Stellingen

1. De indeling van koolmezen in de categorieën 'snelle' en 'langzame' exploreerders op basis van continue variabelen is zinvol.
   Dit proefschrift

2. Brutale en voorzichtige koolmezen hebben verschillende gedragsstrategieën, die beide even goed kunnen leiden tot het verkrijgen van een territorium.
   Dit proefschrift

3. Het gebruik van morfologische kenmerken als maat voor dominantie is onterecht. Dominantie is immers geen eigenschap van een individu; zij wordt bepaald in interactie met anderen en is omkeerbaar.
   N.a.v. Røskaft E, Järvi T, Bakken M, Bech C and Reinertsen RE, 1986. Animal Behaviour 34: 838-842

4. Optimaliseringsmodellen van gedrag in stressvolle situaties zijn alleen toepasbaar als rekening wordt gehouden met verschillende gedragsstrategieën.

5. De metingen aan het metabolisme van mezen door Hogstad lijken meer te maken te hebben met stress dan met rust. Zijn conclusie dat dominante mezen een verhoogd rustmetabolisme hebben is dan ook aanvechtbaar.
   Hogstad O, 1987. Auk 104: 333-336.

6. In het geval dat Engelstalige studies over koolmezen voor vrouwenstudies worden aangezien, hebben Latijnse soortnamen hun nut.

7. Het aantal te bejagen dwergvinvissen in de Noordoostatlantische oceaan lijkt bepaald door natte vingerwerk en nationale belangen.

8. Blijkens de EU visserij-akkoorden is overbevissing voor de kust van West-Afrika minder erg dan overbevissing in de Noordzee.

9. Het idee dat groei van de economie nodig is om de natuur te redden sluit naadloos aan bij de huidige opvatting over de maakbare natuur, welke zonder beleidsplan nergens meer een voet tussen de deur krijgt.
   N.a.v. 'Onze maakbare natuur' door Koos van Zomeren, NRC 12 april 1997

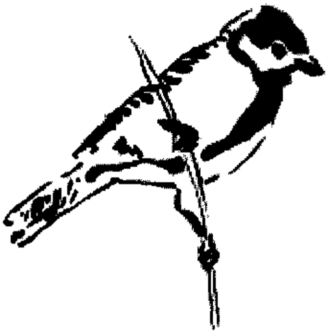
10. De maatschappelijke en financiële onderwaardering van het leraarschap trekt een wissel op de toekomst.

11. De arbitraire termijn van vijf jaar dat een emeritus hoogleraar nog als promotor kan optreden is voor sommige promovendi uiterst nuttig.

Stellingen bij het proefschrift 'Bold or Cautious: behavioural characteristics and dominance in great tits' van Monica Verbeek. Wageningen, 19 juni 1998

Bold or Cautious

Behavioural characteristics and dominance in great tits



Promotor: **Dr. P.R. Wiepkema**
Hoogleraar in de Ethologie
Landbouwuniversiteit Wageningen

Co-promotor: **Dr. P.J. Drent**
Senior Onderzoeker
Nederlands Instituut voor Oecologisch Onderzoek
Centrum voor Terrestrische Oecologie, Heteren

Bold or Cautious

Behavioural characteristics and dominance in great tits

Proefschrift

ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
op vrijdag 19 juni 1998
des namiddags te vier uur in de Aula

door
Monica Verbeek

Cover design and lay-out by Carlos Luís

ISBN 90-5485-883-4

The research reported in this thesis was carried out at the Centre of Terrestrial Ecology of the Netherlands Institute of Ecology, P.O. Box 40, 6666 ZG Heteren, The Netherlands.

DANKWOORD

Het mezen is gedaan! Als iemand mij tevoren verteld zou hebben hoe lang het zou gaan duren, had ik waarschijnlijk ongelovig gelachen en op mijn voorhoofd getikt. En als ik de afgelopen zes jaar niet steeds opnieuw zeer optimistisch en naïef had gezegd dat het 'bijna af' was, was dit proefschrift waarschijnlijk nog niet verschenen. Dat het er nu toch is, heb ik ook te danken aan verschillende mensen.

Afgezien van de 'pietjes' zoals in Heteren de mezen genoemd werden, zijn er nog drie Pieten betrokken geweest bij dit werk. Van hen wil ik als eerste prof. Wiepkema danken. Hij weet waarschijnlijk zelf niet dat hij al flink wat jaren geleden een belangrijke rol speelde waardoor ik uiteindelijk aan dit proefschrift ben begonnen. Toen ik tegen het eind van mijn kandidaats studie biologie een keer naar huis fietste, verlangend naar mijn bed na een nacht lang feesten, zag ik een paar studiegenoten van mij tussen de optrekkende mistflarden fris en monter de uiterwaarden inlopen, gewapend met verrekijkers en speurend naar vogels. Toen wist ik het zeker: ik zou nooit een Echte Bioloog worden. Terwijl ik me in de maanden daarna bezon op wat ik dan wel zou kunnen gaan doen, maakte ik mijn kandidaats af. Een van de laatste colleges die ik daarvoor nog moest volgen was ethologie, gegeven door prof. Wiepkema. Het was een verademing. Dit was pas echt interessant en nog boeiend voorgeschoteld ook. Ik vond ethologie zelfs zo leuk, dat ik besloot toch maar mijn studie biologie af te maken. Toen ik daarna de kans kreeg dit promotie onderzoek te doen, vond ik het dan ook erg fijn dat prof. Wiepkema mijn promotor wilde zijn. Veel van wat ik van hem had geleerd, heb ik op de koolmezen kunnen toepassen. Zijn vragen en opmerkingen op de juiste momenten hielpen mij telkens een stap verder. Dankzij zijn steun durfde ik, na anderhalf jaar besteed te hebben aan metabolisme metingen en hormoonbepalingen, het toch nog voor de resterende tijd over een heel andere boeg te gooien en naar gedragsverschillen te gaan kijken. Ik ben erg blij dat ik, op de valreep, als allerlaatste, nog bij hem mag promoveren.

Kennis over koolmezen heeft Piet Drent me bijgebracht. Ook van zijn uitgebreide veldervaring en zijn bereidheid in tijden van grote drukte bij te springen heb ik dankbaar gebruik gemaakt. Ik heb nog steeds grote bewondering voor het geduld en de aandacht waarmee hij en Peet Drent jaarlijks een enorme hoeveelheid jonge meesjes met de hand groot brachten tot gezonde, sterke mezen door ze elk half uur van zonsopgang tot zonsondergang te voeren. Ik hoop dat de familie Drent er niet teveel onder heeft geleden. Piet wil ik vooral danken dat hij, ondanks zijn aanvankelijke scepsis, mij alle vrijheid gaf om af te wijken van de oorspronkelijke onderzoeksvraag. Inmiddels heeft hij er een prachtig vervolg aan gegeven.

De laatste Piet die hier genoemd moet worden is de Goede. Zijn scherpe observaties van de gebeurtenissen in de volière groepen hielpen mij bij het begrijpen en ontrafelen ervan. Achteraf bezien realiseer ik me dat ik erg veel van hem heb gevraagd door met hem wekenlang achter elkaar ontzettend lange dagen te maken in de zomers dat er gegevens verzameld moesten worden. Gezellige dagen, dat wel. Ook Anne Boon heeft keihard meegewerkt. Dankzij haar geduldig gepeuter aan gegevens als student kreeg ik weer vertrouwen in mijn onderzoek. En dankzij haar gezellig geleuter als assistent vond ik het uren mezen turen minder lang duren. De laatste zomer vormden we met zijn drieën een goed team, en ik ben blij dat Anne en Piet mij ook nu bij willen staan als paranimf.

Marcel Klaassen wil ik als redder in nood danken voor zijn enorme hulp bij het bouwen van de opstelling waarmee ik het metabolisme van heel veel mezen heb gemeten. Ik hoop dat hij niet al te teleurgesteld is dat er, ondanks zijn geduldige uitleg en goede adviezen, uiteindelijk vrijwel niets van die gegevens in het proefschrift zijn opgenomen. Dat lag zeker niet aan hem! *I am very grateful for the hospitality of Hubert Schwabl, who kindly offered me the use of the laboratory at the Max Plack Institut in Andechs. He patiently taught me how to analyse hormone levels in small amounts of bird blood, and after a while I was even able to do that after a lunch at the beer cloister of Andechs. Unfortunately, I could not use the results in this thesis.*

I would like to thank Prof. John Krebs for making the right remark about bold dominants at the right time, which had put me on the right track for the data analysis. He kindly discussed several research plans, and I am grateful that he was prepared to be a member of the PhD committee.

Ab Wijlhuizen en Wil Keultjes bouwden de volières. Vooral 'Keul' was zeer vindingrijk in het met simpele middelen bouwen van de meest vreemde opstellingen, altijd geleverd met begeleidend relativerend commentaar. Bovendien was zijn kennis van het houden van vogels onontbeerlijk en wist hij door zijn praktische tips de verzorgingstijd van de steeds grotere hoeveelheid mezen voor ons enigszins te beperken. Ook Nettie Holman heeft daarbij geholpen door ongelooflijke hoeveelheden badjes en bakjes in- en uit de afwasmachine te ruimen. Ik geloof dat niet iedereen in het instituut het op prijs kon stellen dat dat tussen de koffiekoppen door ging.

Verder wil ik Hans van Balen danken dat hij me destijds de kans gegeven heeft dit onderzoek te gaan doen, ook al was ik ietwat verdacht want geen Groningse student. Jan Woldendorp schonk mij een half jaar extra de tijd, zodat ik nog een derde zomer gedragsgegevens kon verzamelen. Zonder de gegevens van die derde zomer was dit proefschrift niet mogelijk geweest. Karin Kurk verzamelde nog enkele extra gegevens van dominantieverhoudingen in volière groepen. Ik dank mijn ex-collega's van de vogelafdeling voor commentaar op manuscripten en de discussies over mijn werk en over vogels in het algemeen. Mijn ex-collega's van Greenpeace toonden steeds begrip als ik weer eens een weekje vrij nam om te 'mezen', al vonden sommigen dat ik die mezen 'rustig moest laten kezen'. *Kathy Robertson was kindly prepared to edit several chapters of this thesis at a short time notice.*

Mijn ouders dank ik voor hun niet aflatende interesse voor al mijn werk en hun hulp tijdens de laatste loodjes. Ook de rest van de familie en mijn vrienden wil ik danken voor hun belangstelling. De voorzichtige vragen naar de voortgang van mijn proefschrift tijdens mijn jaren bij Greenpeace heb ik toch best op prijs gesteld. Lucas, tenslotte, heeft een belangrijke bijdrage geleverd aan dit proefschrift. Niet alleen vanwege zijn steun en begrip voor mijn mezenmanie al die jaren, zelfs tijdens avonden en weekenden. Maar ook omdat hij me met technische zaken op statistisch gebied hielp, een hele scherpe discussiepartner was en feilloos zwakke plekken wist aan te wijzen in eerdere versies van dit proefschrift. Dank!

Lissabon, april 1998

CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

CHAPTER 1

GENERAL INTRODUCTION

Social dominance

Most animals have a rich repertoire of social interactions. They group together for safety, take care of their young and so on. They also fight with each other for resources such as food, mates or shelter. Within families or other social groups, the same individuals will meet each other frequently which can lead to repeated fights between two individuals. If one of them consistently wins, the pair has a dominance relationship with a dominant winner and a subordinate loser. In a group, most individuals are involved in such dominance relationships, which leads to the establishment of a social hierarchy.

Since dominant individuals generally enjoy better access to resources, dominance in pair-wise fights or place in the hierarchy (social rank or status) can be one of the factors determining who in a population will become sexually mature, who will reproduce, who will leave the population and who will die (Huntingford and Turner, 1987). Therefore dominance can play an important role in the life of an individual. Reproduction and survival determine the lifetime reproductive success of an individual. This, in turn, determines its contribution to the gene pool in the next generation, which represents the fitness of that individual (Daan and Tinbergen, 1997). Dominance thus influences processes at the population level. Effects of social dominance can become stronger as the density (numbers per unit area) of the population increases and competition becomes more important. This is often the case in bird populations. For example, in blue grouse, the dominant individuals have better chances of obtaining breeding territories and at high population density some individuals are excluded from breeding territories and even may not reproduce (Zwickel, 1980). In willow tits, dominant birds obtain more food in winter than subordinate birds, and at high densities more juvenile willow tits, who are subordinate, die in winter (Ekman, 1984). Consequently, the size of the population is likely to remain within certain limits. If each member of a population gained only a part of the food, presumably more animals would die and the size of the population would oscillate. Since the effects of social dominance are often density dependent, they can act to control the size of the population, being more influential at high population densities and slowing down the rate of population increase.

If social dominance is so important, then who becomes dominant? This question is the starting point for this thesis. Several factors determine social dominance (for an overview see Pusey and Packer, 1997). Rivals may differ in size, weight, strength or fighting ability and a large animal may simply beat a smaller one.

The value of the resource may be different for rivals; a hungrier animal will fight harder. If one rival is resident in an area longer, he generally wins over the one who arrived later. Experience in fights can also be important. An individual who has lost earlier fights, has a higher chance of losing again, while winners will probably win again, even over a bigger opponent. The influence of these factors on social dominance has been thoroughly studied in many species, both in theoretical models and in empirical studies with laboratory experiments or in natural situations.

Apart from these well-studied factors, consistent individual levels of aggression can affect social dominance. Aggressive individuals generally win over non-aggressive ones. The phenomenon, that individuals can be characterised by their aggressiveness and the subsequent effect on social dominance, has mainly been studied in artificially selected domesticated or laboratory animals. Individual levels of aggressive behaviour in mice and rats, measured in tests against standard opponents, differ considerably and have a genetic basis (Lagerspetz, 1964; van Oortmerssen and Bakker, 1981). These levels are associated with individual rank in a group (van Oortmerssen *et al.*, 1985; Fokkema, 1985). Experiments with genetically selected aggressive and non-aggressive mice show that they differ in their physiological and behavioural response to social interactions (Benus, 1988). Aggressive mice react in an active way and either attack or flee, while non-aggressive mice react in a more passive way and when attacked they withdraw and become immobile. These different types of reactions, active versus passive, were also found in non-social situations (Benus *et al.*, 1987; Benus *et al.*, 1990). In fact, the aggressive and non-aggressive mice appear to be two different types of animals, showing consistent differences in behaviour whenever challenged by their environment. They have different behavioural strategies to cope with environmental challenges (Benus *et al.*, 1991; Koolhaas *et al.*, 1997). These different coping strategies are reflected in a whole variety of behaviour, ranging from aggression and exploration (Benus *et al.*, 1991) to nest building (Sluyter, 1995). Different coping strategies are found in a growing number of mammal species like tree shrews (von Holst, 1986), beech martens (Hansen and Damgaard, 1993) and pigs (Schouten and Wiepkema, 1991; Hessing *et al.*, 1994). Until now, they have not been studied in birds.

Genetically selected domesticated or laboratory animals have reduced genetic variation and grow up in an environment with little variety compared to the natural situation. So far, the possibility that coping strategies, or more generally individual consistent behavioural characteristics, could also exist in natural populations has not been thoroughly studied (but see van Oortmerssen and Busser, 1989; Sapolsky, 1990). This question deserves more attention, because behavioural characteristics such as aggressiveness can influence social dominance, which in turn can have important consequences for the fitness of an individual and for the composition and dynamics of the population. By studying coping strategies in a natural population, it is possible to link the current thorough knowledge of coping strategies with their ecological function for survival and reproduction. This thesis aims to take a first step by studying the existence of individual consistent behavioural characteristics and their effect on social dominance in the great tit (*Parus major*), a resident territorial bird.

Social behaviour of great tits

Great tits are a suitable model species since their social behaviour is well studied, ranging from detailed descriptions of threat postures to the yearly fluctuations in aggression (e.g. Hinde, 1952; Blurton Jones, 1968; de Laet, 1985). Moreover, social dominance plays an important role in the life of individual great tits and on population level (e.g. Drent, 1983; Krebs, 1971). Many choices in this study depend on current detailed knowledge of the social behaviour of great tits. An outline of the most relevant aspects of this behaviour is presented in the following.

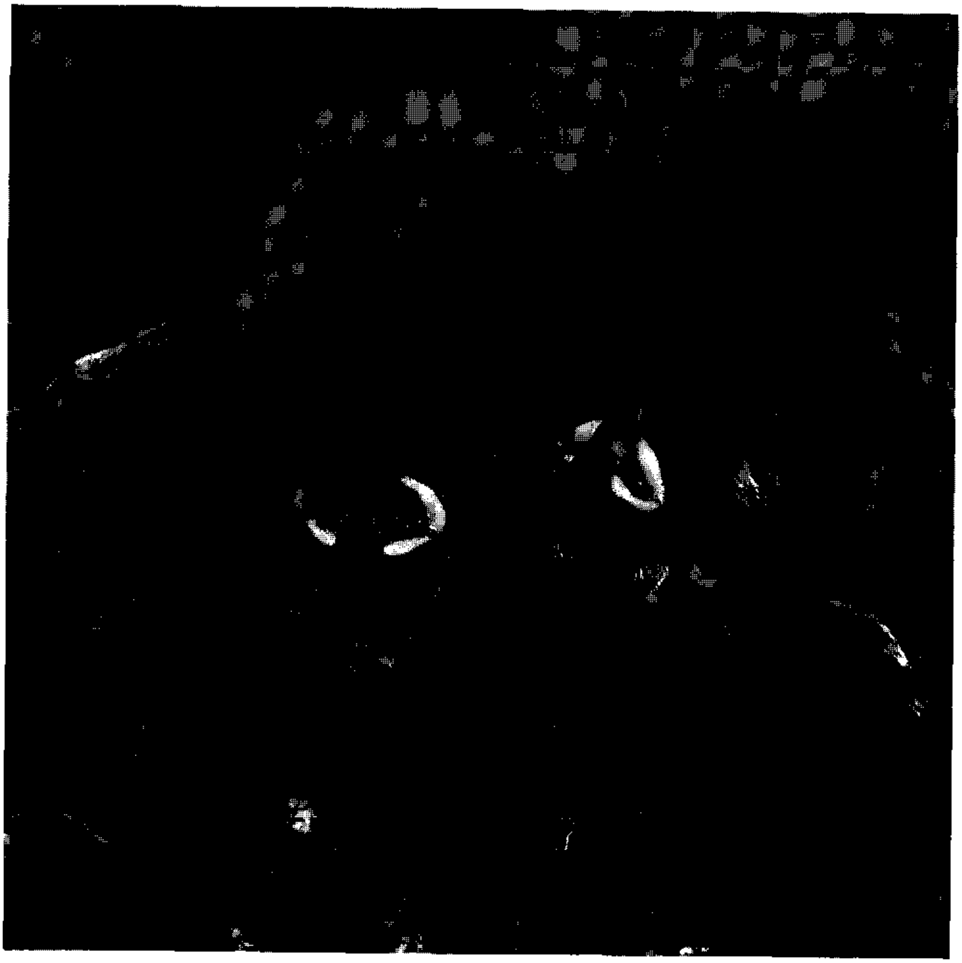
Aggressive behaviour develops only gradually. Young great tits become independent of their parents on average 14-21 days after fledging (de Goede, 1982; Verhulst and Hut, 1996). Once independent, juveniles flock together, either near their place of birth or after migration to areas rich in food (Dhondt, 1979; Drent, 1984). In this period, exploratory behaviour is a major activity (Baker, 1993). Only after some weeks do the first aggressive interactions over food and space take place. Gradually a dominance hierarchy develops in the flock of juveniles (Drent, 1983).

During moulting in August/September, a sexual differentiation in aggressive behaviour develops and males usually win over females (Drent, 1983). All males that have survived to that point (on average 40-50%; Drent, 1984) will try to occupy empty territories between settled adult birds. Birds with a high social rank in the resident flock have the best chance of success (Drent 1983). Females will fight with each other to find a mate with a high social rank or a territory. Once settled, the territorial male defends the site throughout its life, as long as foraging conditions inside and around the territory permit. This is not a territory in the strict sense. At the site they are dominant over all other birds, but they tolerate flocks of birds without territory and even join them to forage and roam over large areas if there is insufficient food in their own territory. Also outside their territory, territorial birds are dominant over birds without territory and have first access to food (Drent, 1983). Territorial birds have a relatively good chance of surviving winter; depending on food availability and winter weather, about 25-70% of the territorial birds are still locally present after winter, but this was as low as 11% in a severe winter when even territory owners dispersed (Drent, 1979; van Balen, 1980). The birds without territory are worse off. Their local winter survival is only 4-25%. These non-territorial birds have the choice to either stay put and wait until a vacancy occurs (usually by death of the owner) or to disperse in the hope of finding less populated areas with vacant territories.

In the spring, with the breeding season coming up, winter flocks break up and all males without territory roam alone or accompanied by a mate. A new wave of attempts to find a territory occurs, but the situation differs from the autumn settlement. In spring it is not the social rank in the hierarchy, but outcomes of short fights between two roaming birds that will determine settlement (Drent, 1983). Territory owners are now more bound to their territory and less tolerant than in the autumn; they chase intruders away more frequently. Although pairs without territory can breed by intruding a territory, behaving inconspicuously and rapidly building a nest, they produce about half the number of fledglings of territorial pairs (Dhondt and Schillemans, 1983).

Outline of the thesis

A first step in the study of possible effects of individual behavioural characteristics on social dominance in great tits, is to determine if great tits do indeed differ consistently from each other in their behaviour and if they can be characterised individually this way. If consistent, behavioural characteristics should be present already early in life before any dominance relationship develops. Probably the first measurable behaviour great tits perform in life is begging in the nest. However, this behaviour of an individual nestling is very much influenced by its temporary level of hunger, by the behaviour of its siblings and by the feeding behaviour of its parents. Therefore it will be difficult to obtain independent measurements of individual nestlings. Such measurements are easier to obtain after the fledglings have become independent of their parents. Then their main activities are exploration and foraging. This study starts in chapter 2 with the examination of consistent individual differences in early exploratory behaviour. It presents measurements of this behaviour in great tits as young as four weeks. In chapter 3 the question is studied whether those juveniles also differ consistently in their first aggressive behaviour later in life, when agonistic interactions can also be seen in natural circumstances. Detailed observations during pair-wise fights are used in that chapter to analyse the relationship between early exploratory behaviour, aggressive behaviour and dominance. Although the relatively 'simple' experimental set-up with pair-wise fights allows such an analysis, in the natural situation dominance relationships between juvenile great tits develop in a flock situation implying complex interactions. This is taken into account in chapter 4, which describes the development of a stable social hierarchy in aviary groups. Juveniles with different exploratory behaviour were put together in the period immediately preceding the territorial strife in autumn. In that chapter an analysis is presented of the relationship between early exploratory behaviour and the initial fighting behaviour in such groups and the resulting stable hierarchy in these groups. Chapters 3 and 4 yield seemingly contradictory results. Chapter 5 offers an explanation for this paradox. This explanation is tested in a pilot study with an experiment in which the familiarity of the aviary for groups of juveniles is manipulated. In the final chapter 6 the results of this study are discussed in the light of coping strategies. Causal aspects such as a genetic basis and phenotypic plasticity are discussed, as well as functional aspects such as possible costs and benefits in different phases in the life of the great tit.



