All these results suggest that individual recognition was a very important aspect of social relationships between captive great tits and, hence, it may be equally important, though less easy to demonstrate, in wild populations. Perfect individual recognition is perhaps the reason why display of any kind was much rarer under aviary conditions than in the wild.

The hypothesis that intrasexual dyadic dominance relationships and dominance hierarchies constructed from them should be less clear-cut in aviary conditions than in the wild, due to the failure of incipient dominant - subordinate asymmetries to be consolidated by dispersal and site-related dominance, was supported in both sexes. However, it is recognized that other aspects of aviary conditions such as the spatial and temporal availability of food resources may be affecting the results obtained. Intersexual dominance relationships still showed an almost complete dominance of males over females, perhaps because the relevant asymmetries in this case are physical rather than spatial.

A final point refers to the importance of subtle, non-ritualized actions as predictors of the outcome of interactions between individuals with intimate mutual knowledge. Van Rhijn & Vodegel (1980) predicted and Bossema & Burgler (1980) showed (in jays *Garrulus glandarius*) that a subtle movement of aggressive intent (in this case, monocular as opposed to binocular looking at the opponent) was sufficient to elicit submission in the opponent. Clearly, costless and bluff-sensitive signals such as these can only be functional in contexts where mutual knowledge is so complete (as in Bossema & Burgler's established groups of five jays) that bluff would be impossible. Without any quantitative data yet analysed to back up my assertion, I am confident that very similar forms of communication were leading to the resolution of many of the 'supplants' and 'avoidances' seen in the aviary groups of great tits. I hope to test this hypothesis in the near future by examining the sequelae of head and body orientation in competing great tits, during interactions recorded on videotape, under both field and aviary conditions.

This study has shown that to have any chance of predicting the agonistic behaviour of a great tit and the outcome of its interaction with a conspecific, a wealth of information about the physical, social, experiential and physiological attributes of the competing birds, the resource under competition, and the location and timing of the interaction, are required. This complex of causal factors can be seen as determining behaviour and outcome via its effect on two, proximate, conflicting internal tendencies which might be labelled 'aggression' and 'fear' (e.g. Blurton Jones 1968; Maynard Smith & Riechert 1984). On its own, however, a proximate model of the causation of agonistic behaviour is of little explanatory assistance to a functional study since to say that display X demonstrates the predominance of aggression over fear tells us nothing about the diversity of causal factors further back along the causal chain. For example, Blurton Jones' (1968) study of the success of the two-tendency conflict hypothesis in accounting for the proximate causation of agonistic display in the great tit does not even distinguish the sexes of the interacting birds, let alone the range of factors relevant to the explanation of agonistic behaviour that have been discussed above. This diversity creates such individual to individual variation in agonistic behaviour that it is only through a knowledge of the history of known individuals that it is possible to reach some functional understanding at a proximate level. The need to take into account individual-level phenotypic variation in explaining higher order processes such as foraging behaviour (e.g. Evans 1988; Partridge 1976), population dynamics (e.g. Sibly & Smith 1985) or the evolution of breeding behaviour (e.g. Clutton-Brock 1988) has been appreciated. The same need applies to understanding and explaining the agonistic behaviour of a species.

In asking whether sociobiology has "revitalized" ethology or "killed" it, Barlow (1989) points out that experimental manipulations of the variables that influence agonistic behaviour have rarely been undertaken as an aid to understanding the ethology of agonistic interaction. Within the passerines alone, there is a huge diversity of documented agonistic display (e.g. Cramp 1988), with a 'core' of postures (e.g. HU, HD, WO - Andrew 1961) of which variants occur across a wide range of taxa. In addition, detailed studies of many species have discovered those variables that influence the outcome of agonistic interactions and have related them to the ecology of the species concerned (e.g. Arcese & Smith 1985; Bekoff & Scott 1989; Bjorklund 1989; Drent 1983; Piper & Wiley 1989; Shawcross & Slater 1984). All that remains for species already known in this detail is for manipulations of those variables to be carried out, and any correlated changes in the agonistic behaviour of known individuals to be recorded. Data from studies of this kind would have great potential for providing explanations of the functions of displays (in terms of the variables they are signalling). A comparative study of the variation in the signalling functions of taxonomically widespread versus taxonomically restricted display elements would then shed light on the evolutionary history of agonistic displays. Functional studies of agonistic behaviour based on a knowledge of the behavioural and social ecology of the species and of individual histories open up many new opportunities for ethological research.

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ADDENDA

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APPENDIX 1. Notes on colour rings used during the study.

Single colours

RED (R)
BLACK (B)
LIGHT GREEN (G)
ORANGE (O)
PINK (P)
YELLOW (Y)
WHITE (W)

Stripes

BLACK/WHITE (BW)
RED/WHITE (RW)
PINK/GREEN (PG)

Combinations avoided

i) W or Y as upper colour ring due to merging with ventral feathers.

ii) BW/W, BW/B and B/BW - all three are confusing in the field.

Notes

i) P tends to fade to almost white over a period of months and the two colours become distinguishable in the field, only with extreme care. The same effect is reported with Y (G. Scott, pers. comm.).

ii) The R/O/Y/P end of the spectrum are all easily distinguishable in the field.

iii) Light blue was not used because it becomes difficult to distinguish from light green at distance. Similarly, both dark green and dark blue become indistinguishable from black at long ranges or in poor light.

iv) The use of RW and BW occasionally proved problematic. Possibly, a single stripe colour (e.g. BW) but with two stripe width variants would have been better, especially in poor light.

v) PG was occasionally difficult to distinguish from R in poor light.

APPENDIX 2. Monthly and yearly summaries of selected meterological data from Pathhead weather station, 55° 53'N 3° 52'W. All temperatures in °C. Figures in parentheses estimated from a max.-min. thermometer at the study site for months in which data was unavailable from Pathhead.