Hand-rearing of great tit nestlings

CHAPTER 2

CONSISTENT INDIVIDUAL DIFFERENCES IN EARLY EXPLORATORY BEHAVIOUR OF MALE GREAT TITS

M.E.M. Verbeek, P.J. Drent and P.R. Wiepkema

Published in Animal Behaviour 48: 1113-1121 (1994)

CHAPTER 2

CONSISTENT INDIVIDUAL DIFFERENCES IN EARLY EXPLORATORY BEHAVIOUR OF MALE GREAT TITS

Abstract

Individual differences in early exploratory behaviour were investigated in hand-reared juvenile male great tits, Parus major, *during the first 18 weeks of their life. The juveniles differed consistently in their reaction to a novel object in a familiar environment, either when tested with different objects or when tested again after a time span of 9 weeks. Birds that approached a novel object more quickly, were also quicker to visit all artificial trees present in a novel environment than birds that approached a novel object more slowly. These behavioural differences extended to the strength of foraging habits, built up during a training in which food was always offered at the same place. After a change in the location of food, the quicker birds would keep going to the place where the food used to be. The slower birds tended to change their behaviour and stop going to the former place. The results show that juvenile great tits differ consistently in various aspects of their exploratory behaviour at least during the first 18 weeks of life. The variation in behaviour was not likely to arise from differences in general activity or physical condition, but seem to refer to differences in the way of which information concerning the environment is collected and dealt with.*

Introduction

To survive, animals must be familiar with their local environment. By exploration, they learn where, for example, food and water can be found, and where they can hide. Being familiar with the area may also influence the outcome of competitive interactions (Krebs, 1982; Drent, 1983; Stamps, 1987; Sandell and Smith, 1991). Therefore, the effectiveness of exploratory behaviour has important consequences for the life of an individual.

Individuals can differ consistently in their reaction to a new situation and their ways of collecting information about their environment, as has been reported for example for wolf cubs, *Canis lupus* (MacDonald, 1983), mice, *Mus musculus*, and rats, *Rattus norvegicus* (Benus *et al.*, 1987), bluegill sunfish, *Lepomis macrochirus* (Ehlinger, 1986; cited in Clark and Ehlinger, 1987) and pigs *Sus scrofa* (Hessing *et al.*, 1994). In rodents, individuals that spend much time on exploration in a novel environment remain alert to stimuli in a known environment, as demonstrated by the rapid adjustment of their behaviour to environmental changes, whereas individuals that spend less time on exploration in a new situation, quickly lose their attention for the environment, as shown by the development of routine-like behaviour (van Oortmerssen *et al.*, 1985; Benus *et al.*, 1987). Routines represent behavioural patterns that are largely independent of actual external stimuli (Benus, 1988). Animals showing routine-like behaviour usually perform the behavioural patterns rapidly and without hesitation, but they are slow to adjust the pattern to changes in the environment.

In several laboratory studies of foraging behaviour in tits, large individual behavioural differences have been reported in hand-reared as well as wild captive ones (Smith and Sweatman, 1974; Partridge, 1976; Krebs *et al.*, 1977; Kacelnik *et al.*, 1981). In most studies, however, it is not obvious whether there is any consistency in the reported behavioural differences, nor is it clear at what age behavioural differences become overt in tits.

During the post-fledging period, exploratory behaviour in juvenile great tits may play an important role in their lifetime reproductive success as suggested by Baker (1993). In this period, mortality is high (≥50%; Drent, 1984), while many juveniles disperse (Dhondt, 1979; Drent, 1984). Exploratory behaviour is a major activity in great tits after fledging, and individual differences in exploratory behaviour may have important consequences for survival.

In this study we examined whether juvenile male great tits show consistent differences in various aspects of early exploratory behaviour over a period of several months. We studied exploration in a novel environment and of a novel object in a familiar environment, as well as the occurrence of foraging habits. This study is part of a project on behavioural characteristics and juvenile dominance. Since agonistic behaviour and dominance differ between sexes during development we restricted ourselves to males.

Methods

Subjects

We conducted this study from June to August in 1990, 1991 and 1992 with 19, 21 and 27 hand-reared juvenile male great tits, respectively. Eight to 12 days after hatching, the subjects were collected from their nests in mixed woods in the Netherlands. In each year nestlings of comparable age were taken (maximum difference of 7 days) to avoid age-related differences in behaviour. The young were hand-reared on a diet of a mixture containing a sour milk product, ground beef heart, baby cereal, multivitamin solution and calcium carbonate, supplemented with pieces of mealworms and larvae of the beet army worm, *Spodoptera exigua* and wax moth, *Galleria mellonella*. The nestlings were fed without handling, using tweezers. During hand-rearing, the young were kept together in groups of siblings in natural nests placed in cardboard boxes. All birds could feed themselves 4-5 weeks after hatching. Survival during hand-rearing was more than 95% in each year.

When the birds were 15 days old, they were sexed by the colour of the primary coverts. Their tarsus length was also measured to the nearest 0.1 mm using a calliper, and their body mass to the nearest 0.05 g using a Mettler laboratory balance. Females were returned to their original nests in the forest. At an age of 5 weeks, just before the first experiment started, the young were weighed again to determine their condition, expressed as weight/tarsus length.

Housing

When the birds could feed themselves, they were housed individually in standard cages of 0.9x0.4x0.5 m, with solid bottom, top, side and rear walls, a wire-mesh front and two perches. Each cage was connected to an observation room via a sliding door of 20x20 cm in the rear wall. The birds were kept under natural light conditions, and they had acoustical and visual contact with other individually housed juveniles 2 m away. They were provided with *ad libitum* drinking (and bathing) water, sunflower seeds and commercial seed mixture, which was supplemented daily with mealworms and the mixture on which they had been reared.

Observation room

The first two experiments were conducted in a light-tight observation room of 4.2x2.5x2.3 m. Along each 4.2 m wall were eight sliding doors connecting the birds' living cages with the room, and one 2.5 m wall had a door with a one-way screen through which the birds were observed. We led birds from their living cages to the observation room and back without handling, by darkening the room or cage when it was to be left. The observation room contained five artificial trees made of wood, with a trunk of 4x4 cm and 1.5 m high and four cylindrical branches 20 cm long. The upper two branches were placed 5 cm below the top on opposite sides of the trunk and perpendicular to the lower two branches that were placed 20 cm lower.

Experiments

In three experiments the birds were tested separately. Behaviour was recorded continuously using an event recorder.

Exploration of a novel environment

To determine whether individuals differed in their exploratory behaviour we recorded individual exploration in a novel environment 1 day after the birds had been housed separately at an age of 4-5 weeks. Observations were made between 0830 and 1400 hours in the observation room and the birds were observed in random order during a 10-min period. One hour before each trial the birds were deprived of food. In this experiment, a bowl with six wax moth larvae was hooked onto the tree nearest to the bird's living cage.

As a measure of exploratory behaviour we used the time it would take a bird to visit all five trees, quantified as the time of first arrival at the fifth tree (referred to as arrival time below). Birds that did not visit all five trees within 10 min were given a score of 10 min. For a better understanding of the behaviour patterns preceding arrival time we also observed the number of tree visits, the number of branch hops during a tree visit, and the time a tree visit lasted. A tree visit was defined as a change of tree or a return to the tree after a flight through the observation room. A branch hop was defined as a hop from one branch to another within the same tree. The correlations between arrival time and the three other behavioural measures were calculated.

Habits in foraging

In 1990, we recorded individual differences in the strength of foraging habits for the same individuals which were used to study exploratory behaviour. Immediately after the first experiment the birds were trained to feed in the tree nearest to the living cage in the observation room. The training procedure involved three phases, each lasting 7 days with 5 successive days of observation, a day of rest and a final observation day. In the first phase, a bowl with six wax moth larvae was hooked onto the tree nearest to the bird's living cage as in the previous experiment. In the second phase the wax moth larvae were covered with a thin layer of sand, making them not immediately visible. In the third phase a bowl with a thin layer of sand was hooked onto each tree, but only the bowl in the tree nearest to the bird's living cage contained wax moth larvae.

After phase 3 the strength of the foraging habit built up during the training was tested by changing the food distribution. In this test each tree contained a bowl with a thin layer of sand just as in phase 3, but the wax moth larvae had been displaced from the nearest tree to the tree furthest away. The strength of an existing foraging habit was quantified by the number of visits to the previous location of the wax moth larvae.

During training and the test, each bird was observed once a day, after a food deprivation of 1 h. Observations were made between 0830 and 1400 hours in random order. The first trial of a new training phase and the final test lasted 10 min; the other trials lasted 5 min. To determine whether individual differences in exploratory behaviour of a novel environment extended to the attention given to changes in a known environment, we calculated the correlation between arrival time and the number of visits to the former food bowl.

Reaction to a novel object in a familiar environment

To determine whether individuals differed consistently in their reaction to a novel object, we replaced one of the two perches in the living cage by a perch with a novel object. In 1990 and 1992, the experiment was carried out when the birds were 9 weeks old, using a penlight battery as object. The test was repeated the next day with an 8 cm pink rubber toy ('pink panther'). In 1992 we repeated these two tests with 17 randomly chosen birds using the same objects when the birds were 18 weeks old, to assess the persistence of the individual reactions. To avoid habituation to the objects, we took a time span of 9 weeks. In 1991, we could only test the birds once with a penlight battery at the age of 12 weeks; however, given the agreement in procedure and results we also consider that test.

All tests were executed between 0900 and 1200 hours. The reaction of each bird was recorded from behind a screen for the first 2 min after the object was introduced. To quantify the bird's reaction we used three measures: (1) the latency time for the bird to sit on the perch with the object (approach time), with a maximum of 2 min if the bird did not sit on the perch within the trial time; (2) the minimum distance to the object; and (3) the total time spent on the perch with the object.

We tried to determine whether the observed behaviour was really induced by the novel object rather than reflecting the ongoing behaviour of the birds. Therefore, in 1992 we measured the approach time to the perch, still without the object, during the 2 min prior to introduction of the object. We compared this pre-test behaviour with the behaviour observed during the test.

Data analysis

Since most parameters were not normally distributed we used nonparametric, two-tailed tests. Most associations between variables were analysed using a Spearman rank correlation coefficient (r_s); however, we used a logistic regression with dummy variables to determine the association between arrival time in a novel environment and the approach time to a novel object (Hosmer and Lemeshow, 1989). This test with categorical data was more appropriate than a rank correlation coefficient, since there were many tied observations, owing to finite trial times in both variables. Furthermore, by using logistic regression it was feasible to test for differences in trends between years.

Results

Exploration of a novel environment

Individuals differed considerably in arrival time. The frequency distribution of the approach time was not normal, being flat with a peak when arrival time was 10 min or more, owing to the finite trial time. Arrival time ranged from 40 s to

10 min (median 432 s in 1990, 511 s in 1991 and 578 s in 1992. Since arrival time tended to differ between years (Kruskal-Wallis one way ANOVA: Kruskal-Wallis statistic=5.11, n=67, p=0.08) we analysed the correlations between arrival time and the other behavioural measures separately for each year.

Arrival time was positively correlated with the average duration of a tree visit, but not with the number of tree visits before arrival time (table 1). This means that a short arrival time was caused by short tree visits, rather than by few tree visits. In agreement with this, the birds with a short arrival time visited more trees in the total trial time of 10 min than the birds with a long arrival time. These latter birds hopped more frequently from branch to branch during a tree visit. This was significant in 1991 and 1992, but not in 1990. During longer tree visits the birds spent their time actively by hopping more between branches in all three years.

In 1990 and 1991 there was no correlation between condition and the arrival time (table 1); however, in 1992 there was a negative correlation, indicating that birds in a better condition had a short arrival time.

Table 1. *Spearman rank correlation coefficients between the different measures of exploratory behaviour in a novel environment for each year and between exploratory behaviour and physical condition.*

	1990 (N=19)	1991 (N=21)	1992 (N=27)
duration of tree visits before AT[1] versus AT	0.60**	0.68**	0.54**
#[2] tree visits before AT versus AT	0.28	0.15	-0.22
# tree visits summed over whole trial versus AT	-0.52*	-0.46*	-0.43*
# branch hops per tree visit before AT versus AT	0.09	0.61**	0.70**
# branch hops per tree visit before AT versus duration tree visits	0.54*	0.86**	0.56**
Body condition (g/mm) versus AT	-0.31	-0.08	-0.41*

[1] Arrival Time: time of first arrival at the last of the five different trees

*p<0.05 **p<0.01

[2] # = number of

Habits in foraging

On the last 3 days of training, all 19 birds ate at least one wax moth during the trial. Most of the birds immediately went to the food bowl and started feeding. Some birds (usually three to five) first visited other trees before feeding; these were not always the same individuals. On the last day of training, the visit frequency to the food bowl ranged from one to seven times (median: 3). Only three of the 19 birds visited all trees. This means that the behaviour of the birds was strongly directed towards the bowl with food at the end of phase 3.

In the test, 17 birds immediately went to the bowl where the food used to be. The remaining two first visited other trees, just as on the last day of training. The visit frequency ranged from two to 18 times (median: 8), which was significantly more often than on the last day of training (Wilcoxon Matched Pairs test: z=3.70, n=19, p<0.01). Some birds visited the old bowl a few times, and then either returned to their living cages before the trial had ended, or went to explore other trees and bowls. Other birds kept on going to the food bowl, even though there was no longer any food in it. In general, the birds visited more trees in the test than they had done the day before (z=2.55, n=19, p<0.01), indicating an increase in exploration.

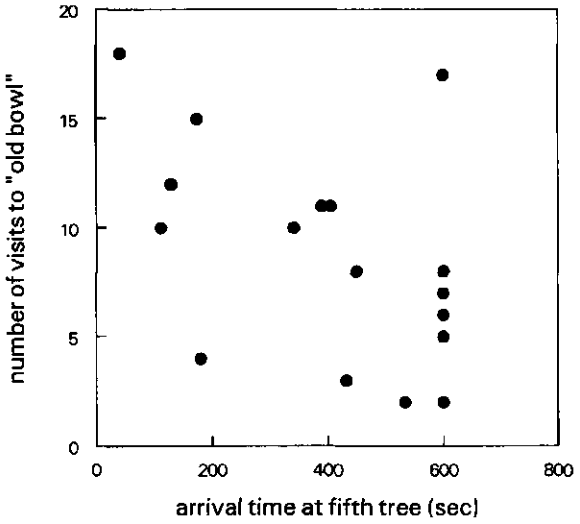


Figure 1. *The number of visits to the former location of the food (old bowl) in the foraging habit test in relation to the arrival time at the fifth tree in the novel environment (r_s= -0.53, n=19, p=0.02).*

Exploratory behaviour and foraging habits

If individual differences in exploration of a novel environment extend to the attention given to possible changes in a known environment, aspects of exploratory behaviour should be correlated with habit strength. Indeed, birds with a short arrival time in the novel observation room kept on visiting the old food bowl more often than birds with a long arrival time (figure 1). An explanation for this correlation could be that birds with a short arrival time made more errors simply because they were more active, visiting more trees including the "wrong" tree. The correlation we found in the exploration test of a novel environment between the number of tree visits during the whole trial and arrival time (table 1) supports this idea. However, there was no significant correlation between the number of tree visits during the testing of habit development and the number of visits to the old food bowl (r_s=0.04, n=19, p=0.87); therefore we reject this explanation. There was no significant correlation between the number of visits to the old food bowl and condition at the start of the experiment (r_s=-0.05, n=19, p=0.84).

Reaction to a novel object in a familiar environment

Considerable individual differences in the approach time were recorded in the first confrontation with a penlight battery. The distribution of the approach times was bimodal, in that most juveniles approached the object either very soon or not at all (figure 2). The approach time ranged from 0 s to 2 min (median 4.7 s in 1990, 7.6 s in 1991 and 39.3 s in 1992). Similar results were found for the approach time to a pink rubber toy. The approach time, the minimum distance and the total time spent on the perch with the objects were strongly correlated within each trial in every year (r_s ranging from 0.69 to 0.99). Birds that approached an object quickly also approached it more closely and spent a lot of time on the perch with it. Because of the strong correlations, only the approach time was used in further analyses to describe the reaction to a novel object.

The observations immediately prior to the test revealed that the approach time to the same perch without the object was not correlated with the approach time in the subsequent test (r_s=0.02, n=27, p=0.92). In addition, the approach time before the test was significantly shorter than in the test (z=2.92, n=27, p<0.01), suggesting hesitation of the individual to approach the object. We therefore concluded that the birds did indeed react to the object.

Persistence in reaction

To assess the persistence of individual differences in reaction to a novel object, we analysed the correlation between the reactions of the birds to the different objects used in 1990 and 1992. Since there were no inter-year differences in level of approach time to the penlight battery (Kruskal-Wallis statistic=2.30, n=46, p=0.13), or to the rubber toy (Kruskal-Wallis statistic=1.59, n=46, p=0.21), we combined the data for the 2 years. The approach time to the battery

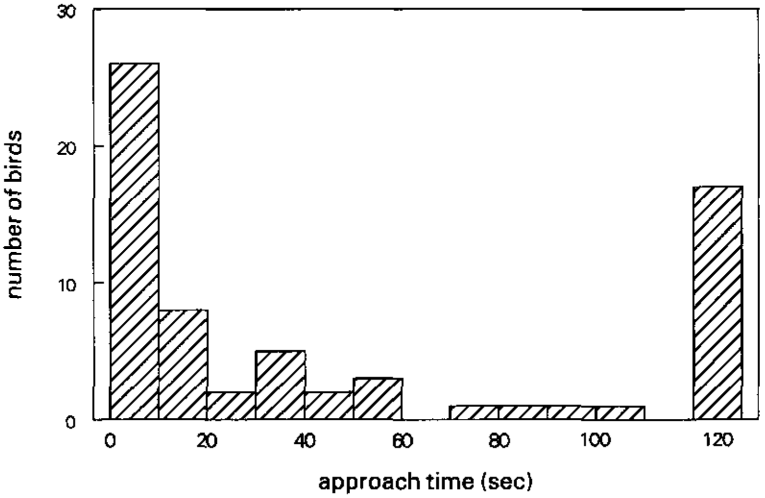


Figure 2. *Frequency distribution of the approach time to a penlight battery. Data are grouped in classes per 10 s; 120 s indicate birds failing to approach within the trial time.*

was positively correlated with the approach time to the rubber toy (r_s=0.55, n=46, p<0.01). This means that the reaction to a novel object was similar for different objects. Since the approach times to both objects were correlated, we used the mean of both approach times for further analyses.

To estimate the time span over which individuals can still be characterised by their reaction to a novel object, we compared the mean approach time measured when the birds were 9 and 18 weeks old (r_s=0.81, n=17, p<0.01). When the birds were 18 weeks old, they approached the object significantly faster than when they were 9 weeks old (z=2.57, n=17, p<0.01). The results show that, although there was a general change in reaction with age, juvenile great tits reacted consistently to a novel object.

Consistency in different aspects of exploratory behaviour

To determine the association between arrival time in a novel environment and the approach time to a novel object using a logistic regression, the birds were classified as follows: (1) early birds with an arrival time of less than 5 min; (2) moderate birds with an arrival time between 5 and 10 min; and (3) late birds with an arrival time of 10 min, who did not arrive at the fifth tree within the trial time. The birds were classified in two classes for the approach time: fast birds approached the object within 1 min, while slow birds approached after 1 min or not at all. As the dependent variable we used the approach time, expressed as the proportion of slow approaching birds. Besides the classes of arrival time we included the factor year and the interactions of the arrival time classes with year in the regression to test for possible inter-year differences. The significance of

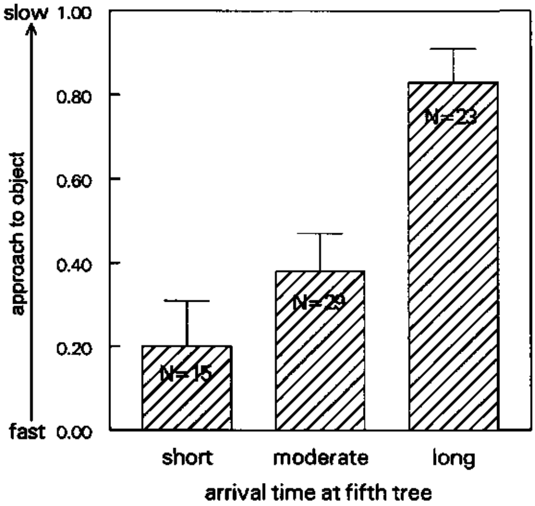


Figure 3. *Approach time to a novel object (expressed as the proportion of slow approaching birds) in relation to arrival time at the fifth tree in the novel environment. Bars represent mean+se; the fitted values from the model are equal to the means. The result of the regression is expressed as: logit (fraction late approachers)= -1.39+0.89x(moderate arrival time)+2.94x(late arrival time); deviance=74.76, df=64. Comparison with a model of an intercept only reveals that this regression is significant with a p<0.01 (Δdeviance=18.11, Δdf=2).*

predictor variables was tested using the change in deviance and degrees of freedom when the variable was dropped from the model.

There was a significant positive relationship between arrival time at 4 weeks and mean approach time at 9 weeks (figure 3). Birds that quickly visited all different trees, also approached a novel object faster than birds which had gone through the new environment more slowly. There was not a noticeable difference in this relationship between years. The results show that the juveniles differed consistently in several aspects of their exploratory behaviour.

Discussion

Consistent Individual differences

In a novel environment some birds quickly visited all trees, paying short visits and hopping little from branch to branch during a visit. Other birds went through the environment more slowly, staying longer at each tree. These latter birds were not simply slower or less active, since in 1991 and 1992 they hopped more within the tree during their longer visits. The data of 1990 do not contradict this, although there was no correlation between number of branch hops per tree visit and arrival time (table 1). More detailed observations (P.J. Drent, unpublished data) suggest that this absence of correlation may be explained by the slower birds did not all reacting in the same way: some would hop frequently during a tree visit, while others would sit still, actively looking around. The absence of a correlation between condition and arrival time in 1990 and 1991 (table 1) suggests that in these years the long arrival time was not the result of physical weakness, which could have caused the later birds to make small hops within trees rather than larger hops between trees. The significant correlation between condition and arrival time in 1992 (table 1) indicates that condition may play a role in the differences in arrival time, at least in that year. The behavioural differences however, suggest that the slower birds were more thorough and cautious in their investigation of the first trees they came to. The faster birds may have explored the novel environment in a more superficial way.

These differences extended to the reaction to a novel object in a familiar environment, measured when the juveniles were 4 weeks older. The quick and superficial explorers approached the object faster than the slow and thorough explorers. This reaction was persistent over several confrontations with different objects, even when the next confrontation took place 9 weeks later. In these latter tests the birds approached the objects faster, suggesting an overall change in fear for novel objects with age. This suggestion is supported by the fact that juvenile great tits of 5 weeks old, approached novel objects slower than juveniles of 9 weeks old (P.J. Drent, unpublished data). We conclude that juvenile male great tits differ consistently in various aspects of their exploratory behaviour at least during the first 18 weeks of their lives.

The different ways of collecting information about a novel environment were associated with the reaction to a change in the feeding situation. The quick and superficial explorers kept going to the former food bowl, while the slower and more thorough explorers changed their behaviour. This indicates that former had more rigid foraging habits. These different reactions were not the result of a difference in activity or physical condition, but presumably reflect different ways of dealing with information about a known environment. The quick explorers may have paid little attention to the known environment, relying on their former experience and sticking to their habits; their behaviour seemed to be routine-like. The slower and more thorough explorers may have remained alert to stimuli in the known environment, and adapted their behaviour to the change in the feeding situation. This suggestion is in agreement with the studies of van Oortmerssen *et al.* (1985) and Benus (1988), and can be tested further by investigating the habituation rate of responses to a repeated stimulus. On the basis of our results we expect consistent individual differences in habituation rate.

Function of Individual differences

Specific research is needed to clarify whether consistent individual differences in exploratory behaviour measured in simple laboratory circumstances are representative for the field situation, for example by manipulating the feeding situation or confronting juveniles with novel objects. If individual differences exist, what could be their adaptive value? One would expect animals to react flexibly in different situations, optimising their behaviour, resulting in similar behaviour of different individuals in a particular situation. Several mechanisms have been proposed to bring about individual differences in behaviour, such as phenotypic differences between individuals that may constrain their behaviour differently, selection for animals to be identifiable as individuals, or selection that favours the adoption of different strategies by different individuals (Slater 1981, Magurran, 1986).

Clark and Ehlinger (1987), in a review of individual differences in foraging behaviour of birds and fish, suggested a trade-off between time spent on sampling different places or food items and the ability to adjust foraging behaviour to environmental changes. They indicated that individuals that spend much time on sampling different places or food items in stead of feeding at the most profitable place or item are adapted to a changing environment. Individuals that always feed at profitable places or on items without losing time by sampling less profitable places are adapted to a stable environment. As such, individual variation reflects a constraint on the optimisation process and the animal whose behaviour is characterised by average measures as predicted by optimisation models may even not exist (Houston and MacNamara, 1985). A study by Smith and Sweatman (1974) on foraging behaviour of great tits also suggested a potential trade-off between the conflicting demands of sampling in a variable environment and the exploitation of the most profitable resources.

Such a mechanism could explain the consistent behavioural differences we found. There may be a trade-off between exploration speed and attention to the environment. Birds that explore quickly but soon lose attention to the environment may be best adapted to a stable environment. They will not lose time by being distracted in their search for food by small changes in the environment that are not essential; however, if an important change occurs they will not be able to adapt their behaviour immediately to the new situation. Birds that explore slowly and thoroughly and keep alert to the environment will readily react to changes in the environment. They may be best adapted to an unstable environment, in which important changes regularly occur. This is in agreement with van Oortmerssen *et al.* (1985) and Benus *et al.* (1987), who suggested that mice and rats that quickly went through a maze and readily developed routines were at an advantage in a stable environment, while those that went through a maze more gradually and remained alert to stimuli in a familiar environment were at an advantage in a changing environment.

The suggested trade-off could also explain the bimodal frequency distribution of the approach time to a novel object we found. Both fast and slow approaching birds would have their individual-specific advantages in different situations, while the moderate approaching bird would be in a relative disadvantage in both situations. Arrival time did not have a bimodal frequency distribution, although the distribution was not normal. This could be because arrival time was a result of several decisions to hop between branches or to go to the next tree, in stead of one decision to go to the novel object or not. An accumulation of decisions causes a less clear frequency distribution (Ehlinger, 1986; cited in Clark and Ehlinger, 1987).

Genetical aspects of individual differences

It is not clear how far the variation in exploratory behaviour is genetic. In 1992 we carried out some extra measurements of reaction to a novel object with 42 juveniles, all siblings from the 27 birds we used for this study. There were significant differences between nests in the approach time to the object (Kruskal-Wallis statistic=27.5, n=69, p=0.04), which means that siblings were more alike in their reaction than non-siblings. This preliminary result suggests that individual differences had already developed in the nestling stage or earlier; they could even have been genetically determined. This suggestion provides an interesting basis for further research such as cross-fostering experiments.

In several mammal species, consistent individual differences have shown to be part of fundamentally different behavioural strategies, that become obvious particularly in stressful situations (von Holst, 1986; Benus *et al.*, 1987; 1990; Bohus *et al.*, 1987; Wiepkema and Schouten, 1988; Schouten and Wiepkema, 1991; Hessing *et al.*, 1994). The consistent behavioural differences we found in juvenile male great tits could also be part of a more general behavioural pattern or strategy. In that case individual differences in exploratory behaviour will also extend to social behaviour.

Testing the reaction to a novel object

CHAPTER 3

EXPLORATION, AGGRESSIVE BEHAVIOUR AND DOMINANCE IN PAIR-WISE CONFRONTATIONS OF JUVENILE MALE GREAT TITS

M.E.M. Verbeek, A. Boon and P.J. Drent
Published in Behaviour 133: 945-963 (1996)

EXPLORATION, AGGRESSIVE BEHAVIOUR AND DOMINANCE IN PAIR-WISE CONFRONTATIONS OF JUVENILE MALE GREAT TITS

Abstract

In the development of social dominance, constitutional behavioural characteristics may play an important role apart from morphological traits. Previous work has shown that juvenile male great tits Parus major *differ consistently in their early exploratory behaviour and can be classified as fast and superficial explorers or slow and thorough explorers. This study investigated whether these individual differences in exploratory behaviour are related to aggressive behaviour, and whether this affects dominance. In an experimental set-up, pair-wise fights were observed. The obtained data were corrected for possible influences of morphological traits. Consistent individual differences in aggressive behaviour were found, indicating that juvenile great tits can be characterised by that behaviour. Fast explorers started more fights than slow explorers, and birds that started more fights also won more fights. An additional experiment with pairs of fast and slow explorers confirmed that fast explorers won more fights than slow explorers. In conclusion, we demonstrated that individual differences in exploratory behaviour are related to aggressive behaviour, which affects dominance. The striking agreement of these findings with studies of rodents and pigs is discussed. It is suggested that the behaviour of fast explorers agrees with an active style of coping with stress, while the behaviour of the slow explorers resembles a passive coping style.*

Introduction

Social dominance has important consequences for fitness since it may affect territory acquisition, mating success, reproduction and survival (e.g. Arcese and Smith, 1985; Hegner, 1985; Houston and Davies, 1985; Ekman, 1990). In contests, dominance is determined by several asymmetries between the opponents in fighting ability and value of the resource to each over which the fight takes place (Maynard Smith and Parker, 1976). In great tits, fighting ability is affected by body size, weight, age and sex (e.g. Garnett, 1981; Drent, 1983; Dhondt en Schillemans, 1983; de Laet, 1985; Sandell and Smith, 1991). The size of the breast stripe of great tits has been proposed to signal fighting ability (Järvi and Bakken, 1984; Järvi *et al.*, 1987; Pöysä, 1988, but see Lemel, 1989; Sandell and Smith, 1991; Wilson, 1992a) and thus to affect the outcome of a fight when contestants lack information about the social status or fighting ability of the opponent (Lemel and Wallin, 1993).

Apart from morphological traits, behavioural characteristics can affect dominance. For example, mice (Oakeshott 1974; van Oortmerssen *et al.* 1985; Blanchard *et al.* 1988), and rats (Fokkema 1985) show consistent individual differences in their independently measured level of aggression, which are positively related to social rank in a group. These individual differences in aggression extend to other behavioural systems such as exploratory behaviour (Benus *et al.* 1987). Non-aggressive mice and rats spend a great deal of time on exploration in a novel environment and remain alert to stimuli in a known environment, whereas aggressive individuals spend less time on exploration, and soon lose their attention to details in the environment and rely on their previous experience (van Oortmerssen *et al.* 1985; Benus *et al.* 1987; 1990). Similar correlations between exploratory behaviour and aggressive behaviour were found in pigs (Hessing *et al.* 1994). In open field tests non-aggressive pigs hardly try to escape, and approach a novel object slowly but explore it intensely, spending much time on exploration, whereas aggressive pigs have a tendency to escape a novel environment and approach a novel object fast, but explore it short and superficially.

In great tits, behavioural characteristics may also affect dominance. Hierarchies are already established in flocks of juveniles, which have important consequences for later dominance and territoriality (Drent 1983). Juvenile male great tits show consistent individual differences in exploratory behaviour (chapter 2). Juveniles that approached a strange object fast and explored a novel environment fast but superficially, had more rigid foraging habits and did not rapidly adjust their behaviour to a change in the feeding situation. On the other hand, juveniles that approached a strange object slowly and explored a novel environment slowly and thoroughly, quickly adjusted their foraging behaviour to an environmental change. The individual differences in exploratory behaviour found in rodents, pigs and juvenile great tits show striking similarities.

The aim of this study was to investigate whether differences in exploratory behaviour are related to aggressive behaviour in great tits, as has been found in rodents and pigs, and whether this affects social dominance. In this study, aggressive behaviour and the outcomes of pair-wise fights were tested between juveniles of which the early exploratory behaviour was known.

Methods

Subjects

In 1990, 1991 and 1992 nestlings of great tits were collected from the wild when they were eight to twelve days old, and hand-reared (for details see chapter 2). We restricted ourselves to males, since agonistic behaviour differs between the sexes during development (Drent, 1983). All underwent the same procedures and experiments.

After hand-rearing (at an age of 4 weeks), the males were housed individually in standard cages of 0.9x0.4x0.5 m, with solid bottom, top, side and rear walls, a wire-mesh front and two perches. The birds were kept under natural light conditions, and had auditory and visual contact with other individually housed juveniles, but not with the ones they would be confronted with in later dominance measurements. They were provided with food and water *ad libitum.*

When the juveniles were 4 weeks old, we observed their exploratory behaviour for 10 min in a novel environment with five artificial trees. We recorded the time it took a bird to visit all five trees, the number of tree visits, the number of branch hops during a tree visit, and the time a tree visit lasted. Based on the results we classified the birds as fast and superficial, moderate, or slow and thorough explorers. In another exploration test at the age of 9-12 weeks, the time the birds took to approach a strange object that was placed in their own cage was recorded during repeated 2 min trials, and they were classified as fast or slow approachers (for details see chapter 2). Birds that were fast in both tests, or fast in one and moderate in the other, were classified as fast. Birds that were fast in one test and slow in the other, were classified as moderate. Birds that were slow in both tests, or slow in one and moderate in the other, were classified as slow. In 1990, 20 juveniles were used; nine slow, one moderate, and 10 fast explorers were classified. In 1991, 24 individuals were tested, yielding five slow, two moderate, and 17 fast explorers. For the experiment conducted in 1992, we randomly selected 14 fast explorers and 14 slow explorers.

Experiments

When the birds were 12-15 weeks old, we measured the aggressive behaviour and social dominance (expressed in terms of who won) in pair-wise confrontations. During a confrontation the birds could have several interactions in which one bird showed agonistic behaviour towards the other, and the other reacted to that with agonistic behaviour. An interaction began as soon as both birds showed agonistic behaviour, and ended when both birds showed other than agonistic behaviour. All interactions together that are shown during one confrontation are referred to as a fight.

The juveniles were tested in a similar cage as the one in which they were housed. For the test the cage was separated into two compartments of 0.4x0.4x0.5 m by a wooden slide, with two perches in each compartment. All observations were made between 1000 and 1500 hours. An hour before the confrontation, one juvenile was put into each compartment, which allowed adaptation to the environment and entailed deprivation of food and water. The confrontation started by removing the slide. An interaction was won if one bird showed aggressive behaviour and the opponent reacted by fleeing or crouching. As soon as one bird was the obvious winner, that is when he won ten interactions more than his opponent, the confrontation was concluded by reinserting the slide. After the confrontation, the birds were returned to their own cage. Each confrontation lasted for at least 10 interactions and at most 15 minutes. This maximum time limit was introduced to reduce the influence of gained fighting experience on the behaviour in subsequent fights. If the confrontation lasted 15 minutes because there was not an obvious winner or there were less than 10 interactions, the winner was appointed afterwards if that bird won at least two third of the interactions.

In 1990, each bird was individually confronted with three randomly chosen other males. Between confrontations, the birds had one day of rest. Confrontations between the same birds were repeated in random order after one week of rest. In 1991, each bird was confronted with each of five randomly chosen other birds. Each bird had one confrontation each day. In 1992, the hypothesis was tested that exploratory behaviour predicts the outcome of a fight. This hypothesis arose from the results produced in 1990 and 1991. Fourteen pairs, each consisting of a fast and a slow explorer, were confronted with each other once.

The confrontations were observed from behind a one-way screen and recorded on videotape. In viewing these tapes, the behaviour of each bird in each confrontation was analysed separately during the first two minutes after the first agonistic behaviour exhibited by the bird. Two minutes were chosen to have enough data to describe the behaviour of the birds, without including the whole confrontation since we were only interested in the first interactions, when the relation between the birds was still unclear. The behaviour was recorded continuously using an event recorder according to the definitions described by Blurton Jones (1968).

To assess initial aggressiveness, we used the time spent in the horizontal posture, expressed in percentage of the two minutes during which the behaviour was recorded. In this posture the legs are deeply bent and the body, head and beak form one horizontal line. The eyes are fixed on the opponent, the neck may be stretched towards the opponent, and the wings may be spread sideways. Often the beak is held open and a hissing sound is made. This behaviour is aggressively motivated, and commonly shown in feeding contests between wild first-year great tits when the opponents have little prior experience with each other

(Wilson, 1992b). The horizontal posture is quite distinct from other behaviour and thus easy to recognise, and the subjects spent much time on it during the tests. To minimise the influence of the various opponents on the behavioural data of each individual used in the analyses, the average percentage of time spent in the horizontal posture by an individual over the different confrontation tests it had was used. We will refer to this measure as the time in horizontal.

A second measure of aggressiveness was the fraction of the total number of confrontations of each bird, in which it was the first to initiate an interaction showing one of the following behaviours: approach, the head-up posture (aggressive posture with the body upright, the neck and legs stretched and the beak pointed upwards in line with the body, showing the breast stripe to the opponent), the horizontal posture or an attack (approach followed by physical contact, i.e. gripping, pecking and/or pulling or biting). We will refer to this measure as the fraction of fights started.

Morphological characteristics

When the nestlings were 15 days old and the tarsus was fully grown (Garnett, 1976), its length was measured to the nearest 0.1 mm using sliding callipers. Preceding the first and following the last confrontation, body mass was measured to the nearest 0.05 g using a laboratory balance, and stage of moult was scored on a scale of 0-10 (0=no moult, 10=moult complete) on the basis of the regular sequence of moult in different parts of the plumage. For both body mass and stage of moult, the average of the two measurements was taken. We selected the age of each bird on the day that half of all confrontations it had, had taken place for use in the data analyses. In 1991 and 1992, we also measured the size of the breast stripe after the last confrontation by taking a standard photograph from a fixed distance. The bird was placed on its back on a mm scaled paper. Using a digital image analysis system we measured the area of the stripe to the nearest 0.1 mm^2 between a line perpendicular to the anterior end of the sternum and a parallel line running 57 mm posteriorly.

Data analyses

In 1990 and 1991 only three individuals from the 44 birds tested were classified as moderate. This is not surprising since there is a correlation between the two measures of exploratory behaviour (chapter 2), indicating consistent individual differences in exploratory behaviour. Whether the three birds that showed inconsistency in their exploratory behaviour are a separate class of birds that really differs from the other birds, or whether this classification is due to artefacts, is not clear. However, this number is too small for proper statistical analysis, and we therefore had to omit these cases from our analysis.

In 1990, the three confrontations of each individual were repeated. The data of the second series of fights in 1990 were used only for analysis of the consistency in aggressive behaviour, not for any analysis using data from both 1990 and 1991 in order to have comparable data.

For analysis of the time in horizontal we used linear multiple regression. To obtain a normal distribution, the time in horizontal was arcsin√ transformed for such regressions (Kleinbaum *et al.*, 1988). We used logistic regression for the analysis of the fraction of fights started and the fraction of fights won. In the analysis of the time in horizontal and the fraction of fights started (both measures of aggressiveness) we included exploratory behaviour, age, tarsus length, weight, stage of moult and breast stripe and their interaction terms due to their possible influence. To test whether trends in aggressive behaviour differed between years, we also included the factor year and all interactions with it. In the analysis of fraction of fights won, we included both measures of aggressiveness in addition to exploratory behaviour, morphological variables and their interactions, and the factor year. Exploratory behaviour was treated as a dummy variable with two categories: fast and slow (Hosmer and Lemeshow, 1989). In the logistic regressions the significance of predictor variables was tested using the change in deviance and degrees of freedom when the variable was dropped from the model (Hosmer and Lemeshow, 1989). In all regression analyses, we followed a stepwise backward procedure (Kleinbaum *et al.*, 1988), after first checking all associations univariately ($\alpha=0.05$, two-tailed). We present the final models, and some more results where appropriate.

Results

Consistency and coherence in aggressive behaviour

Forty percent of the total recorded time was spent on agonistic behaviour, most of which (30.1%) was in the horizontal posture. Analysis of the repeated contests with the same (randomly chosen) pairs in 1990 showed that the difference in the time in horizontal was significantly higher between juveniles than between the repeated contests of one individual (One-way ANOVA; $n=60$, $df=59$, $F=5.11$, $p<0.01$). This indicates that the juveniles differed consistently in the time in horizontal. The repeated contests were most frequently initiated (sign test; $n=30$, $z=1.77$, $p<0.04$) and won (sign test; $n=30$, $z=3.47$, $p<0.01$) by the same bird, indicating, once again, consistent behavioural differences between individuals.

A linear regression with the data from 1990 and 1991 showed a positive correlation between the fraction of fights started and the time in horizontal (figure 1), which did not differ significantly between the years. This relation indicates coherence in the structure of aggressive behaviour.

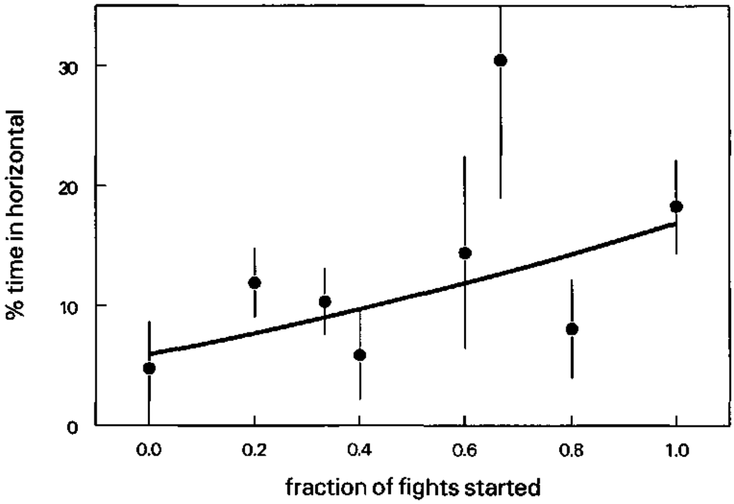


Figure 1. *The percentage of time spent in the horizontal posture (%hor) in relation to the fraction of fights started (fstart). Means and s.e. for each fraction of fights started are shown. Results of the regression: $\arcsin\sqrt{\%hor}=0.25+0.18 \times fstart$; $n=41$, $R^2=0.1$, $p=0.04$.*

Morphology, exploration and aggression

Predictors of the fraction of fights started

The fraction of fights started correlated significantly with exploratory behaviour (figure 2). Fast and superficially exploring birds were in confrontations more often the first to show aggressive behaviour than slow and thoroughly exploring birds. This indicates that individual differences in early exploratory behaviour are related to agonistic behaviour. Age, tarsus length, weight, stage of moult or size of breast stripe and their interaction terms were not significantly related to the fraction of fights started, nor was there a significant difference between the years.

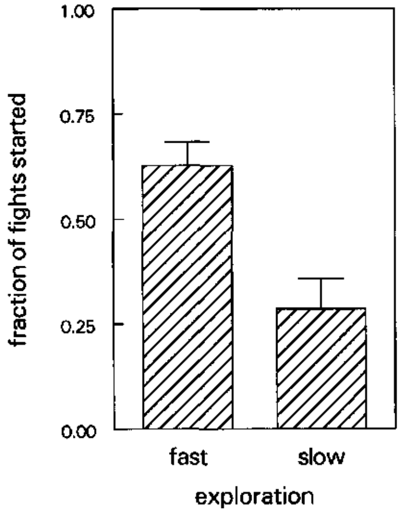


Figure 2. *The fraction of fights started in relation to early exploratory behaviour. Bars represent the mean and s.e.. The model is expressed as: logit (fraction of fights started)=0.52-1.51x(dummy: slow explorers); deviance=66.35, df=39. Comparison with a model with the intercept only, shows that this model is significant with a $p<0.01$ (Δdeviance=18.75, Δdf=1).*

Predictors of the time in horizontal

Weight, age and stage of moult were significantly related to the time in horizontal in the final multivariate model. The time in horizontal increased with body mass (figure 3a) and age (figure 3b), whereas it decreased with stage of moult (figure 3c). This means that heavy juveniles spent more time in horizontal than lighter juveniles, older more than younger, and juveniles that had just begun to moult more than juveniles that were about halfway through their moult. The interaction terms of these variables revealed no significant relation to the time in horizontal, indicating that these findings were not the result of correlations between weight, age and stage of moult. Tarsus length or size of breast stripe were not significantly related to the time in horizontal, nor was there a significant difference between years.

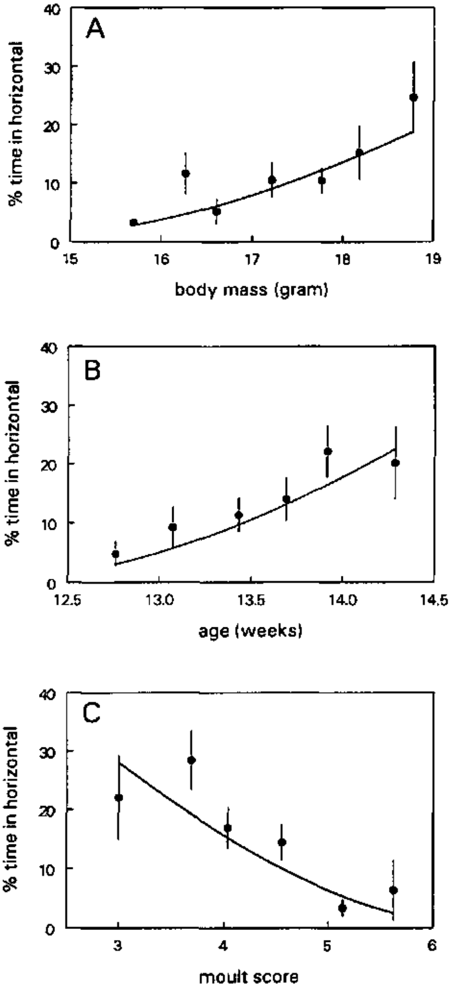


Figure 3. *The percentage of time spent in the horizontal posture (%hor) in relation to body mass (a), age (b), and stage of moult (c), given for a constant average value of the other two parameters. Means and s.e. are shown over each class of 0.5 gram (a), over each class of 2 days (b), and over each class of 0.5 score of moult (c). The final model is expressed as:*
arcsin√%hor=-3.39+0.09xbody mass+0.21xage-0.15xmoult; n=41, R^2*=0.26, p=0.01.*

The univariate analysis showed a relation between early exploratory behaviour and the time in horizontal: fast explorers spent more time in horizontal than slow explorers (t=-2.08, p=0.04). However, after correction for weight, age and stage of moult, exploratory behaviour was not significantly related to the time in horizontal (although there was a strong tendency: t=-1.94, p=0.06) and was therefore not included in the final model (figure 3).

Exploration and morphology
Since both exploratory behaviour and morphological traits predict aggressive behaviour, there could be a relation between these factors. The existence of such a relation could also imply that the relation between exploratory behaviour and fraction of fights started was actually caused by a morphological trait that was related to both exploratory behaviour and

aggressive behaviour. However, a two sample t-test showed that there was no significant difference between fast and slow explorers in weight (mean weight in grams ± s.d.: slow explorers :17.5±1.1; fast explorers: 17.6±0.7; n=41, p=0.67) and tarsus length (mean length in mm±s.d.: slow explorers :19.9±0.6; fast explorers: 19.9±0.7; n=41, p=0.96), or size of breast stripe (mean size in cm^2± s.d.: slow explorers :3.08±1.1; fast explorers: 2.91±0.8; n=22, p=0.69). Nor were there significant differences between fast and slow explorers in stage of moult as shown by a Mann Whitney U-test (U-statistic: slow explorers: 200.5; fast explorers: 177.5; n=41, p=0.76) or age (U-statistic: slow explorers: 155.5; fast explorers: 222.5; n=41, p=0.36). Summarising, there was no relation between exploratory behaviour and any of the morphological traits.

Exploration and dominance

Predictors of chances of winning

Analysis of the fraction of fights won from random opponents showed a significant relation with the two variables representing initial aggressiveness. The fraction of fights won increased with the fraction of fights started (figure 4a), and with the time in horizontal (figure 4b).