Year	Month	Mean Daily Min. Temp.	Mean Daily Mean Temp.	Days with air min. <0°C	Days with grass min. <0°C	Days of ice/snow cover
1985	SEP	8.8	12.5	0	0	0
	OCT	7.1	10.6	0	7	0
	NOV	0.2	2.7	13	22	3
	DEC	2.9	5.0	6	8	0
1986	JAN	-0.6	1.8	16	23	9
	FEB	-3.6	-1.1	22	24	24
	MAR	1.0	4.5	8	15	5
	APR	1.4	4.7	4	13	2
MEANS		2.2	5.1			
TOTALS				69	112	43
1986	SEP	6.6	11.3	1	7	0
	OCT	6.7	9.9	0	1	0
	NOV	3.8	7.0	4	9	0
	DEC	2.0	4.2	3	16	1
1987	JAN	-1.0	0.8	15	25	11
	FEB	0.8	2.7	12	18	6
	MAR	0.4	3.5	14	19	2
	APR	4.7	9.0	0	5	1
MEANS		3.0	6.1			
TOTALS				49	100	21
1987	SEP	7.9	12.3	0	1	0
	OCT	4.4	8.1	1	6	0
	NOV	3.2	5.9	4	10	1
	DEC	2.5	5.0	9	13	0
1988	JAN	1.3	3.7	6	19	1
	FEB	1.6	3.8	6	17	2
	MAR	1.6	4.8	9	17	1
	APR	3.4	7.6	6	12	0
MEANS		3.2	6.4			
TOTALS				41	95	5
1988	SEP	9.0	12.1	0	2	0

	OCT	6.2	9.3	2	8	0
	NOV	2.3	5.7	5	22	5
	DEC	4.4	6.9	0	14	0
1989	JAN	4.2	6.5	0	18	0
	FEB	2.7	5.6	3	-	0
	MAR	2.7	6.8	5	-	0
	APR	1.5	6.5	4	-	0
MEANS		4.1	7.4			
TOTALS				19	(88)	5

APPENDIX 3. List of statistical and other abbreviations used throughout the study.

Statistics

X^2 = chi-square

W = Statistic of MINITAB Mann-Whitney-Wilcoxon test

H = Statistic of Kruskal-Wallis test

t = Student's t

r_s = Spearman rank correlation coefficient

r = Pearson rank correlation coefficient

R^2 = coefficient of determination

Data

n = sample size

x = mean

SD = standard deviation

SE = standard error

u = median

p = probability that observed deviation of a distribution from null expectation could have arisen by chance.

NS = not significant; used to indicate any deviation of the observed distribution from null expectation that has a p-value of greater than 0.05. Other critical p-values are used in a few tests.

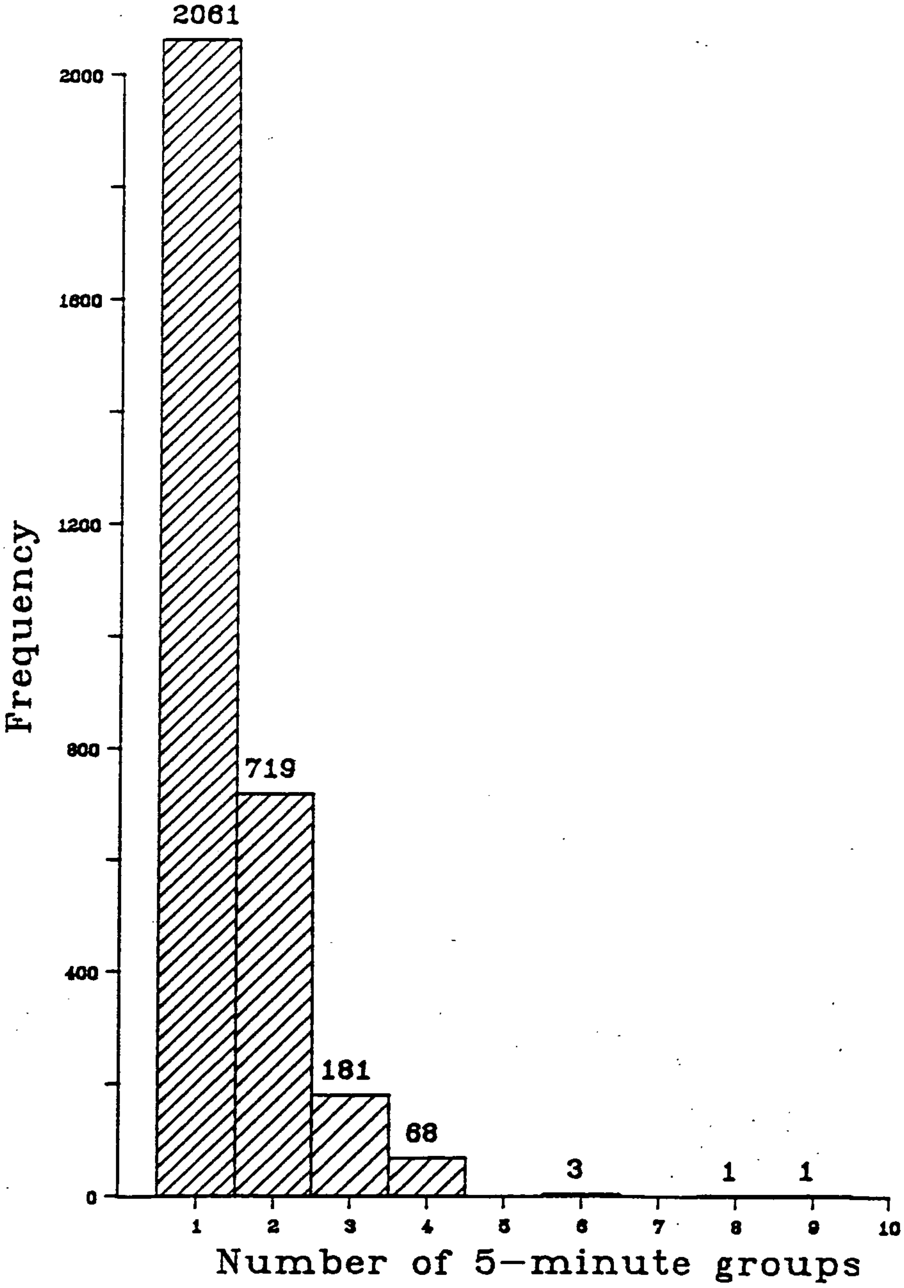
Miscellaneous

km = kilometres, m = metres, cm = centimetres, mm = millimetres

g = grams

h = hours

APPENDIX 4. Turnover of great tits at feeding stations during the 1987/88 winter. Data from all three sites pooled. X-axis = the number of consecutive five-minute intervals during which each bird recorded was present. 68% of all birds observed remained at a feeding station for less than five minutes. Less than 3% stayed for longer than 15 minutes.



APPENDIX 5. Correlations between two measures of frequency of occurrence of individual birds at feeding stations. Analysis is based on 1988/89 data from the Yew and Wood sites. The sexes are treated separately. Measure 1 = "percentage of observation days on which individual recorded". Measure 2 = "percentage of 5-minute groups in which individual recorded". The second measure is derived from the first by dividing each day's observation period into successive 5-minute intervals.