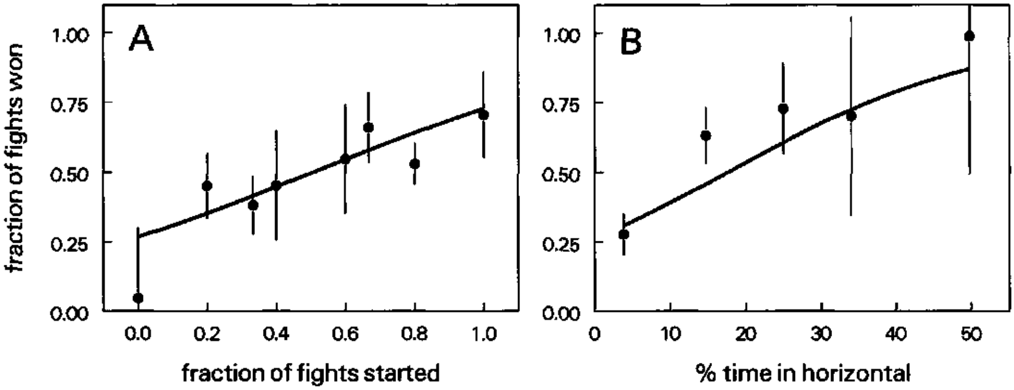


Figure 4. *The fraction of fights won in relation to the fraction of fights started (fstart), and the percentage of time spent in the horizontal posture (%hor), given for a constant average value of the other parameter. Means and s.e. are shown over each fraction of fights started (a), and over each class of 10 percent time in horizontal (b). The final model is expressed as:*

logit (fraction of fights won)=-2.14+1.97x(fstart)+0.09x%hor; deviance=60.18, df=38. Comparison with a model with the intercept only, shows that this model is significant with a p<0.01 (Δdeviance=44.28, Δdf=2).

When tested univariately, exploratory behaviour was significantly related to the fraction of fights won; fast and superficially exploring birds won more fights than slow and thoroughly exploring birds (this relation compared with a model with the intercept only: Δdeviance=5.41, Δdf=1, p=0.02). After correction for the fraction of fights started and the time in horizontal, however, the significant relation disappeared (Δdeviance=0.73, Δdf=1, p=0.39). Therefore exploratory behaviour is not included in the final model. Morphological traits were not significantly related to the fraction of fights won, either when tested univariately or multivariately.

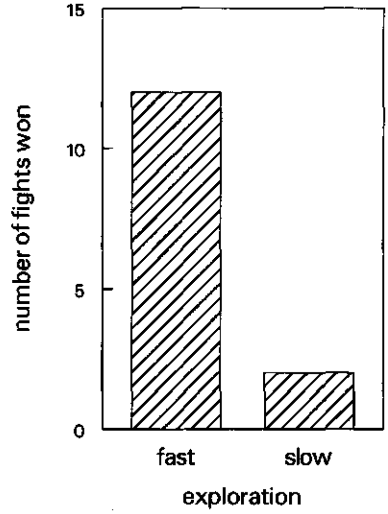


Figure 5. *Fights between pairs, each consisting of a fast and a slow explorer, are significantly more often won by fast explorers than by slow explorers. This result of a logistic regression can also be tested with a χ^2-test: n=14, χ^2=7.14, df=1, p<0.01.*

Exploration and winning: an experiment

In the contests between random opponents, fast explorers started more fights than slow explorers, and birds that started more fights also won more fights. Besides, fast explorers won a larger fraction of fights than slow explorers when tested univariately. We expected therefore fast explorers to win from slow explorers in pair-wise fights. We tested this hypothesis in an experiment with 28 birds in which 14 pairs, each consisting of a fast and a slow explorer, had one confrontation. The outcome of the fights was analysed with a logistic regression, in which we included exploratory behaviour and morphological traits. We did not include both measures of aggressiveness in the analysis; since the birds only fought once, the influence of the opponent on the aggressive behaviour shown was presumed to be large. In the final model only exploratory behaviour is included; none of the morphological traits was significantly related to the outcome of the fights. The result of the regression analysis is expressed as: logit(winning)=-1.79+3.58x (fast explorers); deviance=22.97, df=26. Comparison with a model with the intercept only, reveals that this model is significant with a p<0.01 (Δdeviance=15.85, Δdf=1). The model shows that, as expected, fast explorers won significantly more fights than slow explorers (see also figure 5). We conclude that early exploratory behaviour predicts future dominance in pair-wise fights.

Discussion

Behavioural differences and dominance

Figure 6 shows an overview of our results. We found consistent individual differences in aggressive behaviour, and a positive relation between both measures of initial aggressiveness (A in figure 6). This means that juvenile great tits can be characterised both by their exploratory (chapter 2) and aggressive behaviour. In the pair-wise contests between randomly chosen birds, fast explorers started more fights (B in figure 6), and showed a strong tendency to spend more time in horizontal during the fights (F in figure 6). This shows a relation between individual differences in exploratory behaviour and aggressive behaviour, which indicates that individual differences in juvenile great tits are consistent in two different behavioural systems.

The birds that started more fights also won more fights (G in figure 6). This suggests that the first blow is half the battle, which has also been shown in several other species (e.g. sticklebacks: Fitzgerald and Kedney, 1987; evening grosbeaks: Bekoff and Scott, 1989; dark-eyed juncos: Jackson, 1991). The univariate correlation between early exploratory behaviour and the fraction of fights won disappeared after correction for both variables of aggressive behaviour. This is not surprising, since aggressive behaviour at the start of a fight is closer to the outcome, in time and function, than exploratory behaviour measured weeks earlier, and exploratory behaviour and fraction of fights started are correlated. The univariate relation between early exploratory behaviour and fraction of fights won in randomly chosen birds, however, was confirmed by the experiment with selected pairs of fast and slow explorers (I in figure 6): fast explorers won from slow explorers. This implies that early behavioural characteristics are important predictors for dominance.

In pigs (Hessing *et al.* 1994) and rodents (Benus *et al.* 1987, 1990) aggressive individuals were found to be fast and superficial explorers and non-aggressive individuals were slow and thorough explorers, which strikingly agrees with our findings. Based also on other experiments both Benus (1988) and Hessing (1994) conclude that these differences represent different behavioural strategies, that become particularly overt in stressful situations, like novel environments, fights, inescapable shocks etc. Also in other species (e.g. dogs: Corson and Corson, 1976; tree shrews: von Holst, 1986; baboons: Sapolsky, 1990) different behavioural and physiological responses to a challenge have been found. In general two strategies to cope with stress have been described: an active or a passive strategy. Active copers show the tendency to actively manipulate the situation that causes stress, whereas passive copers try to adjust to the situation. In the mentioned studies of rodents and pigs, aggressive individuals showed an active coping strategy; their behaviour was aimed at getting away from the source of stress or at removal of the source of stress itself. They initiated fights faster (Benus, 1988) and more often (Hessing *et al.*, 1993), and when defeated they fled more often (Benus, 1988) than passive copers. Non-aggressive individuals showed a passive coping strategy; their behaviour was aimed at adjusting themselves. They did not initiate fights fast or often, and when defeated they showed much immobility.

In juvenile great tits, the early exploratory behaviour and aggressive behaviour in pair-wise fights of the fast explorers seem to agree with an active coping style, while the behaviour of the slow explorers resembles a passive coping style.

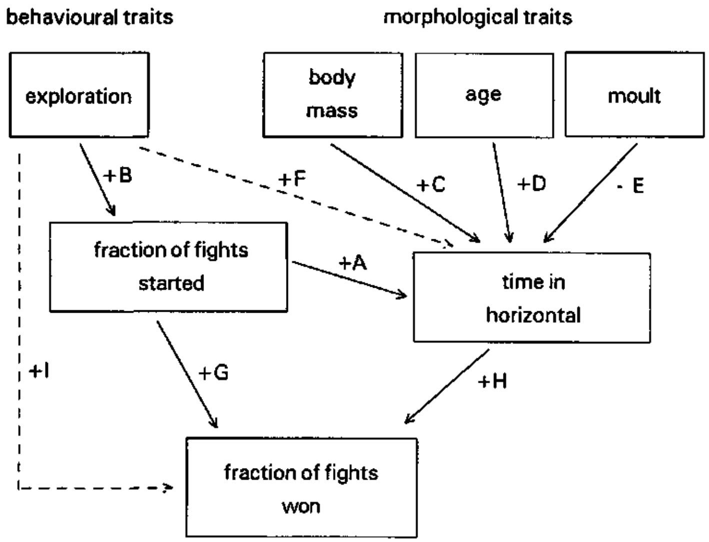


Figure 6. *Summary of the results in a flow diagram. All independent relations we found are indicated with solid arrows. Arrow A refers to the relation shown in figure 1, arrow B to figure 2, arrows C, D and E to figure 3, arrow G and H to figure 4, and arrow I to figure 5. This latter arrow is dotted, because the relation is not independent from those indicated by arrow B and G. Arrow F is also dotted and not shown in a figure, because the relation is significant when tested univariately, but not any more after correction for body mass (C), age (D) and moult (E). + indicates a positive relation, - a negative. For relations with exploration, + indicates that fast explorers showed a higher value of the related variable than slow explorers.*

Morphology and aggressive behaviour

Body mass, age, and stage of moult (independently of each other) predicted the time in horizontal (C, D, E in figure 6), which in turn predicted the fraction of fights won (H in figure 6). We did not find a direct relation between body mass, age or stage of moult and the fraction of fights won, although this has been observed by several authors (Kluyver, 1951; Garnett, 1976; Drent, 1983; Järvi and Bakken, 1984; Sandell and Smith, 1991).

The relation between body mass and the time in horizontal (C in figure 6) suggests that the positive correlation between social status and body mass found in the field situation is mediated by differences in level of aggressive behaviour.

Developmental differences between the combatants may be underlying the relation between age and time in horizontal (D in figure 6). At the time of testing the gonadal system was probably still developing (Balthazart, 1983). This would cause the plasma concentration of testosterone to still be rising to a peak value that is normally reached in September (Röhss and Silverin, 1983), corresponding with an increase in aggressive behaviour in juveniles from June to November (Drent, 1983; de Laet, 1985). It is possible that older juveniles had higher testosterone levels and, therefore, higher levels of aggressive behaviour, expressed in time in horizontal.

The relation between moult and time in horizontal (E in figure 6) is probably mediated by levels of thyroid hormone (Huntingford and Turner, 1987). This hormone induces moulting and has a negative influence on the gonadal system, causing a reduction in testosterone and thus in level of aggression (Assenmacher, 1973). This might explain why juveniles that had just started moulting were more aggressive than juveniles that were halfway through the moult. Moulting causes increased vulnerability, making high levels of aggressive behaviour inappropriate (Huntingford and Turner 1987).

We found no relation between aggressive behaviour or fraction of fights won and the width of the breast stripe, although we expected to corroborate the results of Lemel and Wallin (1993). Great tits show their breast stripes to each other through the head-up posture. On average, of the total time spent on agonistic behaviour, very little was spent in the head-up posture (5.3%). This may indicate that the breast stripe was not an important signal in the context of our experiments. Drent (1983) noticed that juveniles show the head-up posture less frequently before moulting than after moulting. Our (unpublished) recordings of time spent in the head-up posture by juveniles before and after moult confirm this observation (Wilcoxon Matched Pair test: $T=3$, $n=8$, $p=0.04$). It is possible that the breast stripe becomes an important signal only after the first moult, when the male juveniles develop a clear dark stripe.

Processes underlying aggressive behaviour

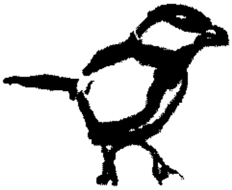
Since the fraction of fights started was predicted exclusively by early exploratory behaviour (B in figure 6, $p<0.01$), and the time in horizontal mainly by body mass, age, and stage of moult (C, D, E in figure 6), this suggests that different processes underlie the two measures of aggressive behaviour. This suggestion is supported by the fact that the relation between both measures of aggressive behaviour was relatively weak (A in figure 6). It is possible that at the start of the fight, differences in organisation of behaviour prevail over the behaviour shown. However, during the fight, when the birds communicate with each other through their agonistic behaviour, the influence of the opponent on this behaviour may become more important. The horizontal posture could be a signal to the opponent about the bird's assessment of its own motivation and fighting ability relative to that of his opponent. In that case, the bird's assessment was supported by its physical and developmental condition (body mass, age and stage of moult). Tests with detailed sequential analysis of actions and subsequent reactions of contestants may shed more light on the underlying processes.

The relatively simple way of determining dominance in pair-wise fights did enable us to demonstrate that individual differences in exploratory behaviour are related to aggressive behaviour, which affects dominance. In the wild juvenile dominance relations develop in flocks, which is a more complex situation. Further experiments with aviary groups and measurements in the field are therefore needed.

A dominant bird (left, in horizontal posture) and a subordinate bird (right, crouching) in an experimental pair-wise confrontation

CHAPTER 4

INDIVIDUAL BEHAVIOURAL CHARACTERISTICS AND DOMINANCE IN AVIARY GROUPS OF GREAT TITS



M.E.M. Verbeek, P. de Goede, P.J. Drent and P.R. Wiepkema

Accepted by Behaviour (1998)

CHAPTER 4

INDIVIDUAL BEHAVIOURAL CHARACTERISTICS AND DOMINANCE IN AVIARY GROUPS OF GREAT TITS

Abstract

In previous work we have shown that juvenile male great tits Parus major *show consistent behavioural differences in exploratory and aggressive behaviour. Fast and superficial explorers (FE) won from slow and thorough explorers (SE) during controlled pair-wise confrontations in small cages. The present study assesses the relationship between early exploratory behaviour and later dominance in aviary groups of juvenile male great tits; such groups might approach natural conditions better than 'simple' pair-wise confrontations. Observations of nine aviary groups showed that a stable hierarchy is only established after a first dynamic phase of several days with many dominance shifts and a peak in number of interactions. In seven other aviary groups we determined the dominance relationships between FE and SE. In a stable hierarchy, SE had on average a significantly higher dominance score than FE. This finding contrasts our previous results in pair-wise confrontations. However, on the first day in the aviary, FE had on average a higher dominance score and initiated more fights than SE. This agrees with our previous results and indicates a gradual development of the situation in the stable hierarchy. Behavioural observations indicate that during this development, FE took more risks in their fighting behaviour and had more difficulty to cope with defeat than SE. In the stable hierarchy they either won or lost from all SE. SE were more cautious and had intermediate dominance scores in the stable hierarchy. These differences in fighting behaviour and the role of individual differences in exploratory behaviour and in coping with defeat are discussed as possible causes for the unexpected results of this study.*

Introduction

Social dominance has important consequences for fitness since it affects territory acquisition, mating success, reproduction, and survival (Huntingford and Turner, 1987). Several factors determine social dominance (for an overview see Pusey and Packer, 1997). Differences between rivals in size, weight, strength or fighting ability can influence dominance. The value of the resource over which fights take place may be different for rivals, which can affect dominance. If one rival is resident in the area, he generally wins from the one that came later.

Experience in fights can also be important. An individual who has lost earlier fights, has a higher chance to lose again, while winners will probably win again, even from a bigger opponent.

Apart from these factors, individual behavioural characteristics can also affect social dominance. For example, mice and rats show consistent individual differences in their levels of aggression, measured in tests against standard opponents. The differences are considerable and have a genetic basis (Lagerspetz, 1964; van Oortmerssen and Bakker, 1981). These levels are associated with social rank in a group (van Oortmerssen *et al.*, 1985; Fokkema, 1985). Experiments with genetically selected aggressive and non-aggressive mice show that they differ in their physiological and behavioural response to social interaction (Benus *et al.*, 1991). Aggressive mice react in an active way and either attack or flee, while non-aggressive mice react in a more passive way and when attacked they withdraw and become immobile. These different types of reactions, active versus passive, were also found in non-social situations (Benus *et al.*, 1987; Benus *et al.*, 1990). Non-aggressive mice and rats spend a great deal of time on exploration in a novel environment and remain alert to stimuli in a known environment. Aggressive individuals spend less time on exploration, and soon lose their attention to details in the environment and rely on their previous experience. Similar correlations between exploratory behaviour and aggressive behaviour were found in pigs (Hessing *et al.*, 1994). In open field tests non-aggressive pigs hardly try to escape, and approach a novel object slowly but explore it intensively, spending much time on exploration. On the other hand, aggressive pigs have a tendency to escape a novel environment and approach a novel object fast, but explore it short and superficially. Based also on other experiments both Benus *et al.* (1991) and Hessing *et al.* (1994) conclude that these individual differences represent different behavioural strategies to cope with stressful situations like novel environments and agonistic interactions.

In great tits, dominance is affected by body size, weight, age, sex, experience, prior residence and possibly size of the breast stripe (Garnett, 1981; Drent, 1983; Dhondt and Schillemans, 1983; de Laet, 1985; Sandell and Smith, 1991; Lemel and Wallin, 1993). Behavioural characteristics also predict dominance. Juvenile male great tits show consistent individual differences in exploratory behaviour (chapter 2; Marchetti and Drent, submitted). Some juveniles consistently approached a strange object quickly in repeated measurements. We will refer to them as 'fast explorers': FE. Other juveniles consistently approached a strange object slowly; the 'slow explorers': SE. FE also explored a novel environment fast but superficially. They developed more rigid foraging habits and did not rapidly adjust their behaviour to a change in the feeding situation. SE explored a novel environment slowly but thoroughly and quickly adjusted their foraging behaviour to an environmental change. They paid more attention to the environment than FE, both in new and in well-known stable environments. These differences in exploratory behaviour were related to aggressive behaviour and dominance. FE initiated more fights and won more often fights than SE in short lasting pair-wise confrontations (chapter 3). These findings strikingly agree with the individual behavioural differences found in mice, rats and pigs and suggest that also in wild juvenile great tits different coping strategies may exist.

Given the ecological importance of dominance and behavioural strategies, one might raise the question in how far our previous and 'simple' experiments in which we measured aggressive behaviour and dominance of juvenile great tits in pair-wise fights in small cages, increase our insight into what happens in nature. There, dominance relations between juvenile great tits are established in flocks during the summer and autumn, implying complex interactions. However, in such flocks the development of dominance relations and behavioural differences are very hard to determine. Therefore we studied aviary groups, where the juveniles have at least more space than in simple cages and will meet a number of different flock mates. The aim of this study is to assess whether early exploratory behaviour may also predict dominance in aviary groups of juvenile male great tits.

Methods

We first studied the general process of the formation of dominance hierarchies in nine aviary groups. Then we formed seven other groups with both FE and SE to examine dominance relationships between them in a stable hierarchy. Because of the preliminary results of four of these seven groups, we observed in more detail the behaviour of FE and SE during the formation of the dominance hierarchies in a subset of three of these seven groups

Birds

The study was conducted with juvenile great tits, collected from the wild as nestlings and hand-reared (for details see chapter 2). We restricted ourselves to males, since agonistic behaviour differs between the sexes during development and females generally lose from males (Drent, 1983).

Before the start of the experiments, all birds were housed individually in standard cages of 0.9x0.4x0.5 m, with solid bottom, top, side and rear walls, a wire-mesh front and two perches. The birds were kept under natural light conditions, and had auditory and visual contact with other individually housed juveniles, but not with the ones they would be confronted with in later dominance measurements. They were provided with food and water *ad libitum.*

Formation of dominance hierarchies

The general process of the formation of dominance hierarchies was studied in nine groups of birds (n=54, group size 5 to 8 juveniles) aged 16-17 weeks at the start of the observations. The birds of each group were introduced simultaneously in the aviary without handling by opening a slide in the rear wall of their individual cages, giving access to the aviary. The aviaries of 2x4x2 m contained a feeding table, a drinking bowl, eight nest boxes, many perches and an artificial tree made of wood (figure 1). The birds were kept under natural light conditions and provided with *ad libitum* sunflower seeds and commercial seed mixture, supplemented daily with mealworms and the protein-rich mixture on which they had been reared. They were observed from behind a one-way screen during two 30 minutes periods, one in the morning and one in the afternoon, for a period of 11 successive days. All aggressive interactions and their outcomes were recorded. For each observation day, we summed the outcomes of the fights between each possible pair of birds. The bird that won 67% or more of the total number of interactions between the pair was considered the winner. The dominance relationship of a pair was considered unclear (a tie) if the percentage of fights won was between 33% and 67%.

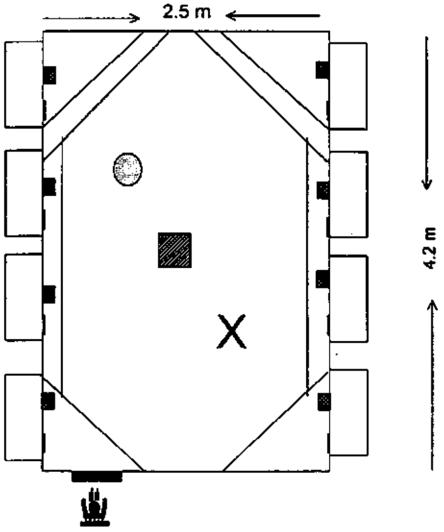


Figure 1. Aviary with feeding table, drinking bowl, nest boxes and artificial tree made of wood.

The birds in these nine groups were of the same age and sex (males) and reared/housed the same way as the other birds in this study. For all birds the social environment of the group was new. We considered the similarities between the birds of these nine groups and the other birds in this study large enough to use their data as a reference to derive criteria for a stable hierarchy.

Relationship between exploratory behaviour and dominance

Exploratory behaviour

To assess whether early exploratory behaviour predicts dominance in aviary groups, we classified 51 birds (other than in the nine groups described above) as FE, SE or intermediate explorers based on two exploration tests. Details of the tests and the results of 26 of the 51 tested birds can be found in chapter 2. At an age of four weeks the birds explored a novel environment with five artificial trees during 10 minutes and we recorded the time it took a bird to visit all five trees. Based on the results we classified the birds as fast and superficial, intermediate, or slow and thorough (figure 2A). In another exploration test at the age of nine weeks, we recorded the time the birds took to approach a strange object that was placed in their own cage during repeated 2 minute trials, and they were classified as fast or slow approachers (figure 2B). Based on these results, 22 of the 51 birds were classified as FE because they were fast in both tests, or fast in one and intermediate in the other. There were 25 SE who were slow in both tests, or slow in one and intermediate in the other. The remaining four birds were fast in one test and slow in the other; they were classified as intermediate explorers. These latter birds were not included in the aviary groups, because there were only very few of them.

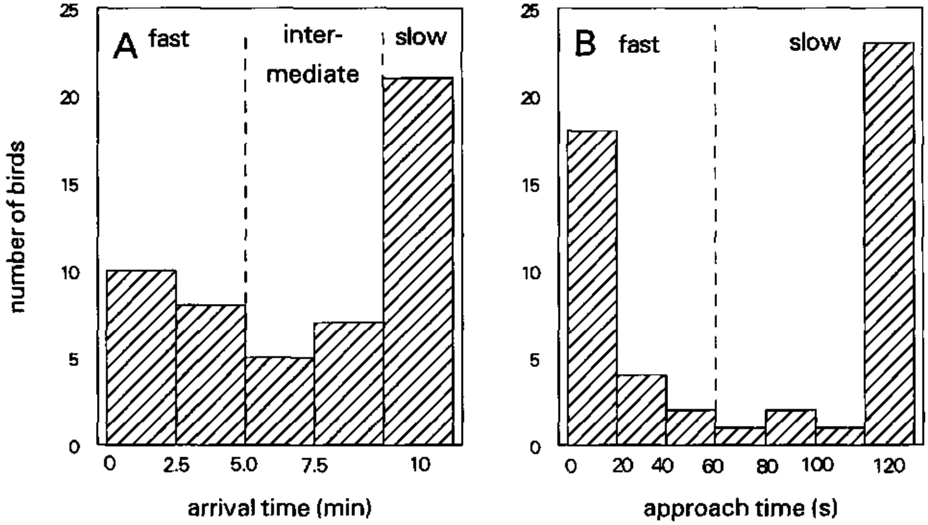


Figure 2. *Frequency distributions of A: the arrival time at the fifth tree in the novel environment (data grouped per 2.5 min; 10 min indicate birds failing to arrive within the trial time) and B: the approach time to a strange object in the home cage (data grouped per 20 sec; 120 s indicate birds failing to approach within trial time). Classification criteria are shown (dotted lines).*

Group observations

We formed seven groups with the 47 classified FE and SE (group size five to eight birds), when they were 16 weeks old. Each group consisted of both FE and SE, with at least two birds per class. As in the nine groups, the birds were introduced simultaneously in the aviary (figure 1). In four of the seven groups behavioural recordings started four days after the birds were introduced in the aviary. We observed one hour a day, four days a week for four weeks and recorded the aggressive interactions and their outcomes. After two weeks a stable hierarchy was established. We summarised the data of the last two weeks to determine the dominance relations in the stable hierarchy, using the same criteria for winning and losing as in the nine groups.

In three of the seven groups we determined dominance relations both at the initial phase of the hierarchy development and after stabilisation of the hierarchy. Immediately after introduction in the aviary we observed the birds continuously for seven hours. During these observations the details of each interaction were recorded: who initiated it, target, behaviour involved (as described by Blurton Jones, 1968), location where the interaction took place and outcome. On that first day we also gathered behavioural data of the birds when they were not having an interaction, by alternately observing each bird for one minute during two continuous periods of three hours with a break of one hour in between. After the first day, we reduced the observations to two 30 minutes periods, one relations. We stopped observations when a stable hierarchy was established and after a minimum of six days. The dominance relations in the stable hierarchy were determined on the basis of the total data set of the last two days.

Although the duration of observations differed between groups, in all seven groups dominance relations were determined after establishment of a stable hierarchy when very few dominance shifts occurred. Therefore we used the combined data of all seven groups to assess the relation between early exploratory behaviour and dominance in a stable hierarchy.

Dominance

Dominance in groups can be expressed in many different ways. An often used measure of dominance is the number of animals from which one wins, expressed as a percentage of the total number of animals one has an interaction with. However, we were primarily interested in a possible relationship between FE, SE and dominance, and this measure could obscure such a relationship because the groups were not all composed of an equal amount of FE and SE. For example, imagine a group with two FE and six SE in which both FE win from all SE. There will still be some SE with a relatively high dominance score because they win from most other SE. To take this into account we adjusted the dominance measure. In this study, the dominance score of a bird is expressed as the number of animals of the other exploration class (than the bird's own) from which the bird won, relative to the total number of animals of the other exploration class with which the bird had interactions. So a SE who wins from all FE he has interactions with, gets a dominance score of 1. A FE who wins from half of all the SE he has interactions with gets a dominance score of 0.5, and a FE who loses from all SE gets a dominance score of 0. Unclear dominance relations (ties) were treated as winning from 0.5 bird.

Other measurements

Besides early exploratory behaviour, several other characteristics may affect dominance. Therefore tarsus length, body mass, age and moult score (on a scale of 1-10) were measured the day before the birds were put together. At the start of the study, most birds were halfway through their moult or even further in their moult, but no bird had finished moulting before the end of the study. In the three groups that were observed continuously during the first day in the aviary we also measured the size of the breast stripe (for details see chapter 3).

Data analyses

The dominance scores, expressed in fractions, often had extreme values since the denominator, the total number of animals of the other exploration class with which the bird had interactions, was usually small. If a bird had a dominance score of one obtained by winning from five other birds, we considered this more meaningful than if it had the same score obtained by winning from two other birds. Given these facts, we considered logistic regression of the dominance score, weighed for the total amount individuals with which the bird had interactions as the most appropriate method of analysis to assess a relation between exploratory behaviour, morphological and physical characteristics and dominance (see also Crawley, 1993). We coded exploratory behaviour as a variable with two categories: FE and SE. We included tarsus length, body mass, age, moult score, and (when possible) breast stripe and their interaction terms with exploratory behaviour in the full model, to assess their possible influence on dominance. To test whether a possible relation between exploratory behaviour and dominance differed between groups, we also included group as a categorical variable and the interaction between group and exploratory behaviour. We followed a stepwise backwards elimination procedure, unless stated otherwise. The significance of predictor variables in logistic regressions was tested using the change in deviance and degrees of freedom when the variable was dropped from the model (Hosmer and Lemeshow, 1989). The contribution to the explained variance of the variables in the final models as presented in the tables (i.e. the change in deviance with accompanying change in degrees of freedom) was determined by removing each variable, in turn, from the final model. When the residual scaled deviance of the final model was considerably larger than the residual degrees of freedom, an F-test was used to test for significance, otherwise a χ^2 test was used (α=0.05, p-value two-tailed).

CHAPTER 4

Results

Formation of dominance hierarchies

In each of the nine groups a stable hierarchy gradually developed. Linear regression analysis showed that during this development, the number of interactions per hour in the groups increased, peaked after approximately 3 days and then decreased again and seemed to stabilise towards the end of the observations (figure 3, solid line). There were no significant differences between the groups in this curve. During the first 2-3 days the majority of interactions in the groups took place between the two highest ranking birds. The number of interactions within this highest pair of birds decreased after several days. There were less interactions between the highest and lowest ranking bird in the hierarchy, and this also decreased after several days. Birds with middle or low ranks had even less interactions with each other than the highest and lowest ranking bird, but interactions between these birds did not decrease during the stay in the aviary. The daily numbers of interactions within pairs in the groups were sufficient to determine dominance relations, and most of these relations showed a clear winner and loser.

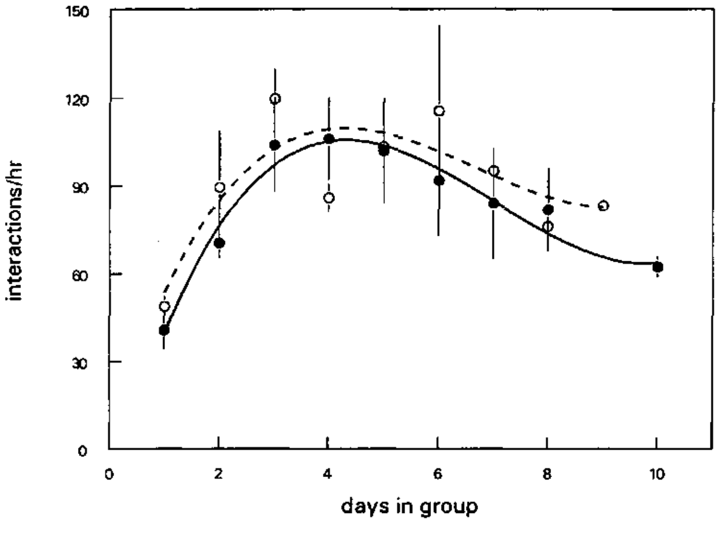


Figure 3. *Number of interactions per hour during the formation of a hierarchy in nine groups (•, mean ± s.e.) and three other groups observed in more detail (○, mean ± s.e; after 6 days ○ represents data of only one group since observations of the other groups had stopped). The regression lines of best fit are given. Solid line for nine groups:*
int/hr= $-16.54+66.42\text{xday}-11.12\text{xday}^2+0.53\text{xday}^3$*; n=65,* $R^2=0.29$*,* $p<0.001$*.*
Dotted line for the three groups observed in more detail:
int/hr= $5.02+57.79\text{xday}-9.91\text{xday}^2+0.49\text{xday}^3$*; n=21,* $R^2=0.37$*,* $p<0.05$*.*

During the formation of a stable hierarchy, dominance relations between two birds could change: from one day to the next, winners could turn into losers or clear relationships could become unclear by the absence of an obvious winner. With such rapid changes, criteria for a stable hierarchy needed to be derived before the relation between exploratory behaviour and dominance could be assessed. Therefore we analysed the general trend in time of the stability of hierarchy in the nine groups with a linear regression analysis. As a measure for instability we used the percentage of the pairs of birds with a dominance shift from one day to the next, relative to the total number of pairs in the group. During the first one or two days after introduction in the aviary many dominance shifts occurred (figure 4, solid line). In the subsequent days instability of the hierarchy decreased to a level below 10% dominance shifts, but never reached zero during the 11 days in the aviary. There were no significant differences in this trend between the nine groups. In these groups it was generally clear within a few days time which individuals were at the top and the bottom places of the hierarchy (after four days on average, ranging from one to eight days). After that, most dominance shifts occurred among individuals with an intermediate dominance score, usually between the same pairs during several days. Based on these data, we regarded a hierarchy stable when during at least two subsequent days less than 10% of the pairs showed dominance shifts, with shifts only occurring among the individuals with an intermediate dominance score. In the nine groups these criteria were met on average after seven days in the aviary (ranging from three to eleven days).

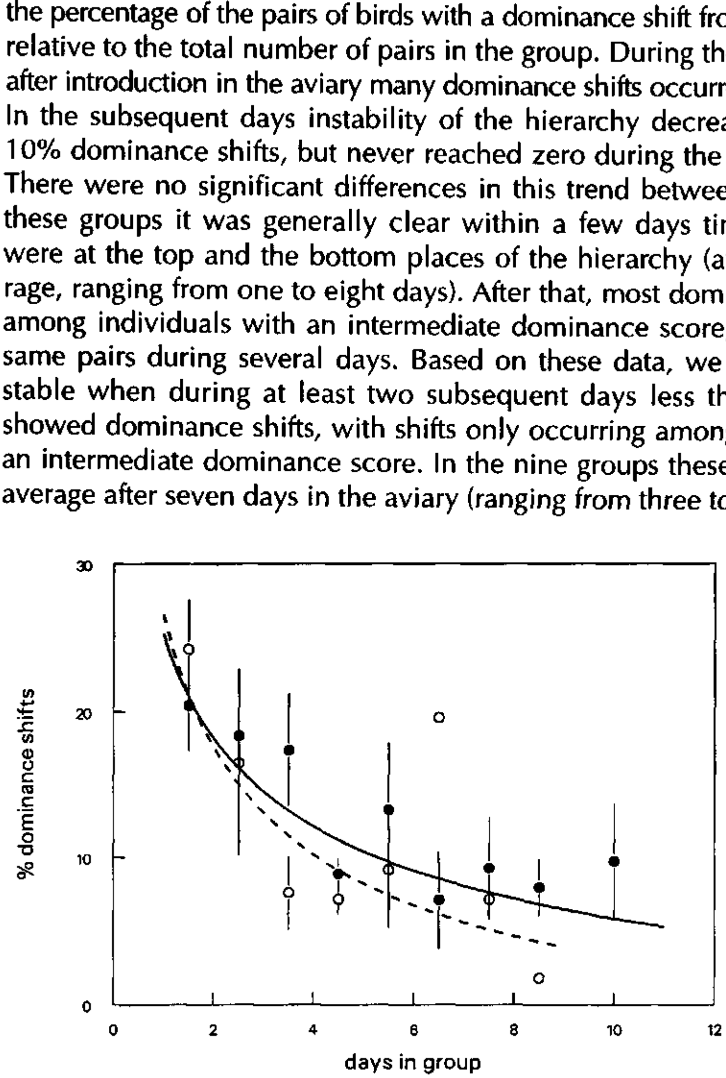


Figure 4. *Development of stability of the hierarchy in nine groups (●, mean ± s.e.) and three other groups observed in more detail (○, mean ± s.e; after 6 days ○ represents data of only one group since observations of the other groups had stopped). The regression lines of best fit are given; for the regression analysis the % dominance shifts were arcsin√ transformed to obtain a normal distribution.*
Solid line for nine groups: $\arcsin\sqrt{(\text{dominance shift})} = 0.53-0.13 \times \ln(\text{day})$; $n=54$, $R^2=0.25$, $p<0.001$.
Dotted line for the three groups observed in more detail:
$\arcsin\sqrt{(\text{dominance shift})} = 0.54-0.16 \times \ln(\text{day})$; $n=18$, $R^2=0.40$, $p=0.005$.

Exploratory behaviour and dominance in a stable hierarchy

After stabilisation of the hierarchy we analysed the relationship between early exploratory behaviour and dominance score in the seven groups with FE and SE. Logistic regression showed that both exploration and the interaction between exploration and moult were significantly related to dominance score (table 1). There was no significant difference between the seven groups in this relation, even though the procedure differed slightly. The significance of the variable 'exploration' shows that on average SE had a higher dominance score than FE (figure 5). The significance of the interaction between exploration and moult means that moult was also related to the dominance score, but this relation differed between FE and SE. FE almost ready with moulting had a higher dominance score than FE about halfway moulting. For SE the relation between dominance and moult tended to be the opposite. Separate analysis of FE and SE showed that the relation between moult and dominance was significant for FE ($p=0.03$) but not for SE ($p=0.14$). There was no significant difference in average moult score between FE (mean score: 6.39) and SE (mean score: 6.68; t-test: $n=47$, $t=-1.54$, $p=0.13$). The variance of moult score of SE (score range: 5.0-8.5, var=0.73) was significantly larger than that of FE (score range: 6.0-7.5, var=0.17; $f=4.40$, $p<0.01$), which one would sooner expect to lead to a significant relation between moult and dominance score in SE than in FE.

Table 1. Logistic regression analysis of dominance in a stable hierarchy. Null model includes the constant only. Final model includes the significant parameters and the lower order terms that are part of significant interaction terms regardless of their significance (moult in this case). The variable 'exploration' had two categories: SE (exploration=0) and FE (exploration=1). See also figure 4.

	(Increase in)			Estimates of coefficients	
Parameter	deviance	df	p	SE	FE
null model	87.95	46			
final model	68.36	43			
constant		1			
exploration	16.49	1	< 0.01	1.218	-19.974
moult	0.23	1	0.71		
explxmoult[1]	16.01	1	< 0.01	-0.152	3.071

[1] explxmoult is the interaction between exploration and moult

The relation between exploration and dominance score confirms that early exploratory behaviour predicts at least partially later dominance. However, the result that on average SE had a higher dominance score than FE is quite surprising, since in pair-wise confrontations in small cages, FE won from SE (chapter 3). A more detailed look at the stable hierarchies formed, showed that there were exceptions of the relationship found. Although most FE had a low dominance score, in five of the seven groups a FE won from all SE. This becomes more obvious if the frequency distribution of dominance scores is considered (figure 6). The frequency distribution of the SE roughly follows a normal distribution where the largest number of birds (18 of 25) have an intermediate dominance score between 0.2 and 0.8. In contrast, the frequency distribution of the FE tends to follow a bimodal distribution where many birds (13 of 22) have extreme dominance scores of 0-0.2 or 0.8-1.0. This means that FE more often either lost or won from all the SE in the group, while SE generally lost from some and won from some FE. This difference in frequency of extreme dominance scores between FE and SE was significant (χ^2=4.63, df=1, p=0.03).

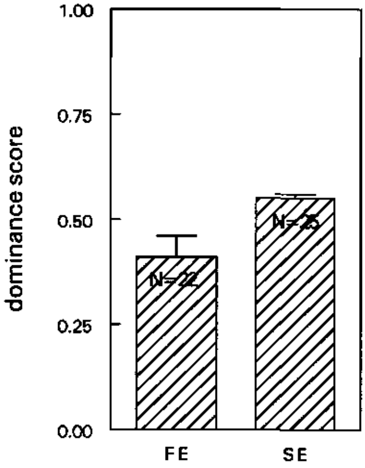


Figure 5. *Mean (+ s.e.) dominance score of FE and SE in a stable hierarchy, given for the average moult score of FE and SE. See also table 1.*

Exploratory behaviour and dominance during hierarchy development

Formation of hierarchy

The data of the nine groups indicated that the stable hierarchy is the result of a preceding instable period. In three of the seven groups (20 birds in total, group size six to seven birds) we observed the birds during the whole period of development of a stable hierarchy, with a special emphasis on the first day since most changes in dominance happen then. The number of interactions per hour in the three groups during the days in the aviary was analysed with linear regression, resulting in the (broken) regression line in figure 3. This regression line did not differ significantly from the (solid) regression line based on the data of the nine groups (n=86, t=1.0, p=0.32). The three groups did not differ significantly in the number of interactions per hour, nor in the relation between time spent in the aviary and number of interactions.

Analysis of the development of stability of hierarchy during the days in the aviary indicated that the regression line based on the data of the three groups (figure 4, broken line) did not differ significantly from the regression line based on the data of the nine groups (n=72, t=-0.82, p=0.42). There were no significant differences between the three groups in the level of dominance shifts or in the relation between time spent in the aviary group and stability of the hierarchy. Many dominance shifts occurred during the first two days, but this instability of hierarchy rapidly dropped, and in two groups the hierarchy was stable within the minimum observation time of six days. In the third group it took nine days before the hierarchy was stable. In this group the percentage of dominance shifts between day 6 and 7 was much higher than would be expected based on the regression line (outlier in figure 4). After the first two to five days, in all three groups dominance shifts only occurred between birds of the middle ranks in the hierarchy. By then the birds in the top and the bottom of the hierarchy had already established stable relationships. Details on the daily dominance relations and shifts in the three groups are shown in diagrams in figure 7. The diagram of group 2 shows that on day 7, dominance relations of all possible dyads in the group could be determined, while in the preceding days this was not the case. Dominance shifts that might have happened already in the preceding days but that were not observed until day 7, are therefore all accumulated in the dominance shift between day 6 and 7, which might explain the outlier in figure 4. Because the hierarchy of the three groups developed in a similar way as in the nine reference groups, we assume the results of this subset are representative

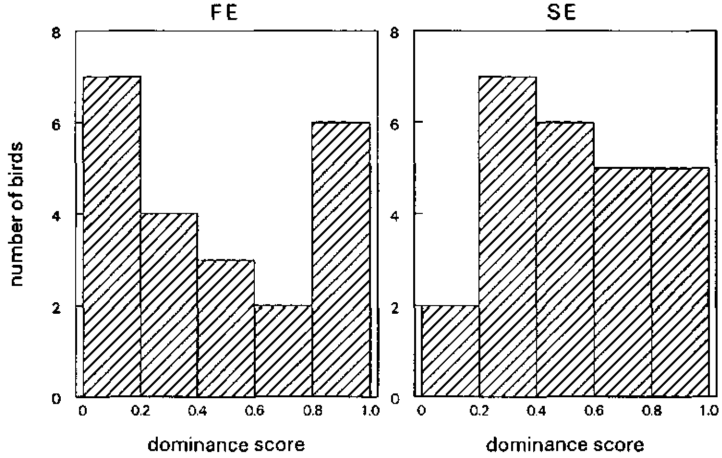


Figure 6. *Frequency distribution of the dominance score of FE and SE in a stable hierarchy. Data are grouped per 0.2 dominance score.*

Exploratory behaviour and dominance on the first day

After introduction in the aviary, the birds generally flew up and down the cage very fast, as in a panic. After a few minutes they turned back to calmer behaviour and started to explore the aviary. Only after some time was spent on exploration, the first aggressive interactions in the group took place (on average after 51 min: after 29, 43 and 81 min respectively). The birds differed considerably in exploration time before they initiated their first interaction. While the first birds initiated their first aggressive interactions within two hours after introduction in the aviary, others only initiated their first interaction after four hours.

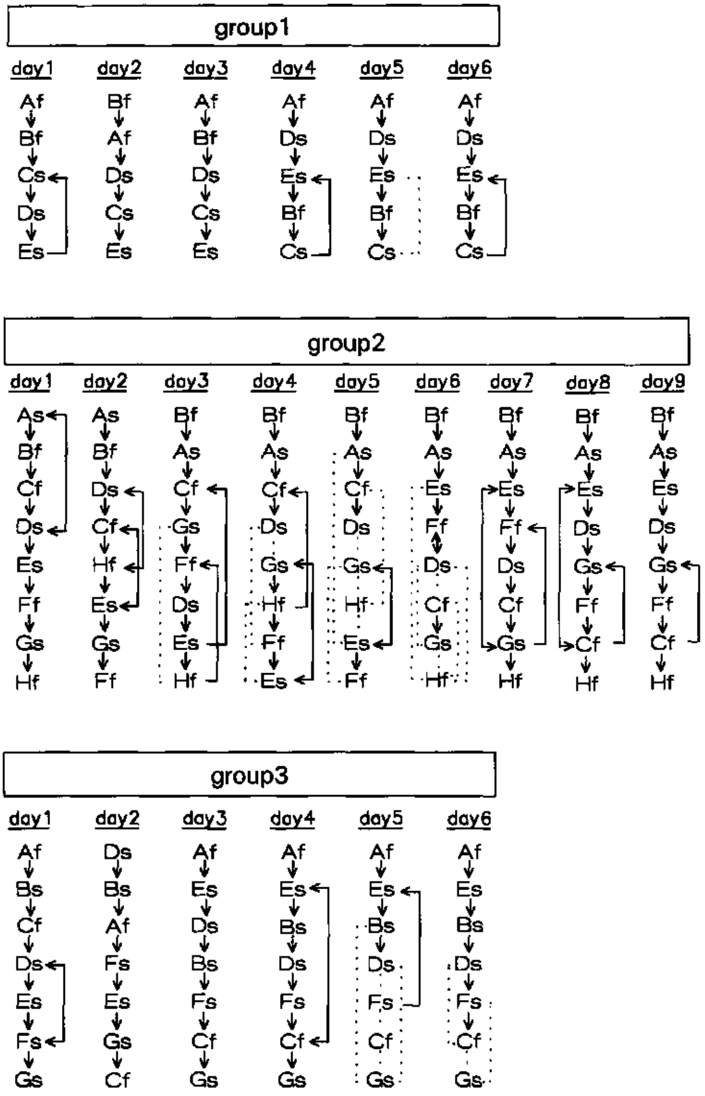


Figure 7. *Daily rank orders during hierarchy formation in three groups. Individuals A-E (group 1), A-H (group 2) and A-G (group 3) are FE as indicated by f, or SE as indicated by s. Dominance relations are indicated by solid arrows pointing to losers. Birds high in the vertical row win from all lower birds, unless indicated otherwise. Solid arrows pointing upwards indicate that the lower ranking bird wins from the higher one. Dotted lines indicate absence of any observed interaction between the two birds on that day. Lines with arrows on each side indicate unclear dominance relations (ties).*

For the logistic regression analysis of the variation in dominance scores on the first day, we summarised all data of interactions we observed that day. Besides exploration, we also included tarsus length, body mass, age, moult score, breast stripe, group and their interaction terms with exploratory behaviour in the analysis. Due to overfit problems, a stepwise backward deletion procedure did not give satisfactory results, so we used a forward selection procedure. Exploration, group and the interaction between exploration and group were significantly related to dominance score (table 2). The significance of the variable 'exploration' shows that on average FE had a higher dominance score than SE. The significance of the variable 'group' indicates that the levels of dominance scores differed between the groups. This was due to the fact that the groups differed in composition of FE and SE, while the dominance score is taking exploration class into account. If all groups would have an equal amount of FE and SE, there would be no difference in dominance score between the groups. Therefore, the different levels of dominance scores have no biological meaning. The significance of the interaction between exploration and group means that the relation between exploration and dominance scores differed between the three groups. Figure 8 shows that in two of the three groups (nrs. 1 and 3) FE had a significantly higher dominance score than SE. In one group (nr. 2) there was no significant difference in dominance score between FE and SE on the first day. The finding that FE were dominant over SE on the first day (at least in 2 groups) agrees with the results of the pair-wise confrontations (chapter 3) and contrasts the relation found in a stable hierarchy (figure 5).

Table 2. *Logistic regression analysis of dominance on the first day in the aviary. For further explanation see table 1. The variable 'exploration' had two categories: SE (exploration=0) and FE (exploration=1). See also figure 6.*

	(Increase in)			Estimates of coefficients		
Parameter	deviance	df	p	group1	group2	group3
null model	51.86	19				
final model	20.00	14				
constant		1				
group	11.32	2	0.04	-8.902	0.251	-2.197
exploration	14.73	1	< 0.01			
explxgroup[1]	22.64	2	< 0.01	18.062	-0.503	4.394

[1] explxgroup is the interaction between exploration and group

Behavioural differences and dominance reversal

While the dominance relationships in the stable hierarchy differed strongly from the ones in the preceding instable phase, in both phases early exploratory behaviour predicted the dominance score. To clarify this we need a closer look at what happened with the FE and SE in both phases.