Site	Sex	r_s	n	p
Yew	Males	0.936	76	<0.001
Yew	Females	0.900	77	<0.001
Wood	Males	0.943	79	<0.001
Wood	Females	0.953	77	<0.001

APPENDIX 6. Cardinal index output files for male and female dominance hierarchies at each site, in each year. All indices are based only on interactions at feeders. The number of interactions whose outcome is a reversal of the overall hierarchical order produced by the program is also given. TS = territorial status in the following spring (Y = on breeding territory, N = not known to be on breeding territory). S = survival to next winter (Y = yes, N = no). TD = distance from site to centre of breeding territory (Chapter 4).

Garden 1986/87. Males.
Interactions = 233.
Reversals = 35.

Rank	Ring	Index	S	TS	TD
1	9024	1.92	N	Y	85.5
2	9055	2.94	N	Y	47.0
3	9094	3.03	N	Y	36.0
4	9090	4.33	N	Y	101.0
5	9065	4.66	Y	Y	463.0
6	9040	4.73	Y	Y	91.0
7	9414	4.94	Y	Y	345.0
8	9402	5.01	Y	Y	146.0
9	9458	5.03	Y	N	
10	9413	5.11	Y	N	
11	9433	5.51	N	N	
12	9419	5.65	Y	Y	299.5
13	9446	5.92	N	N	
14	9435	5.95	Y	N	
15	9017	5.98	N	Y	192.0
16	9412	6.01	Y	N	
17	9474	6.02	N	N	
18	9427	6.06	Y	N	
19	9439	6.10	Y	Y	592.5
20	9472	6.34	Y	N	
21	9073	6.39	N	N	
22	9482	6.51	Y	N	
23	9415	6.70	N	N	
24	9437	6.79	Y	N	
25	9440	6.83	Y	N	
26	9064	6.86	N	N	
27	9481	7.11	N	N	
28	9473	7.55	N	N	
29	9441	7.68	N	N	
30	9477	8.25	Y	Y	385.5
31	9430	8.76	Y	N	
32	9456	13.8	Y	N	
33	9464	14.1	Y	N	
34	9476	14.3	N	N	
35	9053	15.6	N	N	

Garden 1986/87. Females.
Interactions = 190.
Reversals = 36.

Rank	Ring	Index	S	TS	TD
1	9067	0.93	Y	N	
2	9079	2.68	Y	Y	36.0
3	9466	4.29	N	N	
4	9428	5.83	N	N	
5	9098	7.04	Y	Y	146.0
6	9467	7.93	Y	N	
7	9029	8.21	Y	Y	85.5
8	9025	8.43	Y	Y	91.0
9	9445	8.48	Y	N	
10	9093	8.72	Y	Y	101.0
11	9431	8.85	Y	Y	299.5
12	9404	8.86	Y	N	
13	9434	9.23	Y	Y	345.0
14	9468	9.30	Y	Y	85.5
15	9475	9.58	N	N	
16	9026	9.69	N	Y	592.5
17	9013	9.72	Y	N	
18	9409	9.77	Y	N	
19	9410	10.1	N	N	
20	9421	10.2	N	N	
21.5	9451	10.3	Y	Y	463.0
21.5	9436	10.3	N	N	
23.5	9049	10.7	Y	N	
23.5	9089	10.7	N	N	
25	9408	10.8	Y	N	
26	9486	11.4	Y	N	
27	9060	11.5	N	N	
28	9461	11.8	Y	Y	385.5
29	9417	12.2	Y	N	
30	9078	12.4	N	N	
31	9432	17.1	Y	N	
32	9019	19.6	N	N	

APPENDIX 6 continued.

Garden 1987/88. Males.
Interactions = 113.
Reversals = 7.

Rank	Ring	Index	S	TS	TD
1	9413	0.17	N	N	
2	9489	8.15	Y	Y	22.5
3	9414	8.19	Y	Y	449.0
4	8403	8.36	Y	Y	73.0
5	9419	8.71	Y	Y	264.5
6	9457	9.05	Y	N	
7	9498	10.20	N	N	
8	9493	11.10	N	Y	51.5
9	8429	11.20	N	N	
10	8443	11.60	Y	Y	128.0
11	9496	12.60	N	N	
12	9435	12.80	Y	N	
13	9065	12.90	Y	Y	470.0
14	8452	13.60	N	N	
15	9439	16.00	Y	Y	528.0
16	9440	18.70	N	N	
17	8455	19.70	Y	?	
18	9491	19.80	Y	Y	448.5
19	8428	20.50	N	N	
20	8447	25.10	Y	N	

Garden 1987/88. Females.
Interactions = 50.
Reversals = 0.

Rank	Ring	Index	S	TS	TD
1	9025	2.61	N	N	
2	8441	3.27	Y	Y	80.0
3	8415	5.59	N	N	
4	8439	7.87	Y	Y	22.5
5	9434	9.29	Y	N	
6	8422	9.50	Y	Y	67.5
7	8409	9.58	Y	N	
8	8472	13.40	N	Y	51.5
9	8489	14.50	Y	N	
10	9488	17.20	N	N	
11	8411	18.60	N	N	
12	9497	21.10	N	N	
13	8448	24.30	N	N	
14	8410	26.00	N	N	

APPENDIX 6 continued.

Yew 1987/88. Males.
Interactions = 67.
Reversals = 7.

Rank	Ring	Index	S	TS	TD
1	9402	0.05	Y	Y	151.5
2	8443	3.73	Y	Y	60.0
3	9493	6.12	N	Y	117.5
4	8455	8.04	Y	?	
5	9413	9.84	N	N	
6	9498	10.90	N	N	
7	9489	11.40	Y	Y	62.5
8	9491	14.30	Y	Y	450.5
9	9038	15.90	N	N	
10	8491	16.50	N	N	
11	8466	17.00	N	Y	279.5
12	8403	17.40	Y	Y	124.0
13	8452	17.70	N	N	
14	8431	19.50	Y	N	
15	8482	21.60	Y	N	
16	9455	23.50	Y	Y	179.0
17.5	8478	23.70	N	N	
17.5	8458	23.70	Y	N	

Yew 1987/88. Females.
Interactions = 52.
Reversals = 5.