During the first day 90% of the interactions was won by the bird that started it (the 'actor') and only 10% was won by the receiving bird (the 'reactor'); a significant difference (n=801, χ^2=516, df=1, p<0.001). Most interactions were supplant attacks. Less aggressive behaviour like approaches or head-up displays (Blurton-Jones, 1968) did not occur very often. In two of the three groups, FE started an interaction significantly more often than SE (n=143, χ^2=55.9 and n=294, χ^2=62.0, df=1, p<0.001); in one group this difference was not found (n=495, χ^2=0.45, df=1, p=0.5).

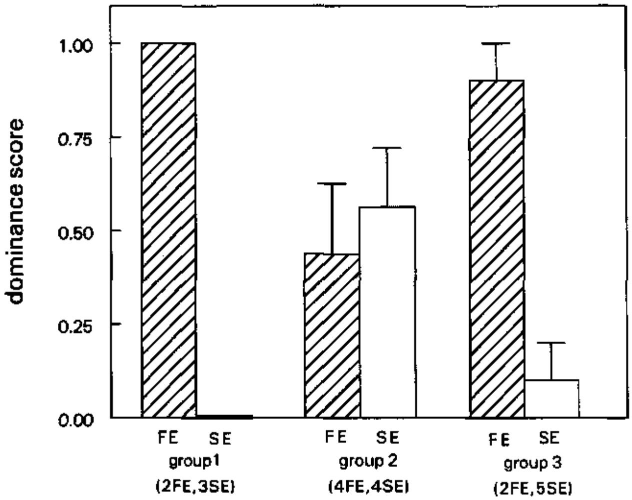


Figure 8. *Mean (+ s.e.) dominance score of FE and SE on the first day in the aviary in the three groups observed. See also table 2.*

In the stable hierarchy of all three groups a FE was dominant over all other birds (figure 7). These three FE were the first (in groups 1 and 3) or second (in group 2) to start the very first interaction after introduction into the aviary, while the other birds were still exploring the new environment. The three FE that started early with interactions, all initiated more interactions during the first day than the other birds in their group (28%-53% of all interactions). Although these three FE occasionally lost an interaction, they mainly won. On the first day they were in the top of the hierarchy (number one or two), and they generally maintained this position until the hierarchy was stable and they were dominant over all other birds in the group (figure 7).

The other five FE in the three groups all had a low dominance score (≤0.33) in the stable hierarchy. Two of them already had a low score (≤0.25) on the first day in the aviary; their very first initiated interaction was with the FE who would become dominant, and both lost. After that they lost most of the following interactions on that day. On the same first day the other three FE all lost from the top FE but won from the other FE in the group (if present) and from most SE. They had a high dominance score the first day (≥0.75). All three, however, suddenly started to lose from one SE they first won from. Within one or two days after that dominance shift they also started to lose from other SE over which they were dominant at first, and they dropped to the lower regions of the hierarchy on the fourth, sixth and second day in the aviary respectively (figure 7).

On two occasions we observed a first dominance shift of a FE that led to a fall in hierarchy. Both times there was a similar order of events. Just before the dominance shift, the FE lost several times in very aggressive interactions from another FE. At the same time a SE won from another SE on a place in the aviary where it spent much time and usually could be found. Then, on the same place where the FE had just lost, this SE initiated and won an interaction with this FE.

The SE used display behaviour (head-up and horizontal; see Blurton Jones, 1968) rather than the normal, more aggressive supplant attack. We observed three more clear dominance shifts between FE and SE during the fall in hierarchy, after the FE started to lose from other SE. In all three the SE initiated the interaction after the FE lost several times from a third bird and/or on a place where it spent much time.

This last observation seemed to be a more general phenomenon. From the data gathered when the birds were not interacting it became clear that some birds constantly moved from one place to the other, while others showed the tendency to stay on one place, exploring it well. Nine of the 12 SE initiated their very first interaction on such a preferred, familiar place where they had spent most time before that interaction (that is, more than 20% of the time before it first initiated an interaction, and at least 5% more time than on other places). Of the eight FE, only two initiated their first interaction on a familiar place, which indicates that SE tended to do this more often than FE (Fisher exact test, n=20, p=0.06).

In most of the observed dominance shifts the FE just experienced loss of several aggressive interactions in a row. Such severe loss did not occur frequently. On the few occasions recorded, the reaction to losing three or more vehement aggressive interactions in a row differed between FE and SE. After a series of losses, the latency time before the loser initiated an interaction himself again was longer for FE (mean 16.0 min, n=4) than for SE (mean 4.9 min, n=16; Mann-Whitney U statistic=9, n=20, p=0.03). This indicates that FE had more difficulty to recover from defeat than SE.

Discussion

Exploratory behaviour and dominance

In the aviary groups a stable hierarchy developed gradually after several days. During the first days there were many dominance shifts as a result of relatively few interactions. Those few interactions mainly took place between the two highest ranking birds. The increase of the number of interactions during the first days suggests that the strife for dominance between all flock mates only really bursted after initial exploration of aviary and/or flock mates, especially by the middle and lower ranking birds. This peak in interactions mainly led to dominance shifts between the middle ranking birds, while by that time it was on average already clear which birds had the top and lowest rank. Then also between the middle ranking birds dominance relations gradually became settled and the number of interactions decreased and seemed to stabilise.

Once a stable hierarchy was established, SE explorers had on average a significantly higher dominance score than FE. This means that on average, SE won from most FE in the group. These results confirm that early exploratory behaviour predicts later dominance, but contrast with the results of our previous experiments with pair-wise confrontations in small cages, where FE won from SE. What could have caused this unexpected result? It is obvious that the circumstances in the pair-wise confrontations were very different from the circumstances in the aviary groups. The size of the cage, the number of opponents and the duration of the stay all differed. Apparently dominance status is a relative concept that can change depending on the situation in which it is measured, as other authors mention as well (Cole and Shafer, 1965; Bernstein, 1981; Huntingford and Turner, 1987; Drews, 1993).

The stable hierarchy was the end result of a gradual formation process. The detailed observations of the three groups indicated what might happen among juveniles forming a new group, although we realise that data of only three groups are strongly anecdotal. At least in respect of the stability of hierarchy and number of interactions, the development of dominance relations in the groups was representative. The data of the three groups showed that the first dynamic phase at the start was quite different from the later stable situation. On the first day FE initiated an interaction more often than (in two groups) or as often as (in one group) SE. On that day FE had a higher (in two groups) or equal (in one group) dominance score than SE. These findings agree with previous results of pair-wise confrontations in small cages, where FE started more fights and won from SE (chapter 3). There were differences between the groups in the relation between exploration and dominance score on the first day, but the data did not allow for further analysis to check whether these differences were caused by differences in group size or in group composition.

Reversal of the relation between exploratory behaviour and dominance

In both the pair-wise confrontations and the stable hierarchies in the groups, early exploratory behaviour predicted dominance. Moreover, at the start of both situations FE initiated more fights than SE and won from SE. For FE the first blow was clearly half the battle. The data available strongly suggest that FE tended to take more risks in their fighting behaviour than SE which were more cautious. FE quickly started interactions and won initially, but our few recordings indicate that if they lost a severe fight, they needed a relatively long time to recover before they initiated an interaction themselves again. In the stable hierarchy FE had extreme dominance scores and either won or lost from all SE in the group, while SE had intermediate dominance scores. SE tended to initiate their first interaction on a specific, familiar place. The few observations of dominance shifts we made, suggest that SE readily reacted to developments in their environment. They initiated an interaction with a FE after that FE seriously lost several interactions with another FE. The SE 'safely' made use of the previous experience of the losing FE caused by the 'first blow' from another FE. Hence, consistent individual differences in exploratory behaviour were related to differences in fighting behaviour, which in turn yielded different dominance relations under different circumstances. In a small cage with only one opponent, the FE who started the fight, usually won. In a large aviary during a longer period and with more opponents the situation was more complex and it was not always enough to give the first blow; the place of interaction and previous experience also played a role.

Especially for SE the specific place of interaction seemed to be important. Previous experiments showed that SE pay more attention to (changes in) the environment than FE (chapter 2), and therefore probably have a more detailed knowledge of their environment. At least in two groups SE were not the first to begin interactions, and they had less interactions than FE on the first day. This suggests that SE once again took more time for exploration. Familiarity with the area enhances the chance of winning a fight (Sandell and Smith, 1991). It could be that because of their thorough and cautious way of exploration, SE became more familiar with a specific place. This may have resulted in the initiation of the first interaction there, and in a dominance shift. Such a process is also described for dominance shifts between aggressive, fast and superficially exploring mice and non-aggressive, slow and thoroughly exploring mice (van Oortmerssen *et al.*, 1985). This hypothesis should be tested with experiments in aviary groups in which knowledge of the environment is manipulated; see also chapter 5.

The previous loss of interactions with another FE seemed to be important for FE who started to fall in the hierarchy. The importance of previous experience for the outcome of interactions has been described for many species (Jackson, 1988; Jackson, 1991). FE needed more time than SE to 'recover' from losing a severe interaction; they seemed to have more difficulty to cope with losing a fight. Defeat can cause stress. A growing number of studies shows that in several species different behavioural responses to stress can be found (Corson and Corson, 1976; von Holst, 1986; Bohus *et al.*, 1987; Wiepkema *et al.*, 1987; Benus *et al.*, 1991; Schouten and Wiepkema, 1991; Hessing *et al.*, 1994). In general two behavioural strategies to cope with stress have been described: an active and a passive strategy. Active copers show the tendency to actively manipulate the situation that causes stress, whereas passive copers try to adjust to the situation. In studies of rodents (Benus *et al.*, 1991) and pigs (Hessing *et al.*, 1994), aggressive individuals with relatively little attention to stimuli in the environment showed an active coping strategy. Non-aggressive individuals that paid much attention to the environment showed a passive coping strategy. In juvenile great tits, the early exploratory behaviour and aggressive behaviour in pair-wise fights and on the first day in the aviary of the FE seem to agree with an active coping style. The behaviour of the SE resembles a passive coping style. If FE would have active coping styles, they would tend to flee from the winner after defeat in order to cope with it. This is, however, quite difficult in an aviary. Instead, just before the dominance shifts we observed, the FE lost many interactions, repeatedly initiated by other FE who chased the losing FE throughout the aviary. Thus, the circumstances could have led to much stress for the FE that lost severely. If SE would have a more passive way of coping with defeat, the circumstances in an aviary would have led to less difficulties for losing SE. A difference in coping strategy could therefore explain why in caged groups FE needed more time to recover from severe loss than SE. In a group the chances to lose an interaction are higher than in a pair-wise fight, simply because there are more opponents. During the long recovery time of FE after severe defeat, chances to lose again may be enhanced which could have resulted in the observed dominance shifts of FE to SE.

Moult was found to predict dominance in a stable hierarchy, at least for FE. This is not unexpected, since thyroid hormone that induces moulting has a negative influence on the gonadal system, causing a reduction in testosterone and thus in levels of aggression (Assenmacher, 1973). This probably explains why FE almost ready with moulting had a higher dominance score than FE halfway moulting. Moulting causes increased vulnerability, making high levels of aggressive behaviour inappropriate (Huntingford and Turner, 1987). The relation between moult and dominance was only found in FE and not in SE. This might be the result of the different fighting behaviour of FE and SE. FE that lost from other FE in the group on the first day, obtained low ranks in the stable hierarchy. On the first day, FE almost ready with moulting might have had a higher chance of winning from other FE that were halfway moulting. This was also the case for SE. For FE however, winning from others on the first day had large consequences for their dominance rank in the stable hierarchy, while for SE this may have been less important since they seemed to have less problems with defeat and they climbed in rank during the development of the stable hierarchy.

Relevance for the natural situation

Aviary groups and natural flocks

In this study we assessed the relation between early exploratory behaviour and dominance in aviary groups in order to have a better simulation of the natural situation than in our previous experiments with well controlled but unnatural pair-wise fights in small cages. Although the aviary groups produced detailed data on the development of dominance relations among juvenile great tits in a new group, there are several differences between an aviary and the natural situation. An important difference is clearly that a bird can not escape an aviary group. This might have caused an artefact, if indeed differences in dealing with a loss have played a role in the development of dominance relations. One should bear in mind however, that also in the natural situation birds can not always "escape" the flock they are in. They may be forced to stay if the benefits of being in a group are larger than the costs of the stress of losing fights. This could be the case when predation pressure is high (Bertram, 1978; Fels *et al.*, 1995). Or when food is scarce and better found in a joint group effort (Krebs *et al.*, 1972), especially if slow and cautiously exploring flock mates are better in finding food (thus being producers in the terminology of Barnard and Sibly, 1981). Recently fledged juveniles usually flock together; there are not many lonely juveniles. Apparently there are large benefits to be in a flock for a recently fledged juvenile great tit.

Another difference is the way the birds are introduced in the groups. In this study the birds were simultaneously introduced in the group in an unfamiliar aviary at an age in which agonistic behaviour has already developed. By the time agonistic behaviour starts to emerge in the natural situation, most juvenile flocks already exist of a core group of four to ten juveniles and those juveniles know each other, but not their agonistic behaviour (Drent, 1983). Not all juveniles join flocks simultaneously. After a hierarchy has settled in the core group of the flock, later arriving juveniles will get a lower position in rank without interfering with the existing dominance relations (Drent, 1983). Juvenile flocks may roam or break up resulting in separately dispersing juveniles to new, unfamiliar areas (Drent, 1984). If several of such lonely juveniles meet, they will form a new flock. Our relatively small aviary groups probably best resemble core groups in roaming juvenile flocks or newly formed groups.

We did not study mixed flock of males and females, the natural situation, because females show less aggressive behaviour and usually lose from males. We therefore assumed that females would not influence dominance relations between males. However, great tits that lose a fight tend to subsequently initiate an interaction with a lower ranking bird to get a winning experience (Drent, 1983). Fast explorers in the lowest ranks of the hierarchy that have difficulties to cope with defeat, may enhance their chances to win by initiating interactions with females that will probably lose from them. This way, the presence of females in a group could influence dominance relations. Observations of fighting behaviour and hierarchies in juvenile flocks with FE and SE in large aviaries or in a natural setting are needed to determine whether our results are relevant for juvenile groups, despite all these possible artefacts.

Implications for the natural situation

The behavioural differences we described in our juvenile male great tits are also found in females and adult great tits (Drent, 1995). They are consistent for each individual and have a genetic basis (Drent, 1997). We proposed that these consistent individual behavioural differences might be part of two different behavioural strategies that become particularly overt in stressful situations like novel physical or social environments. Since both FE and SE exist, the different strategies should be advantageous in different circumstances. If relevant for the natural situation, our results suggest that it may require a different behavioural strategy to become dominant in pair-wise fights than in a flock. Great tits face both situations in life. After the breeding season until late winter, juveniles tend to flock in groups. In winter adults join flocks temporarily. In late winter and spring flocks break up and all juveniles and adults are generally alone or in (breeding) pairs, being territorial or trying to occupy a territory. Although many factors play an important role, it could be that under equal conditions SE may obtain a high rank and be better off in the flock situation, while FE have a better chance of winning when they roam alone and compete with other lonely great tits.

This study raises many questions about the development of and influences on dominance in an aviary group of male juvenile great tits. It is clear that the influence of consistent individual behavioural differences on dominance relations in different situations needs further research, both in the field and in well-controlled laboratory experiments.

A dominance relationship in a flock of great tits.
The dominant bird on the left shows his black breast band in a "head-up" posture to the crouching subordinate bird on the right.

CHAPTER 5

EFFECTS OF THE SOCIAL AND PHYSICAL ENVIRONMENT ON THE RELATION BETWEEN BEHAVIOURAL CHARACTERISTICS AND DOMINANCE

CHAPTER 5

EFFECTS OF THE SOCIAL AND PHYSICAL ENVIRONMENT ON THE RELATION BETWEEN BEHAVIOURAL CHARACTERISTICS AND DOMINANCE

Abstract

The previous chapters gave contrasting results: fast and superficial explorers (FE) show more initial aggressive behaviour and win from slow and thorough explorers (SE) in pair-wise confrontations, but in a group in an unfamiliar aviary dominance partially shifts from FE to SE. This pilot study examines two possible explanations for this contrast, involving familiarity with the environment and the behaviour of flock mates. SE may become dominant over FE in a group in an unfamiliar aviary, because they pay more attention to the unfamiliar environment than FE, which may increase chances to become dominant. Such dominance shifts are not expected in familiar aviaries. The effect of familiarity with the environment was tested by familiarising birds separately with an aviary in which they were subsequently put together. The exploratory and agonistic behaviour of FE and SE and their subsequent dominance relations in groups in familiar aviaries were compared with that in groups in unfamiliar aviaries, presented in the previous chapter. Additional observations in pair-wise confrontations in familiar and unfamiliar aviaries were used to strengthen the behavioural comparisons. In familiar aviaries FE and SE did not differ in their exploratory behaviour. In unfamiliar aviaries SE seemed to pay more attention to the physical environment than FE and initiated more often their first interaction on a familiar place. In all test situations FE quickly initiated interactions, which led to initial dominance over SE in the groups. FE stayed on average dominant over SE in the familiar aviaries after stabilisation of the hierarchy, while in the unfamiliar aviaries SE had become on average dominant over FE. The behaviour of flock mates also affected the dominance relations between FE and SE in the groups. FE had more difficulty to cope with defeat than SE as indicated by their longer recovery time after severe defeat. In the groups in familiar aviaries, SE made more often than FE use of previous loss of the opponent by initiating an interaction with a dominant bird that had not recovered yet from severe defeat. This suggests that SE pay more attention to their social environment. These behavioural differences resulted in a stable hierarchy in which FE either lost or won from all SE in the group, while SE had intermediate dominance scores. This pattern was found in both familiar and unfamiliar aviaries. Familiarity with the environment only influenced the proportion of FE in the highest and lowest places, resulting in different average dominance ranks of FE and SE.

CHAPTER 5

Introduction

From the previous chapters it is clear that juvenile male great tits show consistent individual differences in exploratory and agonistic behaviour, which predict social dominance. Fast and superficial explorers (FE) show more initial aggressive behaviour and win from slow and thorough explorers (SE) in pair-wise confrontations (chapter 3). When FE and SE are put together in an aviary group a similar situation exists during the first day, but in the subsequent days dominance partially shifts from FE to SE (chapter 4). As a result, SE are on average even dominant over FE in a stable hierarchy. Apparently the same behavioural characteristics can lead to different dominance relations in different situations.

Observations of dominance shifts in aviary groups indicated that the place of interaction and experience in preceding interactions played a role in the shifts (chapter 4). This leads to at least two possible explanations for the different dominance relations in pair-wise confrontations and aviary groups. One explanation considers the fact that both in pair-wise confrontations and in aviary groups, exploratory behaviour predicts dominance. This suggests that factors associated with exploratory behaviour could have caused the different dominance relations between FE and SE. Especially for SE the place of interaction seemed to be important. In aviary groups SE had less interactions on the first day than FE, suggesting that SE once again took more time for exploration. They tended to initiate their first interaction in the aviary on a specific familiar place. It could be that because of their thorough and cautious way of exploration, SE may gradually get a more detailed knowledge of the environment than FE. Familiarity with the area increases the chance to win a fight (Sandell and Smith, 1991). Thus, differences in exploratory behaviour could eventually lead to a dominance shift from FE to SE. In the short pair-wise confrontations in small cages SE did not have the possibility to develop a more detailed knowledge of the environment, so in that situation the FE stayed dominant. This hypothesis can be tested by manipulating the familiarity with the environment. In an environment that is unfamiliar to the birds in a newly formed group, several SE gradually become dominant over the initially dominant FE (chapter 4). If this dominance shift is indeed caused by a gradually developed difference in knowledge of the environment between FE and SE, then such a shift should be less likely in an environment that is familiar to all birds in the newly formed group. In that situation, all birds would have a good knowledge of the environment before they were put together, so a development of an asymmetry in knowledge between FE and SE would be less probable. The hierarchy will then remain the same as at the start, with fast attacking FE being dominant over SE.

Another explanation is based on the importance of previous experience for the outcome of interactions (Jackson, 1988; Jackson, 1991). In aviary groups dominance relations between two birds are always established in the presence of other birds; this is not the case in pair-wise confrontations. Previous experience with flock mates may influence the dominance relation between two individuals. FE and SE seem to differ in their reaction to losing a severe fight (chapter 4). FE need more time to 'recover' from such a loss than SE before they initiate an interaction themselves again. During that recovery time, chances to lose again may be enhanced. Such temporarily enhanced chance on losing might be enough to tip the balance in a dominance relation. One could imagine that in a group situation, a third bird might take advantage of a previous severe loss in an interaction of two other birds by subsequently initiating an interaction with that loser. Such use of previous losing experience of the opponent implies particular attention to the social environment. SE, who are more alert to their physical environment than FE (chapter 2), might also pay more attention to their social environment and may make more use of previous loss of opponents. Thus, differences in reaction to severe defeat, combined with differences in attention to the social environment could eventually lead to a dominance shift from FE to SE.

This chapter presents a pilot study to examine the effect of familiarity with the environment on the exploratory and agonistic behaviour of FE and SE and their subsequent dominance relations. Both proposed explanations of familiarity and social effects are not mutually exclusive and may even support each other. Therefore, attention is also paid to the possible influence of flock mates on agonistic interactions. The behaviour and dominance relations of FE and SE were observed in three groups in familiar aviaries. The observed behaviour is compared with the behaviour of FE and SE in groups in unfamiliar aviaries, as described in chapter 4. Additional, more detailed behavioural recordings of FE and SE in pair-wise confrontations in familiar and unfamiliar aviaries are used to support the behavioural comparisons. A possible effect of familiarity on dominance relations is tested in one analysis with data of both familiar (this chapter) and unfamiliar (chapter 4) aviary groups.

Methods

Birds

Great tit nestlings were collected from the wild when they were eight to twelve days old, hand-reared and housed individually in standard cages in the way described in chapter 2. Thirty nine male juveniles were classified for their exploratory behaviour based on two exploration tests, as described in chapters 3 and 4. Sixteen birds were classified as FE, 5 as intermediate and 18 as SE.

Pair-wise confrontations in aviaries

At the age of 13 weeks 32 bird were selected to conduct pair-wise confrontations in an aviary. Each of the 16 pairs consisted of a FE and a SE. These confrontations took place in aviaries of 2x4x2 m containing a feeding table, a drinking bowl, 8 nest boxes, many perches and an artificial tree made of wood. Along the 4-m walls were sliding doors, connecting the aviary with the birds' living cages, as shown in chapter 4 (figure 1). The birds were led from their living cages into the aviary and back without handling, by darkening the aviary or cage when it was to be left. For eight pairs the aviary was unfamiliar; only during the exploration test in an novel environment they had been out of their living cage. The birds of the other eight pairs were separately familiarised with the aviary. Eight, six and four days before the confrontation each bird spent 2 hours alone in the aviary and the last two days before the confrontation each spent 1 hour.

Immediately after introduction in the aviary between 8.30 am and 12.00 am, the behaviour of the birds was observed for 2 hours, and then for a third hour after a break of 2 hours. The outcome of each agonistic interaction was recorded, as well as who initiated it (actor), where it took place and the behaviour involved (both action and reaction), using the descriptions of Blurton Jones (1968). Behavioural data of the birds when they were not interacting were also gathered, by alternately observing each bird for 1 minute. After the confrontation that lasted 5 hours, the birds returned to their living cages.

Several physical traits are known to affect dominance in great tits: body size, weight, sex, size of breast band and age (e.g. Garnett, 1981; Drent, 1983; de Laet, 1985; Sandell and Smith, 1991; Lemel and Wallin, 1993). To check for the possible influence of those traits, body mass, tarsus length (body size), the size of the breast band, moult score (on a scale of 0 (no moult) to 10 (moult complete)) and age were measured one day before the pair-wise confrontation (for details see chapter 3).

Group observations in familiar aviaries

Four weeks later, when the birds were 17 weeks old, three aviary groups of six or seven individuals were formed, using 10 FE and 10 SE that had been observed in the pair-wise confrontations, both in the familiar and unfamiliar aviaries. Each group consisted of FE and SE, with at least two birds per class. All birds were familiarised with the aviary before they were put together, following the same scheme as with the pair-wise confrontations in familiar aviaries. The day before the observations started tarsus length, body mass, breast band, age and moult score were measured again.

Between 9.00 am and 10.30 am the groups were introduced into the aviary without handling; all birds of a group entered the aviary simultaneously. Immediately after introduction in the aviary the birds were observed continuously for 7 hours. The outcome of each interaction was recorded, as well as the birds involved, who initiated it and where it took place. The nature of the interaction was also recorded: calm with actions like display behaviour or approaches and reactions like fleeing or crouching, or vehement with supplant attacks, physical fights and chases. On that first day also behavioural data were gathered of the birds when they were not having an interaction, by alternately observing each bird for one minute during two continuous periods of three hours with a break of one hour in between. After the first day, the observations were reduced to one hour a day. Each observation day the outcomes of the interactions between each possible pair were summed. The bird that won 67% or more of all interactions was considered the winner. If the percentage of interactions won was between 33% and 67%, the dominance relation was considered as unclear. After a minimum of six days, observations were stopped when a stable hierarchy was established. For this purpose the percentage was determined of the total number of possible pairs of birds in the group with a dominance shift from one day to the next. A hierarchy was considered stable if this percentage was less than 10% during at least two subsequent days, with shifts only occurring among the individuals with an intermediate dominance score (chapter 4).

Using the dominance relations between each possible pair of birds in the group (dyad), the dominance score of each bird was determined. Such a dominance score is expressed as the number of animals of the other exploration class (than the birds own) from which the bird won, relative to the total number of animals of the other exploration class with which the bird had interactions. This means that a SE who wins from all FE he has interactions with, gets a dominance score of 1, and a FE who wins from one of the four SE he has interactions with gets a dominance score of 0.25. Unclear dominance relations were treated as winning from 0.5 bird. The reasons for this choice of dominance score are given in chapter 4.

Except for the familiarisation with the aviary before introduction in the group, the collection, upbringing, housing and experimental procedure described above is exactly the same as in the previous study of juvenile male great tits in aviary groups in an unfamiliar aviary (chapter 4). This makes a comparison of the results of both studies possible.

Analyses

The behavioural data were analysed with non-parametric tests. Differences between FE and SE or familiar and unfamiliar aviaries were tested with a Mann Whitney U-test, unless stated otherwise. A logistic regression was used for the analysis of the dominance scores, which often had extreme values (0 or 1). The dominance scores were weighed for the total amount of individuals with which the bird had interactions (for reasons given in chapter 4). Dominance scores of birds in both familiar and unfamiliar aviaries were combined in one regression analysis. A full model was fitted including all variables and their interactions with exploratory behaviour. Variables and interactions were then sequentially dropped from the model in a backward selection procedure. Whether the removal of a variable caused a significant increase in deviance was tested with a F-test, because the deviance was high compared to the number of degrees of freedom. Exploratory behaviour, familiarity and their interaction were included as categorical variables (factors). To control for possible influences on dominance score of tarsus length, body mass, breast stripe, age and moult score, these variables and their interactions with exploratory behaviour were included in the full model. All p-values are two-tailed with a significance level of 0.05. Results with $0.05<p<0.1$ are mentioned as suggestive tendencies, since this is a pilot study with a small number of birds.

In one of the three aviary groups a bird died on the second day in the aviary. Since he did not show deviant behaviour on the preceding day, the data of this bird are included in the results of the first day. One pair, tested in an unfamiliar aviary, did not have any aggressive interaction during the three hours of observation. Data of this pair are excluded from the analyses. Of another pair, tested in a familiar aviary, not all behavioural data were recorded due to a technical failure. The results of the pairs were insufficient to test for effects of familiarity on dominance. This was not only due to the small number of birds, but also to the relatively short observation period which in retrospect did not allow the dominance relations to stabilise. Effects on dominance were only tested for the groups, a situation that resembles the natural situation better.

Results

Effect of familiarity with the environment

The supposed effect of familiarity will be assessed in a comparison of data gathered from groups and pair-wise confrontations in familiar versus unfamiliar aviaries. The results of the groups in unfamiliar aviaries have already been presented in chapter 4. Of these latter results only some that are important for the present comparison will be mentioned shortly.

Behavioural observations

After introduction of the groups in the familiar aviary, it lasted on average 24 min (7, 27 and 37 min respectively) before the very first interaction was initiated. This interval lasted on average 51 min in groups in unfamiliar aviaries (chapter

4). In the pair-wise confrontations, the pairs in the familiar aviary started their very first interaction significantly sooner (mean latency time (mlt)=5 min) than the pairs in the unfamiliar aviary (mlt=24 min; n=15, p=0.02), who first spent some time exploring the new environment.

In two groups a FE initiated the very first interaction, in one group a SE started. On average, FE initiated their first interaction sooner than SE (FE: mlt=58 min, SE: mlt=109 min, n=20, p=0.05). Despite this earlier start of FE, there did not seem to be a significant difference between FE and SE in the number of interactions initiated during the whole first day in the familiar aviary (mean FE: 71.1; mean SE: 48.2, n=20, p=0.12). This contrasts the results of unfamiliar aviary groups, where FE initiated more interactions than SE (table 1, chapter 4). The results of the groups are supported by those of the pair-wise confrontations. In these confrontations the very first interactions were more often initiated by the FE than by the SE (χ^2=5.4, df=2, n=15, p=0.02). In the familiar aviary there was no difference between FE and SE in the number of interactions initiated during the whole pair-wise confrontation (mean FE: 18.1, mean SE: 20.2, n=14, p=0.95). In the unfamiliar aviary however, FE initiated more interactions than SE during the confrontation (mean FE: 11.4, mean SE: 5.0, n=14, p=0.02; table 1). After correction for the earlier start in the familiar aviary, the pairs in the familiar aviary had more interactions per observed hour (mean 40.4) than in the unfamiliar one (mean 16.4; n=15, p=0.03).

Table 1. *Overview of differences in behaviour between fast explorers (FE) and slow explorers (SE) in familiar (fam) and in unfamiliar (unfam) aviaries, both in pair-wise confrontations (pair) and aviary groups (group). The results of groups in unfamiliar aviaries are taken from chapter 4.*
-: the difference between fast and slow explorers was not found
+: the difference between fast and slow explorers was found with $0.05<p<0.10$
++:the difference between fast and slow explorers was significant with $p\leq0.05$

Behaviour	pair		group	
	fam	unfam	fam	unfam
Effect of familiarity				
- FE initiated more interactions than SE (on the first day)	–	+ +	–	+ +[1]
- SE initiated their first interaction more often on a familiar place than FE	–	+	–	+
Effect of flock mates				
- FE had a longer recovery time after a severe loss than SE	+ +[2]	+ +[2]	+	+ +
- SE made more use of previous loss of their opponents than FE	not possible in pairs		+ +	

[1]: difference found in two of the three groups

[2]: difference found in combined data of fam and unfam, small N made separate analysis impossible

Some birds showed the tendency to stay on one place, exploring it well, while others constantly moved from one place to the other. The birds that tended to stay in one place, often initiated their very first interaction on that preferred, familiar place. A place was classified as 'familiar' to a bird if the bird spent there more than 20% of the time before it first initiated an interaction, and at least 5% more time than on other places. In the groups in familiar aviaries, it could only be determined for 6 FE and 5 SE if they initiated their first interaction on such a familiar place. The data do not suggest a difference between FE and SE in this tendency; 2 of the 6 FE and 3 of the 5 SE initiated their first interaction on a familiar place (Fisher exact, n=11, p=0.6). A total of 11 birds is however too small a number to support a conclusion of no difference. In groups in unfamiliar aviaries SE tended to initiate their first interaction more often on a familiar place than FE (table 1, chapter 4). The results of the pair-wise confrontations suggest a similar pattern, although again the data are not sufficient for firm conclusions. In the pair-wise confrontations in a familiar aviary, 3 out of 7 SE initiated their first interaction on a familiar place, while in FE 2 out of 6 did, which again does not suggest a difference between FE and SE (Fisher exact, n=13, p=1.0). In the unfamiliar aviary however, the data suggest that more SE (3 out of 6) than FE (0 out of 7) initiated their first interaction on a familiar place (Fisher exact, n=13, p=0.07; table 1). Since a similar difference between FE and SE was suggested in pair-wise confrontations and groups in unfamiliar aviaries, independent of each other, the probabilities from the independent tests of significance can be combined (Sokal & Rohlf, 1969). Combination of the probabilities of the tests of pairs (p=0.07) and groups (p=0.06, chapter 4) showed that in unfamiliar aviaries, SE initiated their first interaction significantly more often than FE on a familiar place (χ^2=10.95, df=4, p=0.03). Since in the familiar aviaries some of the birds used in the pair-wise confrontations were later also used in the groups, the results of these two situations could not be combined. The small sample sizes did not allow for exclusion of the birds that were observed in both situations.

Dominance in groups

During the first days in the familiar aviary many dominance shifts occurred, but stability quickly increased. After 6, 8 and 9 days respectively, a stable hierarchy had developed, which is a normal pattern in aviary groups of juvenile great tits (chapter 4). Because of the dominance shifts, the initial dominance relations between FE and SE could be different from the relations in a stable hierarchy, as in unfamiliar aviaries (chapter 4). Since the effect of familiarity is expected to develop gradually, the analysis of dominance scores was done with data gathered on the instable first day, as well as with data of the stable situation using the summarised outcomes of the last two observation days. Possible effects of familiarity with the aviary are quantified by using the data of familiar and unfamiliar aviaries in one logistic regression analysis. The effect of familiarity on the relation between exploration and dominance was tested by including the interaction of exploratory behaviour and familiarity in the analysis.

***Table 2.** Logistic regression analysis of dominance on the first day in the aviary of three groups in a familiar aviary (this chapter) and three groups in an unfamiliar aviary (chapter 4). Exploratory behaviour was coded as a variable with two categories: FE (exploration=1) and SE (exploration=0). For further explanation see text. The results are also shown in figure 1.*

Parameter	(Increase in) deviance	df	p	Estimate of coefficient
null model	99.92	39		
final model	73.41	38		
constant		1		
exploration	26.51	1	<0.001	1.933

Note: Null model includes the constant only. Final model includes the significant parameter(s).

For the analysis of the dominance scores on the first day in the aviary, data of the three groups in the familiar aviary (n=20) and data of three groups in an unfamiliar aviary (n=20, chapter 4) were used. Of all predictors included in the full model, only exploration correlated significantly with dominance score (table 2). In both familiar and unfamiliar aviaries, FE were dominant over SE on the first day (fig. 1). There was no significant effect of familiarity or one of the physical variables on dominance, nor on the relation between exploration and dominance. Possible differences in this relation between the six groups were tested by including group as a categorical variable, and the interaction of the variables 'exploration' and 'group'. We did this test with a forward selection procedure, because inclusion of the predictor variable 'group' in the full model was not possible due to overfit problems. However, in none of the six groups the relation between exploration and dominance differed significantly from the general picture that FE were dominant over SE.

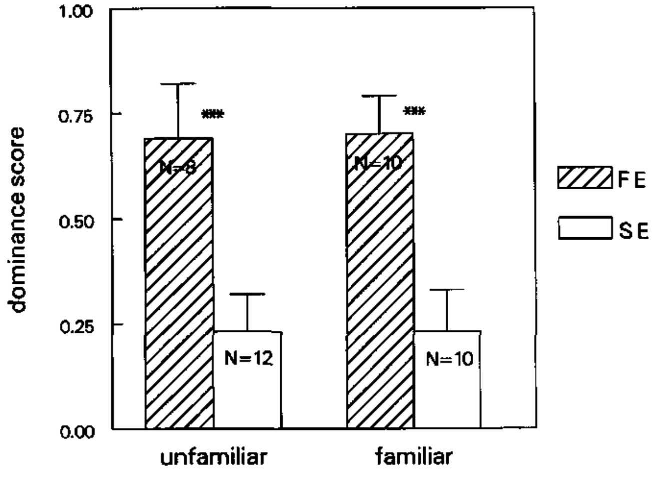


***Figure 1.** Mean (+ se) dominance score of FE and SE on the first day in groups in familiar aviaries and unfamiliar aviaries. ***:p<0.01. See also table 2.*

To determine if the situation was the same after stabilisation of the hierarchy, the dominance scores in the stable situation were analysed. For this analysis data of the three groups in the familiar aviaries (n=19) and data of seven groups in unfamiliar aviaries (n=47, chapter 4) were used. The same predictor variables were included as in the analysis of dominance score on the first day, except for breast band, because not of all birds in the unfamiliar aviary the size of the breast band had been measured. Exploration and the interaction of exploration and familiarity contributed significantly to the explained variation in dominance scores (table 3). This indicates that while in an unfamiliar aviary SE were on average dominant over FE (as was reported in chapter 4), in a familiar aviary this relation was reverse: FE were on average dominant over SE (figure 2). None of the physical variables affected dominance significantly. Nor were there significant differences between all 10 groups in the relation between exploration and dominance.

Table 3. *Results of the logistic regression analysis of dominance in a stable hierarchy of three groups in a familiar aviary (this chapter) and seven groups in an unfamiliar aviary (chapter 4). Familiarity with the aviary was coded as a variable with two categories: familiar aviary (familiarity=1) and unfamiliar aviary (familiarity=0). Further explanation in text and note of table 2. The results are also shown in figure 2.*

	(Increase in)			Estimates of coefficients	
Parameter	deviance	df	p	familiar	unfamiliar
null model	127.49	65			
final model	112.25	62			
constant		1			
familiarity[1]	4.20	1	0.14	-0.693	0.207
exploration	6.99	1	0.05		
explxfam[2]	8.50	1	0.03	1.386	-0.413

[1] Although not significant, familiarity is included because it is part of the interaction
[2] Interaction of exploration and familiarity

In the previous study of groups in unfamiliar aviaries, we found that FE had either extreme high or low dominance scores in the stable hierarchy, while SE had more intermediate dominance scores (chapter 4). In the stabilised hierarchies in familiar aviaries a similar pattern may exist, even though the groups in familiar and unfamiliar aviaries had different relations between exploration and average dominance score. In figure 3 the frequency distribution of the dominance scores in the stable hierarchy is shown separately for FE and SE. The frequency distribution of the SE roughly follows a normal distribution where most birds (8 of 10) have a dominance score between 0.25 and 0.75. The frequency distribution of the dominance scores of FE tends to follow a bimodal distribution where many birds (7 of 9) have extreme dominance scores of 0-0.25 or 0.75-1. This difference in frequency of extreme dominance scores between FE

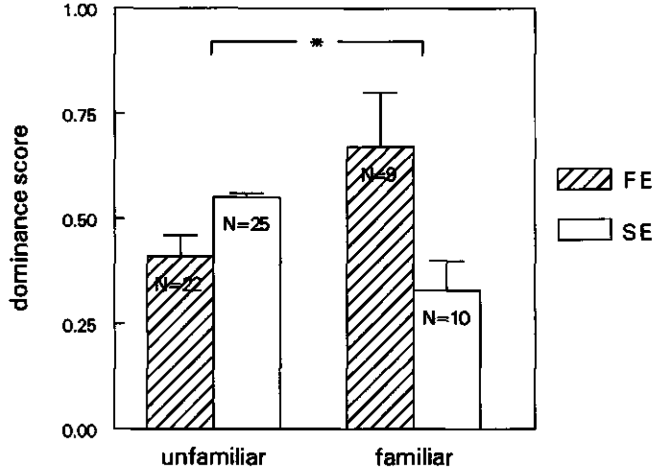


***Figure 2.** Mean (+ se) dominance score of FE and SE in a stable hierarchy in groups in familiar aviaries and unfamiliar aviaries. **:p=0.03. See also table 3.*

and SE was significant (Fisher exact test: n=19, p=0.02). This indicates that also in stable hierarchies in familiar aviaries FE more often either lost or won from all explorers in the group, while SE generally lost from some and won from some.

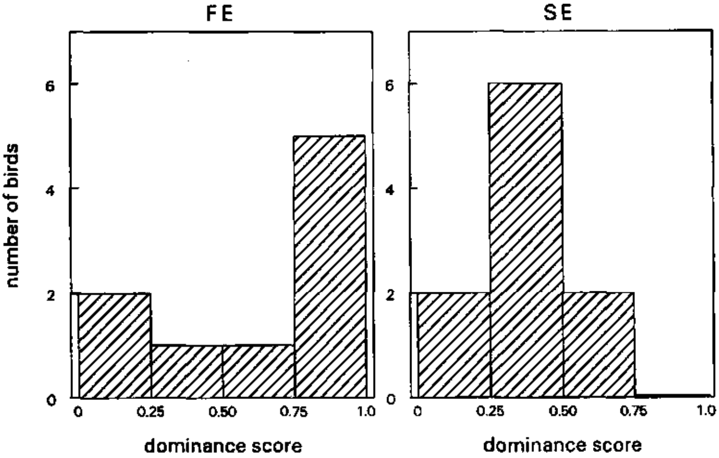


***Figure 3.** Frequency distribution of the dominance score of FE and SE in a stable hierarchy in groups in familiar aviaries. Data are grouped in classes of 0.25 dominance score.*

Effect of flock mates

Besides familiarity, flock mates may also affect agonistic interactions and dominance. Differences in reaction to severe defeat, combined with differences in attention to the social environment could eventually lead to a dominance shift from FE to SE. In the pair-wise confrontations in aviaries 54% of the interactions was calm, involving display behaviour or approaches. The rest of the interactions (46%) was initiated by more vehement actions like supplanting attacks, chases or physical contacts. There were no differences in the kind of agonistic behaviour shown between familiar and unfamiliar aviaries or between FE and SE, although FE tended to initiate an interaction more often with a supplant attack than SE (mean FE: 31.9, mean SE: 18.0, n=28, p=0.06).

Although interactions were not very aggressive in general, there were occasional outbursts with one bird initiating a series of supplants or physical fights followed by a chase though the whole aviary. The reaction to losing such a severely aggressive interaction was determined by measuring the time interval between the loss of at least three supplants followed by a chase and the first interaction the loser initiated again. This 'recovery time' differed between FE and SE. Figure 4 shows that FE had a longer 'recovery time' than SE (n=12, p=0.02). Since only two of those aggressive outbursts occurred in the unfamiliar aviary, it was not possible to determine if this reaction differed between familiar and unfamiliar aviaries.

In the groups in familiar aviaries, 33% of the interactions on the first day was calm and 67% vehement, mainly with supplant attacks. Also for these birds possible differences in recovery time between FE and SE were assessed. Since the recorded behavioural data in the group situation were less detailed than in the pair-wise confrontations, the criterion for severe loss had to be less precise, namely the loss of at least three vehement interactions recorded within three minutes. The results are less clear than in the pair-wise confrontations and only suggest that also in the groups FE had a longer recovery time than SE (n=25, p=0.07; figure 4). In groups in unfamiliar aviaries this difference between FE and SE was significant (chapter 4, table 1).

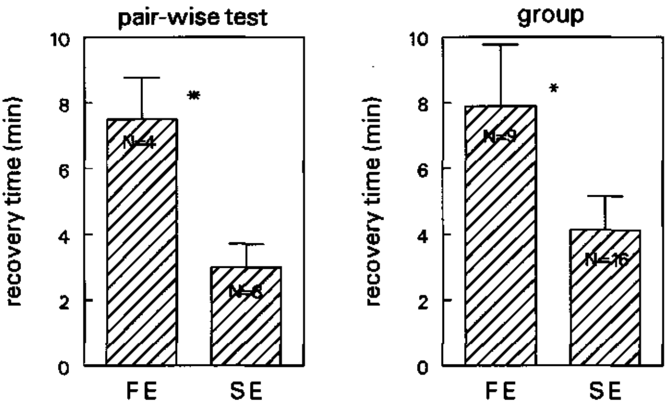


Figure 4. *Recovery time after severe defeat, measured as the time interval between severe loss and the first interaction the loser initiated again. Mean (+ se) of FE and SE in pair-wise confrontations and groups in familiar aviaries. **:p=0.02 *:p=0.07.*

An intriguing possibility is now that FE and SE might differ in the extent to which they make use of previous loss of opponents. To test this, it was determined for each possible dyad in the group which of the two birds usually initiated and won the interactions during the first day in the familiar aviary, disregarding those dyads where both birds initiated an interaction equally often. During the first day in the aviary there were many switches in who initiated the interaction (the actor). Subordinate birds that had not initiated any interaction (reactors) could suddenly turn into actor and try to change the dominance relation. This was sometimes effective and the sudden initiative could lead to a reverse in dominance. Within one dyad, reactors that suddenly turned into actors, could later again become reactors, especially if the dominance relation did not change. Within 23 dyads, a total of 104 switches in initiative in which reactors became actors were observed. In those 23 dyads, only 16 birds (10 slow and 6 fast explorers) were turning into actor, because one bird A could turn into actor in its relation with bird B, as well as in its relation with bird C. In each of the switches in initiative it was determined if the bird that had been the actor but now was the reactor, had lost at least three vehement interactions in the 15 minutes previous to the switch, without initiating any interaction. This happened in 27 of the 64 times that a SE which had been reactor suddenly turned into actor, and in 5 of the 40 times that a FE switched from reactor to actor. Since the birds differed considerably in the number of switches to actor, these findings could be the result of one very alert SE. Therefore for each of the 16 birds the percentage of all switches to actor of that bird preceded by loss of the opponent was determined. This percentage was significantly higher in SE than in FE as shown in figure 5 (n=16, p=0.05; see also table 1). This strongly suggests that in their fighting behaviour SE made more often use of previous loss of opponents than FE.

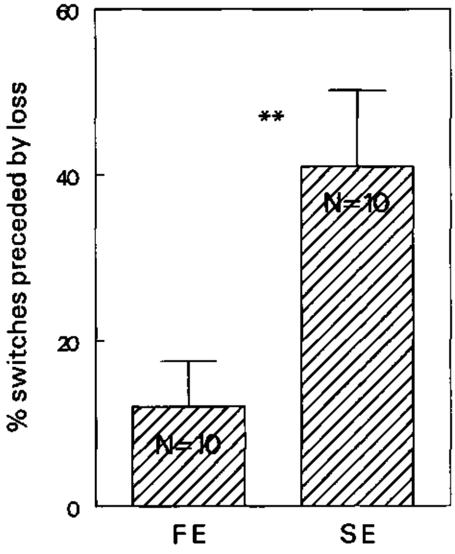


Figure 5. *Mean (+ se) percentage of all switches from reactor to actor of FE and SE that was preceded by severe loss of the opponent. Subordinate birds that had not initiated any interaction in a dyad (reactors) could switch to being actor, initiate an interaction with the dominant bird of the dyad, and try to change the dominance relation. To enhance the chance to win, subordinate birds could make use of previous loss of a dominant opponent, by initiating an interaction before the opponent has recovered from the defeat. **:p=0.05.*

Discussion

Effect of familiarity with the environment

Although this pilot study was carried out with only a small number of birds, the results show clear effects of familiarity with the environment on the exploratory and aggressive behaviour of FE and SE and their subsequent dominance relations. In the pair-wise confrontations, birds in unfamiliar aviaries first spent time exploring the new environment and started interactions later than birds in familiar aviaries. The results of the aviary groups seem to support this, although the small number of groups does not allow for statistical analysis. This difference in latency time before the first interaction indicates that exploration was more important in the unfamiliar than in the familiar environment, which implies that the procedure to familiarise the birds with the environment was adequate. More time spent on exploration in the unfamiliar aviary might also explain why there were less interactions per hour in the unfamiliar than in the familiar aviary during the pair-wise confrontations. Moreover, adequate knowledge of the aviary could have led to a higher tendency to fight in defence of a specific, familiar place in the aviary and thus to more interactions in the familiar aviary.