Rank	Ring	Index	S	TS	TD
1	8410	5.07	N	N	
2	9487	8.70	N	N	
3	8448	9.09	N	N	
4	9486	10.10	N	N	
5	9490	13.20	Y	Y	?
6	9461	13.90	Y	Y	353.0
7	8409	17.10	Y	N	
8	8426	20.40	Y	N	
9	8436	21.30	Y	N	
10	9034	26.30	N	Y	179.0

APPENDIX 6 continued.

Wood 1987/88. Males.
Interactions = 37.
Reversals = 3.

Rank	Ring	Index	S	TS	TD
1	8451	3.99	N	N	
2	9402	5.49	Y	Y	81.0
3	8467	5.68	N	N	
4	9038	6.34	N	N	
5	8482	10.89	Y	N	
6	8431	12.20	Y	N	

Wood 1987/88. Females.
Interactions = 75.
Reversals = 7.

Rank	Ring	Index	S	TS	TD
1	9098	5.34	Y	Y	81.0
2	8440	5.43	Y	Y	60.5
3	9487	10.00	N	N	
4	8410	10.80	N	N	
5	8454	11.00	Y	N	
6	9411	11.70	N	N	
7	8460	12.20	N	N	
8	8424	12.70	N	N	
9	9448	12.80	N	N	
10	9461	13.50	Y	Y	237.0
11	8473	13.80	Y	N	
12	8412	14.20	N	Y	182.0
13	9490	14.80	Y	Y	?
14	8459	15.10	N	N	
15	8448	21.20	N	N	
16	9497	25.30	N	N	
17	8432	26.90	N	N	

APPENDIX 6 continued.

Garden 1988/89. Males.
Interactions = 746.
Reversals = 96.

Rank	Ring	Index	TS	TD
1	9494	4.61	Y	79.0
2	8499	5.89	Y	28.0
3	302	7.24	Y	140.5
4	316	7.89	N	
5	333	7.90	N	
6	380	7.93	N	
7	310	8.16	Y	68.5
8	320	8.29	Y	170.5
9	311	8.53	Y	176.5
10	8479	8.62	Y	196.5
11	309	8.99	Y	145.5
12	322	9.46	N	
13	9419	9.48	Y	269.5
14	9065	9.63	N	
15	9435	9.68	N	
16	351	9.70	N	
17	9040	9.84	Y	68.0
18	315	10.1	N	
19.5	379	10.3	N	
19.5	8558	10.3	Y	135.5
21	9097	10.4	N	
22	366	10.6	Y	335.0
23.5	367	10.7	N	
23.5	329	10.7	N	
26	8492	11.0	Y	414.5
26	373	11.0	N	
26	358	11.0	N	
29	363	11.2	N	
29	389	11.2	N	
29	6305	11.2	Y	603.0
31	387	11.3	N	
32	9439	11.4	Y	497.0
33	400	11.7	N	
34	6329	11.9	Y	121.5
35	347	12.2	N	
36	361	12.6	N	
37	342	13.3	N	
38	8543	15.0	N	
39	369	16.0	N	
40	6313	17.4	N	
41	6330	17.6	N	
42	6306	19.2	N	
43.5	394	19.3	N	
43.5	8447	19.3	N	
45	6346	19.8	N	

Garden 1988/89. Females.
Interactions = 366.
Reversals = 76.

Rank	Ring	Index	TS	TD
1	8441	4.35	Y	79.0
2	330	5.19	N	
3	8539	5.50	N	
4	332	5.78	Y	170.5
5	319	5.86	N	
6	9013	6.05	N	
7	399	6.09	N	
8	381	6.21	Y	28.0
9	352	6.25	Y	68.5
10	314	6.38	N	
11	313	6.62	N	
12	8422	6.69	Y	68.0
13	307	6.80	N	
14	346	6.84	N	
15	355	6.86	N	
16	305	6.97	Y	176.5
17	395	7.15	Y	335.0
18	6321	7.40	Y	497.0
19	301	7.41	N	
20.5	390	7.51	N	
20.5	384	7.51	N	
22	348	7.58	N	
23	376	7.69	N	
24	9461	7.78	Y	369.5
25	349	7.88	N	
26	8430	7.91	N	
27	377	8.42	N	
28	9452	8.58	N	
29	337	9.39	N	
30	386	10.6	Y	145.5
31	9486	13.6	N	
32	356	13.9	N	
33	8453	14.8	N	
34	359	15.5	N	
35	393	16.4	Y	373.0

APPENDIX 6 continued.

Yew 1988/89. Males
Interactions = 230.
Reversals = 23.

Rank	Ring	Index	TS	TD
1	8499	1.98	Y	79.0
2	315	5.17	N	
3	9402	6.33	Y	100.5
4	366	7.46	Y	402.0
5	302	7.62	Y	63.5
6	9489	7.66	Y	38.0
7	380	8.29	N	
8	309	8.86	Y	117.0
9	9419	9.13	Y	339.0
10	340	9.70	Y	304.0
11	6326	10.1	N	
12	8496	10.2	Y	164.5
13	9491	10.3	Y	450.5
14.5	329	10.6	N	
14.5	9412	10.6	N	
17	8558	10.8	Y	161.0
17	310	10.8	Y	114.0
17	6316	10.8	N	
19	345	11.1	N	
20	6330	11.2	N	
21	400	11.4	N	
22	8482	11.5	N	
23.5	9472	11.6	N	
23.5	9457	11.6	N	
25	8476	11.7	N	
26	358	13.0	N	
27	6314	13.1	N	
28	379	13.9	N	
29	6331	14.3	N	
30	9427	14.4	N	
31	8479	14.6	Y	129.0
32	320	14.7	Y	243.5
33	347	15.2	N	
34	8488	19.2	N	
35	6346	19.8	N	
36	8447	23.2	N	

Yew 1988/89. Females.
Interactions = 73.
Reversals = 1.

Rank	Ring	Index	TS	TD
1	9490	3.88	Y	63.5
2	6338	3.96	N	
3	330	4.36	N	
4	8550	9.34	N	
5	305	9.87	Y	177.0
6.5	8539	10.2	N	
6.5	8430	10.2	N	
8	8424	13.6	N	
9	6325	15.2	N	
10	395	15.6	Y	402.0
11	6335	17.0	N	
12	9429	18.5	N	
13	306	19.0	N	
14	313	22.2	N	
15	348	22.6	N	
16	384	25.7	N	

APPENDIX 6 continued.

Wood 1988/89. Males.
Interactions = 215.
Reversals = 30.

Rank	Ring	Index	TS	TD
1	302	2.16	Y	40.0
2	9402	8.07	Y	45.5
3	8496	8.63	Y	101.5
4	8479	8.69	Y	89.5
5	9455	8.88	Y	191.0
6	8558	9.62	Y	200.5
7	345	10.30	N	
8.5	9097	10.60	N	
8.5	380	10.60	N	
10	8482	10.70	N	
11	340	11.00	Y	254.0
12	400	11.10	N	
13.5	373	11.30	N	
13.5	367	11.30	N	
15.5	6314	11.40	N	
15.5	333	11.40	N	
17	329	11.50	N	
18	387	12.00	N	
19	9457	12.10	N	
20.5	358	12.20	N	
20.5	8499	12.20	Y	141.0
22	9491	12.50	Y	464.0
23	9427	12.70	N	
24	366	13.00	Y	468.5
25	6343	13.10	N	
26.5	8488	13.20	N	
26.5	9038	13.20	N	
28	389	13.30	N	
29	9472	13.60	N	
30	310	13.70	Y	167.0
31	379	13.90	N	
32	6326	14.10	N	
33	8447	14.30	N	
34	347	18.90	N	
35	9482	21.20	N	
36	6316	23.00	N	
37	6305	26.20	Y	486.0

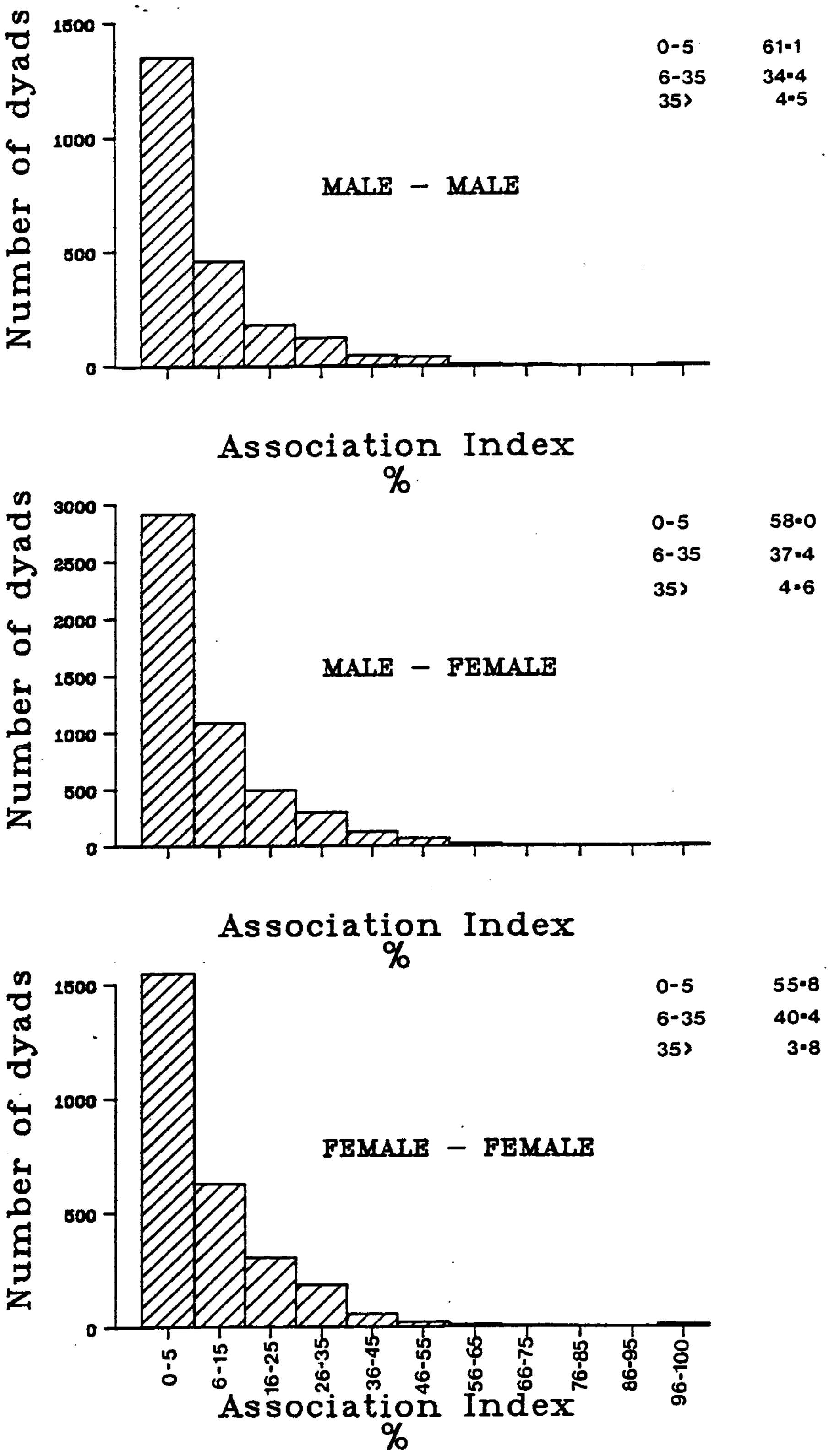
Wood 1988/89. Females.
Interactions = 56.
Reversals = 0.

Rank	Ring	Index	TS	TD
1	393	8.80	Y	280.5
2	8454	5.01	N	
3	9490	5.26	Y	40.0
4	8440	7.19	Y	89.5
5	8539	10.10	N	
6	8550	12.80	Y	136.0
7	304	16.00	Y	101.5
8	397	18.90	N	
9	395	19.00	Y	468.5

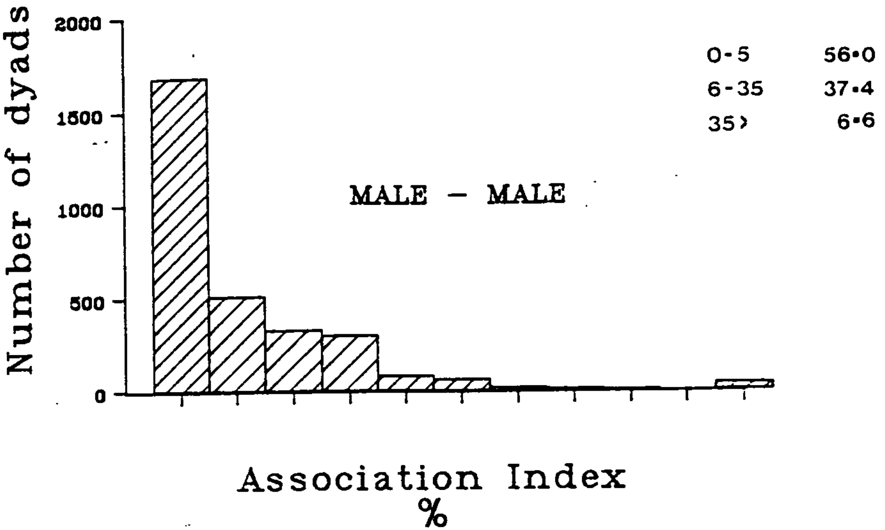
APPENDIX 7. Proportion of dyads showing a reversal of the overall dominant-subordinate asymmetry between sites. Analysis based on 1988/89 data. The two intrasexual data sets are pooled.

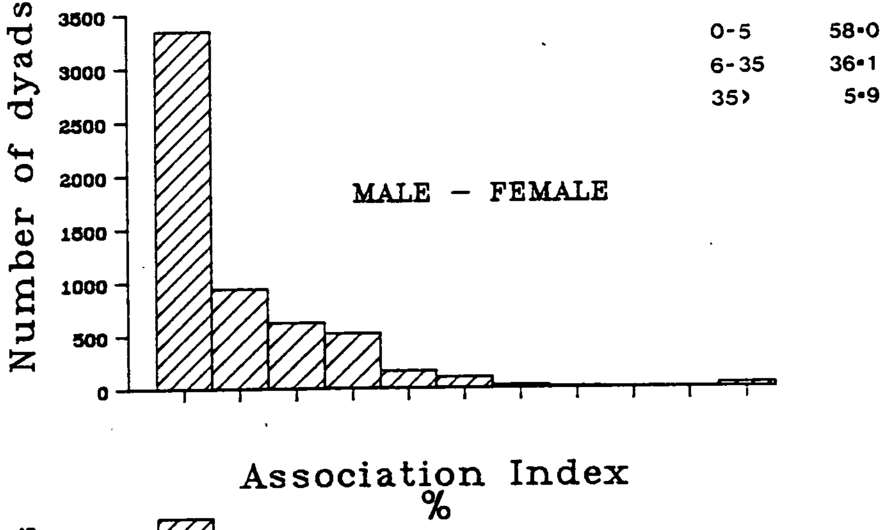
	Number of Dyads	Number(%) showing reversal
GARDEN - YEW		
	27	6(22.2)
YEW - WOOD		
	24	9(37.5)
GARDEN - WOOD		
	11	5(45.5)

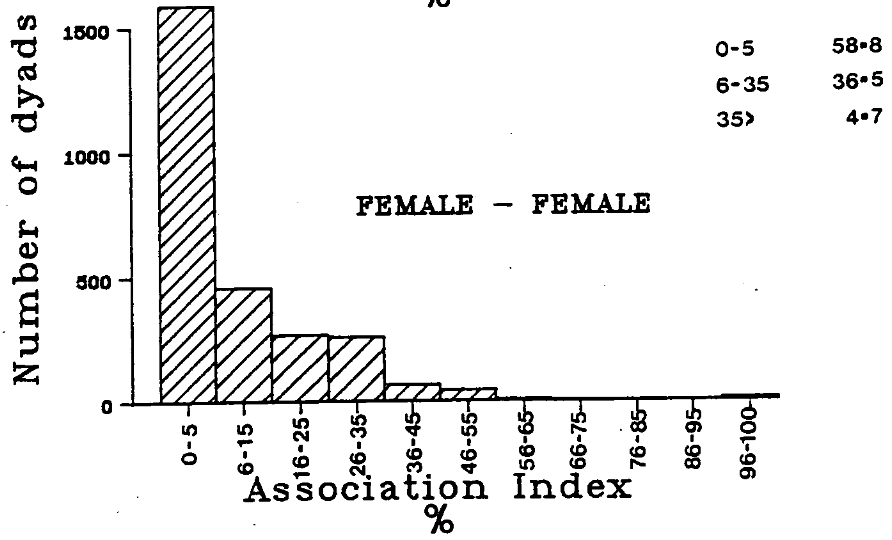
APPENDIX 8. (i). Distribution of twice-weight association indices for all dyads at the Garden (this page), Yew (page ii) and Wood (page iii) sites in 1988/89. For each site, association indices were calculated for all the dyads of a data set containing all birds that were seen once or more at the site. The proportion of dyads falling into each of three broader categories of association (0 - 5%), (6 - 35%) and (>35%) is also annotated. See Chapter 6.5. for further discussion and Chapter 4.2. for details of the calculation of association indices.



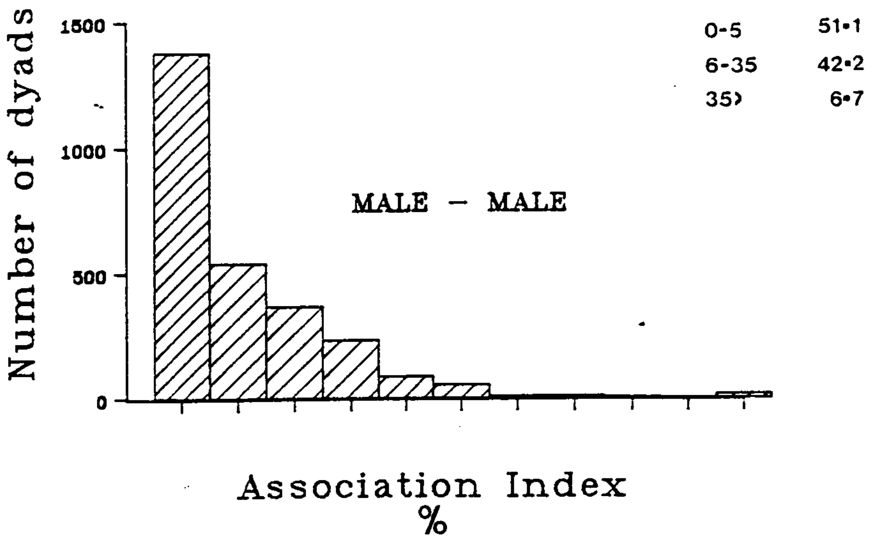
APPENDIX 8, (ii).

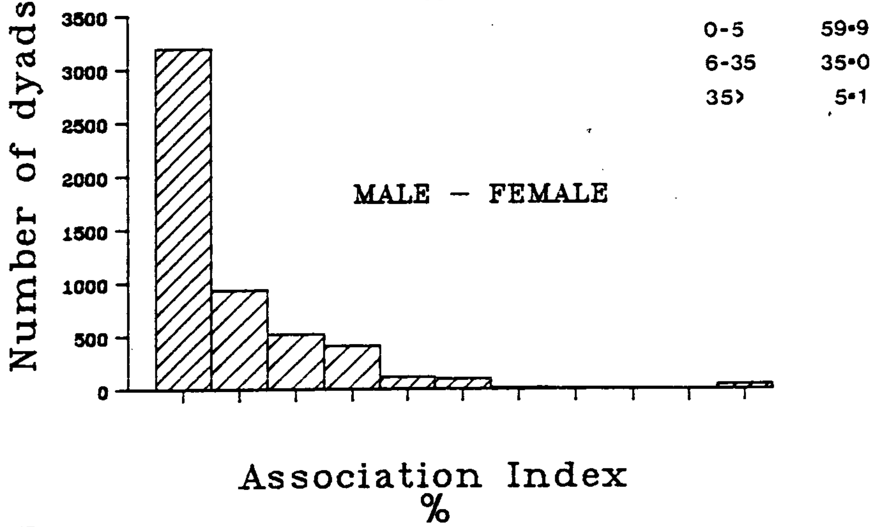


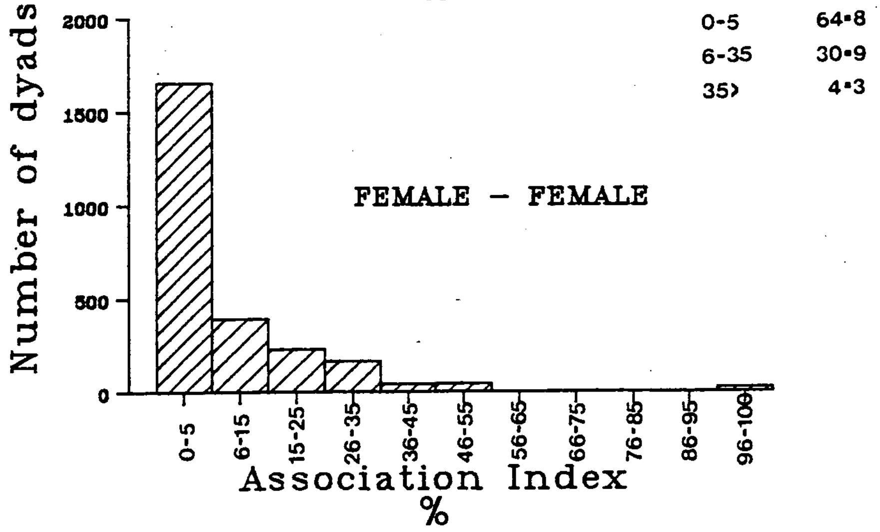




APPENDIX 8, (iii)



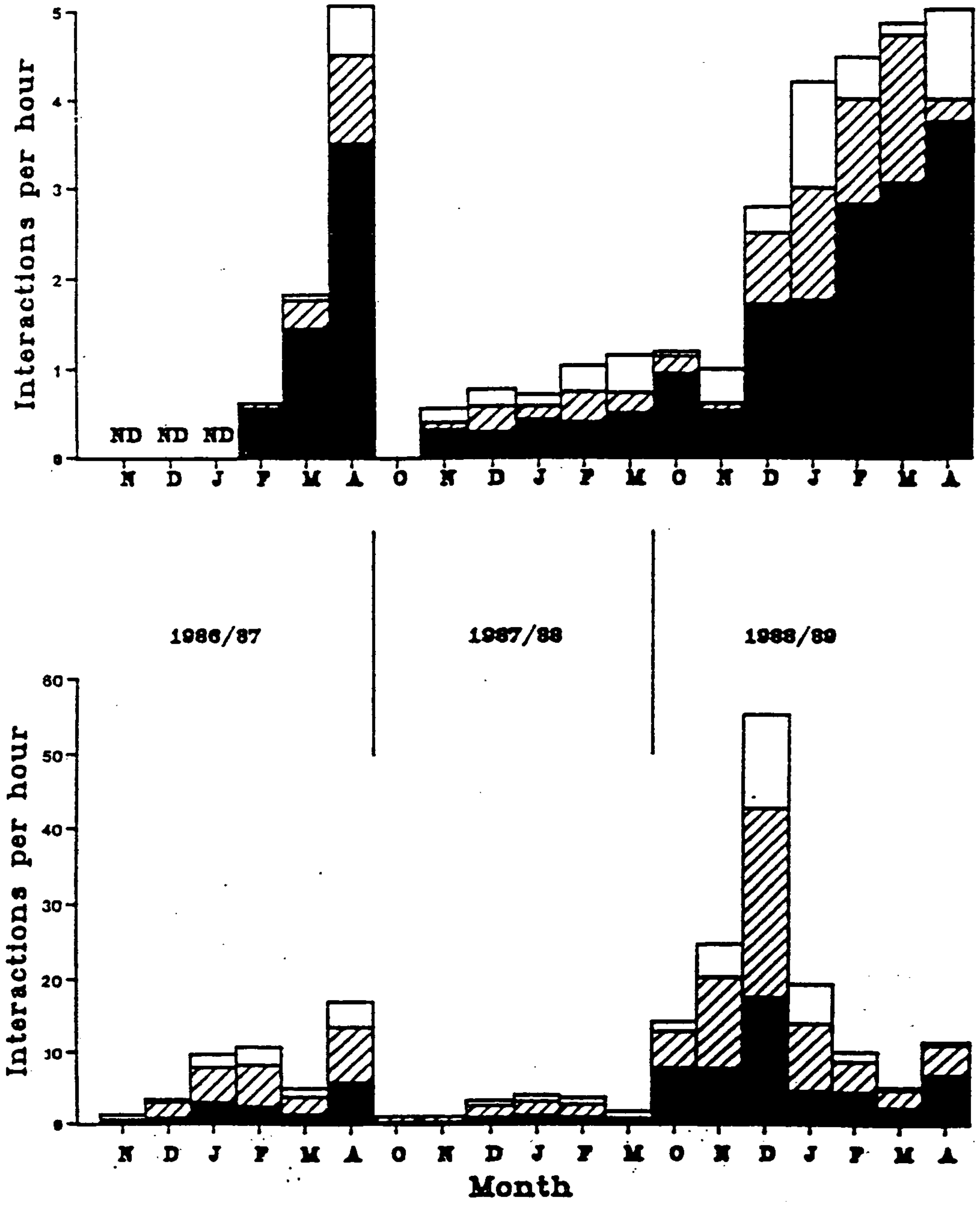




APPENDIX 9. Distribution of interactions between great tits according to year, month, context (F = food, T = 'non-feeder', i.e. territorial) and the sex of the interacting birds. Data from observation and videotape, and from all sites, combined. Raw scores are standardized to 'Number of interactions per hour' in parentheses.

Month/Year	Context	Male/Male	Male/Female	Female/Female	Total
NOV 86	F	5(0.23)	9(0.41)	14(0.63)	28
DEC 86	F	15(0.83)	39(2.17)	7(0.39)	61
JAN 87	F	109(2.97)	177(4.83)	68(1.85)	354
FEB 87	F	115(2.41)	273(5.71)	123(2.57)	511
	T	27(0.56)	3(0.06)	0(0)	30
MAR 87	F	47(1.38)	80(2.35)	40(1.17)	167
	T	49(1.44)	11(0.32)	2(0.06)	62
APR 87	F	73(5.70)	100(7.80)	45(3.51)	218
	T	45(3.51)	13(1.01)	7(0.55)	65
OCT 87	F	3(0.31)	8(0.81)	0(0)	11
	T	0(0)	0(0)	0(0)	0
NOV 87	F	8(0.32)	20(0.81)	0(0)	28
	T	8(0.32)	2(0.08)	4(0.16)	14
DEC 87	F	19(0.92)	34(1.65)	14(0.68)	67
	T	6(0.29)	6(0.29)	4(0.19)	16
JAN 88	F	72(1.18)	120(1.96)	51(0.83)	243
	T	26(0.43)	9(0.15)	8(0.13)	43
FEB 88	F	68(0.98)	121(1.74)	63(0.90)	252
	T	28(0.40)	24(0.34)	20(0.29)	72
MAR 88	F	8(0.37)	11(0.50)	19(0.87)	38
	T	11(0.50)	5(0.23)	9(0.41)	25
SEP/OCT 88	F	164(7.69)	112(5.25)	29(1.36)	305
	T	20(0.94)	4(0.19)	1(0.05)	25
NOV 88	F	101(7.61)	167(12.59)	59(4.45)	327
	T	7(0.53)	1(0.08)	5(0.38)	13
DEC 88	F	245(17.50)	352(25.14)	177(12.64)	774
	T	24(1.71)	11(0.79)	4(0.29)	39
JAN 89	F	72(4.50)	152(9.49)	84(5.24)	308
	T	28(1.75)	20(1.25)	19(1.19)	67
FEB 89	F	37(4.35)	36(4.24)	12(1.41)	85
	T	24(2.82)	10(1.18)	4(0.47)	38
MAR 89	F	36(2.29)	37(2.36)	6(0.38)	79
	T	48(3.06)	26(1.66)	2(0.13)	76
APR 89	F	27(6.75)	17(4.25)	2(0.50)	46
	T	15(3.75)	1(0.25)	4(1.00)	20

APPENDIX 10. Rates of interaction in feeder (lower) and non-feeder (upper) contexts over the three winters. Data from all sites pooled. Solid shading = male - male. Hatching = male - female. Unshaded = female - female.



APPENDIX 11. A comparison of the frequencies of occurrence at the site of observation, of male great tits performing different behaviour elements. Each interaction in the data set is treated as an independent event, and each element is treated independently. For each element, a distribution of frequency of occurrence scores is produced, each score representing the frequency of occurrence of one bird performing that element in one interaction. The distributions for all eleven elements are then compared using a Kruskal-Wallis test which shows that the probability of observing performance of an element varies significantly with the frequency of occurrence of the performing bird. The right-hand column compares the distribution of supplants with that of each other element, using the multiple comparison technique for examining individual pairs of medians (Siegel & Castellan 1988, pp.213-215). In this case, it can be seen, for example, that WO tends to be performed by significantly less frequently occurring birds than do supplants. ND/ND refers to 'non-interactive' encounters in which neither bird performs any of the other elements. Frequency of occurrence is measured as "percentage of observation days on which the bird was seen" (Chapter 4.2.2.). Caveats regarding statistical independence in these tests are discussed in Chapter 6.4.2, and the data sets used are described in the same section.

Element	Sample	Median Frequency of Occurrence	Multiple comparison test
HU	103	44.07	NS
HD	16	29.04	NS
HB	40	39.93	NS
EB	37	50.00	NS
WO	159	45.00	<0.05
TF	161	45.65	NS
OB	32	42.69	NS
TB	113	45.76	NS
ATT	93	49.28	NS
SA	641	52.17	NS
ND/ND	94	45.00	<0.05

Kruskal-Wallis H (adjusted for ties) = 29.13, df = 10, $p<0.001$

APPENDIX 12. A comparison of the frequencies of occurrence at the site of observation, of two subsets of male great tits: i) those performing element 'X' and, ii) those not performing element 'X'. The analysis is based on the same data set as used in Appendix 11. Each interaction is treated as an independent event, and each element is considered separately. For each element, a distribution of frequency of occurrence scores is thus produced for 'element performed' and 'element not performed' categories respectively, with one datum being added to one of the categories for each interaction observed. The complementary pairs of distributions are compared for each element independently using a series of Mann-Whitney-Wilcoxon tests. In each test, the critical p-value for rejection of the null hypothesis of no difference is reduced (see Chapter 6.4.2.) because of the use of serial multiple comparisons on the same data set. Before analysis, all supplants are removed from the data set because their overwhelming contribution to each 'element not performed' category would mask more subtle correlations of the use of one display element in preference to another. In other words, each 'element not performed' category could equally be termed an 'other display performed than X' category. In this case, it can be seen that performers of TB and ATT are significantly more frequently occurring than non-performers, but that these are the only two elements where a significant deviation from random expectation is found at the revised critical p-value of 0.005. Other caveats regarding statistical independence in this and related tests are discussed in Chapter 6.4.2. and the data sets used are described in the same section.

Element	Median Frequency of Occurrence 'Performed'	 'Not Performed'	p
HU	45.76 (n=96)	42.19 (n=578)	0.039
HD	29.04 (n=16)	42.19 (n=658)	0.321
HB	42.19 (n=35)	42.19 (n=639)	0.308
EB	50.00 (n=36)	42.19 (n=638)	0.069
WO	45.00 (n=147)	42.19 (n=527)	0.130
TF	47.52 (n=150)	42.19 (n=524)	0.015
OB	34.78 (n=27)	42.19 (n=647)	0.296
TB	45.76 (n=103)	41.30 (n=571)	0.001
ATT	49.28 (n=93)	41.30 (n=581)	<0.001