The results indicate that SE paid more attention to an unfamiliar aviary than FE, as was indeed to be expected on the basis of the previous experiments that led to the classification (chapter 2). The combined results of pair-wise confrontations and groups in unfamiliar aviaries showed that SE initiated their first interaction more often on a familiar place than FE. Furthermore, FE initiated more interactions than SE in the unfamiliar aviaries, suggesting that SE spent more time exploring the new environment while FE focused more on aggressive interactions. Because of the different attention to the unfamiliar environment, SE may gradually get more detailed knowledge of the environment than FE. Both differences between FE and SE were not found in the groups and pair-wise confrontations in the familiar environment, where exploration was less important because both FE and SE already had a good knowledge of the environment.

The effect of familiarity on dominance relations between FE and SE only became clear after some time. As in pair-wise confrontations in small cages, FE took the initiative in fights. In the pair-wise confrontations in the aviaries, FE initiated the very first interaction more often than SE. In the groups in the familiar aviaries, they initiated their first interaction sooner than SE. The first blow was half the battle for the FE. On the first day in groups, FE were dominant over SE both in familiar and in unfamiliar aviaries. In the stable situation, familiarity with the environment affected the dominance relations between FE and SE in groups. SE tended to be on average dominant over FE in the unfamiliar aviaries (chapter 4). In the familiar aviaries however, the situation had remained the same as on the first day: FE were dominant over SE. These results indicate that the hypothesis on effects of familiarity is valid.

The relation between exploration and dominance in groups in the unfamiliar aviary as shown in figure 2 was not significant directly, but only after correction for the effect of moult on dominance (chapter 4). In the analysis together with the groups in familiar aviaries however, the effect of moult disappeared and only the effect of familiarity was retained in the final model. This could be because familiarity had a stronger effect or because moult did not play a role in the groups in familiar aviaries. The latter explanation is not probable since the variance of moult score in familiar aviaries (score range 5.5-10; var=2.46) was significantly larger than that in unfamiliar aviaries (score range 5.0-8.5; var=0.48, f=5.18, p<0.01). One would therefore sooner expect an effect of moult in familiar aviaries than in unfamiliar ones. The alternative explanation of a strong effect of familiarity that marginalises the effect of moult seems more likely.

The exploratory and agonistic behaviour observed in the pair-wise confrontations in familiar aviaries agreed with that observed in the groups in familiar aviaries. This could have been caused by the fact that about half of the birds in the groups was also tested in the pairs in familiar aviaries. However, the other half of the birds was tested before in pair-wise confrontations in unfamiliar aviaries. The behaviour of these birds in the pair-wise confrontations differed from their behaviour in the groups. Therefore it seems more likely that the similarities were caused by the familiarity with the aviary. Social experience in the pair-wise confrontations might have affected later dominance relations in the groups, even though there were four weeks between the tests. In most cases both birds of the pairs were in the same group, but there was no difference in dominance relations between dyads of FE and SE that had a previous confrontation with each other and dyads that did not. Still we can not rule out the possibility that previous experience influenced the behaviour and dominance in the groups.

The effect of familiarity with the environment on dominance relations suggests that SE are best adapted to a new environment, or an unstable environment in which important changes regularly occur (see also chapter 2). FE seem to be best adapted to a familiar and stable environment. A juvenile great tit can encounter both situations, it can for example either stay in the area where it's nest was, or disperse (Dhondt, 1979; Drent, 1984; Verhulst *et al.*, 1997).

Effect of flock mates

There are several indications that flock mates play a role in the establishment of dominance relations. In all test situations, FE needed more time than SE to recover from losing a series of aggressive interactions before they initiated an interaction themselves again. Apparently, FE had more difficulties to cope with such a loss than SE. This may have been caused by differences in coping style between FE and SE. In several species two behavioural strategies to cope with environmental challenges have been described: an active and a passive strategy (von Holst, 1986; Benus *et al.*, 1991; Schouten & Wiepkema, 1991; Hessing *et al.*, 1993; Hessing *et al.*, 1994; Hansen & Damgaard, 1993). Active copers show the tendency to actively manipulate the situation that causes stress, whereas passive copers try to adjust to the situation. The general behaviour of passive copers is more guided by environmental stimuli than the behaviour of active copers. The aggressive and exploratory behaviour of FE seem to agree with an active coping style, while the behaviour of SE resembles a passive coping style (as discussed in chapter 3, 4). Therefore we would expect FE to actively cope with defeat by fleeing from the winner. This can be quite difficult in an aviary with a fence if there are not many places to hide. The circumstances might have led to much stress for losing FE. If SE have a passive coping style, their behaviour is aimed at adjusting themselves to the situation. This way of coping with loss fits much better the confinement of an aviary.

SE appeared to pay much attention to their social environment and took advantage of the recovery time after a severe loss. More often than FE, SE initiated an interaction with a dominant bird just after that bird lost a series of aggressive interactions from a third bird. This way, once a FE lost severely from another bird, he had an enhanced chance to also lose from SE. This could eventually lead to a dominance shift from FE to SE in groups.

Although a flock of juveniles in the natural situation is not surrounded by a fence, it may still be quite difficult for FE to flee from the winner after severe defeat and 'escape' the flock, as discussed in chapter 4. If the benefits of being in a group are larger than the costs of the stress caused by difficulties to cope with defeat, the birds are forced to stay. Since most juveniles tend to stay in flocks, the benefits are likely to be large and the results of the aviary groups can be relevant for the natural situation.

Synthesis

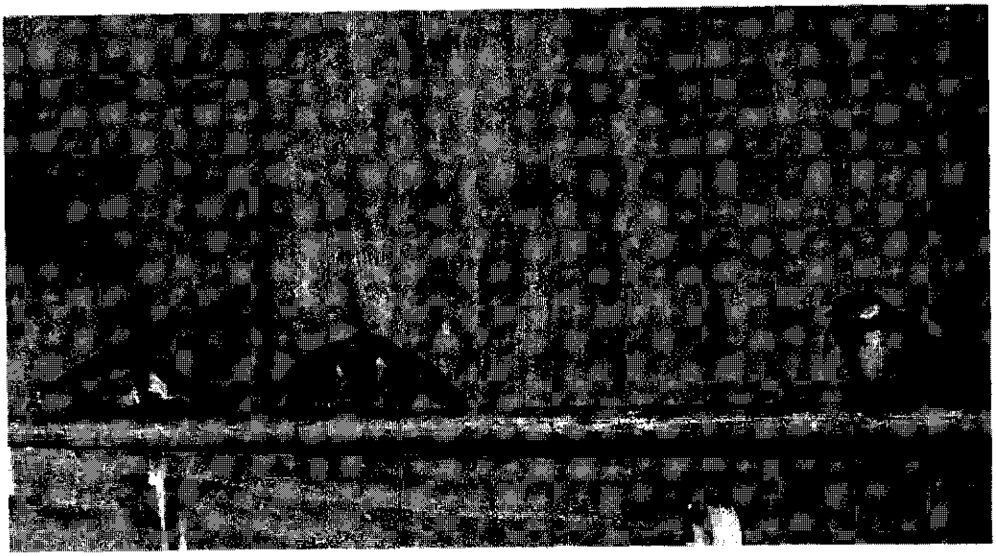
The results support both hypotheses proposed; these hypotheses are not mutually exclusive. Both familiarity with the environment and the behaviour of flock mates modify the dominance relations between FE and SE, and each factor seems to enhance the effect of the other factor. In unfamiliar aviaries SE pay more attention to the environment than FE, resulting in a dominance shift from FE to SE that does not take place in familiar aviaries. It can be argued that after several days, an unfamiliar aviary has become familiar and also FE will have good knowledge of the environment. This might lead to reclaiming the dominant position. However, FE with a low position in the hierarchy will suffer many defeats from all the birds with higher ranks. Since FE have great problems to cope with severe defeat compared with SE, reclaiming their dominance position may be very difficult.

The different reactions of FE and SE on the behaviour of flock mates also induce dominance shifts from FE to SE. However, one would then expect a similar situation in all groups with SE being dominant over FE. This was not the case in groups in familiar aviaries. Still the groups in familiar and unfamiliar aviaries showed a similarity in their hierarchies after stabilisation. Although on average the relation between exploration and dominance score differed, in both situations FE had more extreme dominance scores than SE in the stable hierarchy. They either lost or won from the SE in the group, while SE had mainly intermediate dominance scores. Based on the results of this study, one would only expect dominance shifts due to the behaviour of flock mates after severe loss of FE. At the first day FE are dominant over SE and will mainly lose from the FE that are in the highest ranks of the hierarchy. The FE that are not severely defeated by other FE will maintain their high positions, while the defeated FE will subsequently also lose from SE and fall in the hierarchy to the lowest positions. Therefore a stable hierarchy with FE in either high or low ranks and SE in the middle ranks seems a more probable result of the proposed influence of flock mates than SE being dominant over FE.

This study shows that the different dominance relations between FE and SE in pair-wise confrontations (chapter 3) and groups (chapter 4, this chapter) are not as contradictory as they seemed. The fighting behaviour differed between FE and SE and was consistent in all test situations. The data strongly suggest that FE take more risks in their fights than SE. FE quickly initiate interactions without paying much attention to their environment. They give the first blow and win initially from SE. But if they lose severely, they have relatively large problems to cope with it. The cautious SE seem to not only make more use in their interactions of information about their physical environment, but also about their social environment. They have fewer problems to cope with severe defeat.

In pair-wise confrontations, these behavioural characteristics result in FE being dominant over SE. Whether FE are also dominant over SE in prolonged pair-wise confrontations in unfamiliar aviaries remains to be investigated, since the results of this study were not sufficient to determine the dominance relations in the pair-wise confrontations. It could be that a gradually developed asymmetry in knowledge of the environment is enough to tip the balance in such a situation without flock mates. In groups, the different fighting behaviour of FE and SE results in a stable hierarchy with FE either being in the highest or the lowest ranks, while SE have the middle ranks. A more detailed knowledge of the environment gives SE an enhanced chance to reverse their dominance relations with defeated FE. Hence, in unfamiliar aviaries only a small proportion of FE has extreme high ranks, while a large proportion of FE has extreme low ranks. In a familiar aviary the situation is reversed with a large proportion of FE with extreme high ranks and a small proportion of FE with extreme low ranks. Hence, familiarity with the environment only influenced the proportion of FE in the highest and lowest places, resulting in different *average* dominance ranks of FE and SE. This study indicates that such average relation is not the most sensitive way to describe a stable hierarchy.

The relevance for the natural situation of this study should be examined in further research on dominance relations between FE and SE in flocks of juveniles in different habitats.



Two fighting great tits, observed by a flock mate

CHAPTER 6

GENERAL DISCUSSION

CHAPTER 6

GENERAL DISCUSSION

Introduction

Although my first interest in behavioural characteristics of juvenile great tits was prompted by their possible effects on dominance, the results of this study indicate that such characteristics may also affect other aspects of the life of great tits that are likely to influence their fitness. This chapter discusses consistent behavioural differences found and touches some aspects of Tinbergen's four questions regarding function, causation, development and evolutionary history (1963, cited in Krebs and Davies, 1987) that could be applied to them and will be in several follow-up studies in the near future.

Consistent behavioural differences

The results presented in this thesis clearly show consistent individual differences in exploratory and agonistic behaviour of juvenile male great tits. The individual differences in exploratory behaviour indicate that fast and superficial explorers (FE) pay less attention to the physical environment than slow and thorough explorers (SE; chapter 2). FE persist more in foraging habits after a change in the environment than SE who soon adjust their behaviour to the new situation. The different behavioural responses to a strange, novel object suggest that FE and SE differ in neophobia. The behavioural differences in social situations indicate that FE take more risks in their fighting behaviour than SE (chapters 3, 4, 5). They quickly initiate agonistic interactions without paying much attention to the social and physical environment, but they have great problems in coping with severe defeat as indicated by a relatively long recovery time after such defeat, before they initiate interactions again (chapters 4, 5). SE are more cautious. Their tendency to initiate their first interaction in a new group on a familiar place (chapters 4, 5) and to initiate an interaction with a dominant bird after that bird has lost a severe interaction (chapter 5) suggests that they make more use of information on the physical and social environment in their interactions. SE have minor problems in coping with severe defeat.

These behavioural characteristics affect dominance relationships, with different outcomes depending on the situation, once again stressing that dominance is not a trait, but a relative concept and the result of many factors (Cole and Shafer, 1965; Bernstein, 1981; Huntingford and Turner, 1987; Drews, 1993). In pair-wise confrontations in small cages, FE win over SE (chapter 3). For FE clearly the first blow is half the battle. In a newly formed group, dominance partially shifts from FE, who start interactions and are initially dominant, to SE (chapter 4). Those dominance shifts to SE seem to occur in new groups in unfamiliar environments but not in familiar environments (chapter 5). This could be due to the thorough attention to the physical environment of SE, which may gradually enhance their chances of winning in an unfamiliar environment. A more important characteristic of the dominance relationships between FE and SE in a stable hierarchy is the fact that FE have either high or low ranks in the hierarchy and either win or lose from most SE in the group, while SE have mainly the middle ranks (chapters 4, 5, figure 1). In unfamiliar aviaries only a small proportion of FE has extreme high ranks, while a large proportion of FE has extreme low ranks. In a familiar aviary the situation is reversed with a large proportion of FE with extreme high ranks and a small proportion of FE with extreme low ranks. Hence, familiarity with the environment only influences the proportion of FE in the highest and lowest places, resulting in different *average* dominance ranks of FE and SE in the stable hierarchy.

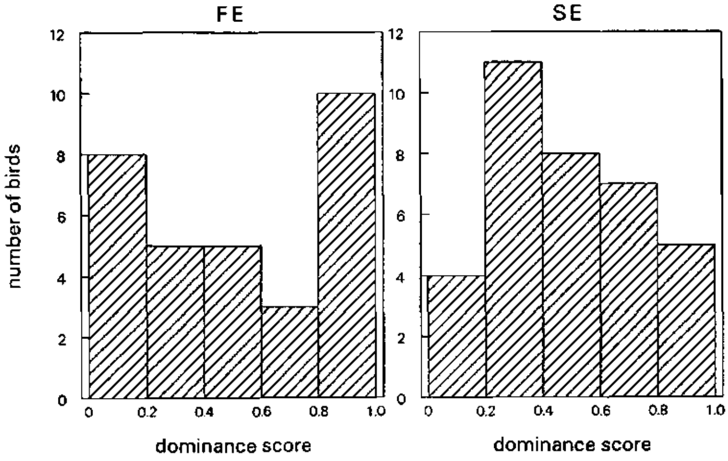


Figure 1. *Frequency distribution of the dominance score of FE and SE in the stable hierarchy. Summarised data of 7 groups in unfamiliar aviaries (chapter 4, figure 6) and 3 groups in familiar aviaries (chapter 5, figure 3), grouped in classes of 0.2 dominance score. FE have more often extreme dominance scores (i.e. <0.2 and >0.8) than SE ($\chi^2=7.12$, $n=66$, $df=1$, $p<0.01$). This is confirmed by a test for equality of variances of the dominance score, applied to $\arcsin\sqrt{}$(dominance score) to obtain normal distribution. The variance of the transformed dominance scores of FE is larger than the variance of SE (FE: $var=0.38$; SE: $var=0.19$; $f=2.05$, $p=0.02$).*

CHAPTER 6

Coping strategies

The striking agreement of the behavioural differences found in male juvenile great tits and in pigs and rodents has already been discussed in preceding chapters (3, 4, 5). In short, the behaviour of FE corresponds to that of aggressive rodents and pigs who generally adopt an active coping strategy to gain control over the social and physical environment when challenged by it (Benus *et al.*, 1987; Benus *et al.*, 1989; Benus *et al.*, 1990, Hessing *et al.* 1993, Hessing *et al.*, 1994). The behaviour of SE on the other hand corresponds to that of non-aggressive rodents and pigs who predominantly have a passive coping strategy. One of the most fundamental differences between the two coping strategies seems to be the degree in which behaviour is guided by environmental stimuli. Aggressive, active copers develop routines in which behaviour, once triggered, is affected very little by environmental stimuli; they seem to anticipate a situation. Non-aggressive, passive copers react to environmental stimuli all the time. This difference in behavioural organisation is reflected in a whole variety of behaviour patterns in which active and passive copers differ, ranging from agonistic and exploratory behaviour (e.g. Benus *et al.*, 1991; Hessing *et al.*, 1994) to nest building behaviour (Sluyter *et al.*, 1995). If the behavioural differences described in this thesis do indeed reflect different coping strategies, then it would be one of the few examples found in a wild, not artificially selected species, and the first indication that coping strategies can also be found in birds. It would provide a good opportunity to study possible fitness consequences and population dynamics of coping strategies. This has received hardly any attention so far (but see van Oortmerssen and Busser, 1989). Great tits are very suitable for this type of research; there is a long tradition of field work on great tit populations, extensive knowledge of their social behaviour and natural history and experience in fitness estimates.

But is it justified to conclude that the results of this thesis provide enough evidence for the existence of specific coping strategies in juvenile male great tits? According to Jensen (1995), four properties of individual variation are particularly important to be clarified before coping theory can be extrapolated from rodents to other species. There should be demonstrations of high behavioural consistency between different exposures to the same situation (1); the reaction to different situations should be consistent (2); the variation should follow a bimodal or multimodal distribution with minimal overlap between strategies (3) and there should be a genotypic difference between the groups of individuals rather than differences acquired in a given situation (for example, in the dominance position of a given group) (4). Given the results presented in this thesis, there is no doubt that juvenile male great tits show consistency in exploratory and aggressive behaviour both in repeated measurements and different situations (chapters 2, 3, 4), at least in the first 18 weeks of their life.

The behaviour in one situation predicts the kind of behaviour that the individual would perform in another situation. Additional observations by Drent showed that the behavioural differences were even consistent during more than a year and were also found in females (Drent, 1995).

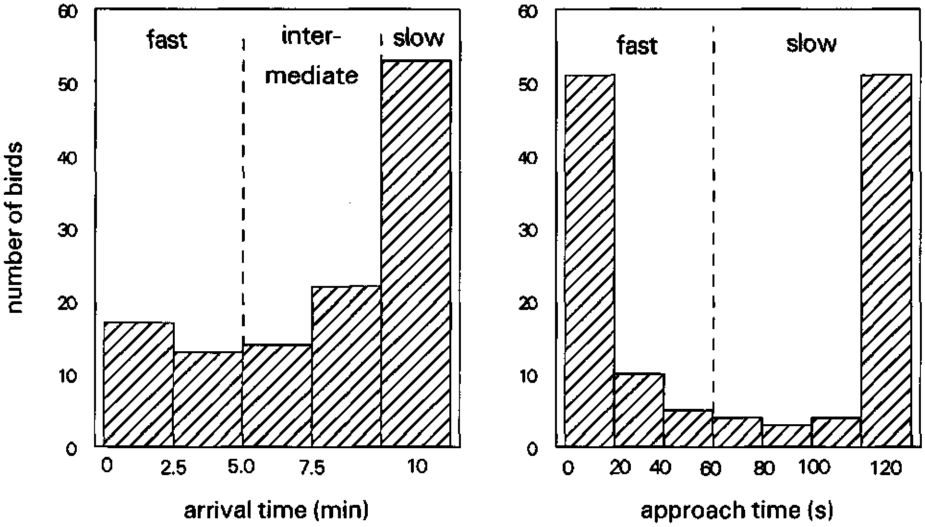


Figure 2. Frequency distributions of the arrival time at the last (fifth) tree in a novel environment (data grouped per 2.5 min; 10 min indicate birds failing to arrive within the trial time) and the approach time to a strange object in the home cage (data grouped per 20 sec; 120 s indicate birds failing to approach within trial time). Summarised data of all birds used in the different experiments in chapters 2, 3, 4, and 5. Classification criteria are shown (dotted lines). Birds that were fast in both tests, or fast in one and intermediate in the other, were classified as FE. Birds that were fast in one test and slow in the other, were classified as intermediate. Birds that were slow in both tests, or slow in one and intermediate in the other, were classified as SE.

The bimodal or multimodal distribution however is debatable. The fact that most individuals could be classified as either FE or SE with hardly any intermediate types was not only due to many individuals with extreme values of exploratory behaviour, but also to the classification criteria used to translate two continuous behavioural measures into classes (figure 2). It is clear that the arrival time at the last (fifth) tree in a novel environment does not have a bimodal frequency distribution, although the distribution is not normal. Therefore the birds were divided in three rather than two classes for arrival time; fast, intermediate and slow. As discussed in chapter 2, the less clear distinction between fast and slow birds may be caused by the fact that the arrival time at the last tree is a result of several decisions to stay in the same tree or go to the next. An accumulation of decisions causes a less clear frequency distribution (Ehlinger, 1986 cited in Clark and Ehlinger, 1987). Therefore, arrival time as a measure of exploratory behaviour is less suitable for the classification of FE and SE. The approach time to a strange object in the home cage shows a clearer distinction between fast and slow birds (figure 2). It is, however, debatable if this approach time is bimodally distributed, for the same reason as is the bimodality of the attack latency time, used in rodents to discriminate between the two coping types (Benus, 1991). It is clear that the second (right) peak in the distribution can be caused by the cut-off time of the observations. All animals that did not approach the object within the two minute trial time are summarised in the second peak, suggesting that they represent a homogeneous subset of animals which might not be the case. Additional measurements with a trial time of up to ten minutes indicated that although some birds approached the object in the extra time, many birds did not approach within this prolonged trial time (Drent, unpubl.). Still it is very likely that all tested birds would eventually approach the object if the trial time was infinite, yielding a Poisson-like distribution with a very long tail and a large variation between the slower birds. Measurements of latency times have this practical set-back, and other measures would be preferred. Perhaps a study with a series of standard tests in different social and non-social situations, analysed by factor or cluster analyses could clarify whether distinct groups of animals that differ in many aspects of their behaviour do exist. Treating the extremes as two different classes proved very fruitful for the purpose of this thesis to guide my thinking, but it cannot be excluded that there are several or even a whole range of classes. However, it is evident that the behavioural variation does not follow a normal distribution; most individuals have extreme values. To regard the behavioural variation as mere deviation of the mean is therefore an underestimation of the biological importance of this variation.

Genotypic difference is the fourth property of individual variation that reflects coping styles, according to Jensen (1995). Preliminary data discussed in chapter 2 suggested that individual differences in exploratory behaviour had already developed in the nestling stage or earlier; they could even be genetically determined. Recently clear evidence for a genetic basis of approach time to a novel object and exploration speed of an unfamiliar environment has been provided by selection experiments combined with cross fostering by Drent (1997). Two lines of great tits, selected for extreme fast or slow exploration have been established and the offspring scores for the selection criterion (a summation of scores of approach time and arrival time) rapidly diverged between the two lines during four generations, indicating a considerable heritability.

This leads to the conclusion that according to the criteria set by Jensen (1995), the consistent behavioural differences of juvenile male great tits indeed represent different behavioural strategies. In this case, the term 'strategy' should not be interpreted as a strict and discrete cluster of behaviour, but in a broader sense as behaviour patterns which an animal uses to achieve its goal or even a series of decisions that an individual makes over a period of time (Davies, 1982; Dunbar, 1984; both cited in Mendl and Deag, 1995). In coping strategies this goal is environmental control (Koolhaas *et al.*, 1997); therefore differences in behaviour can only be expected in situations with environmental challenges, where the animal perceives a temporary loss of control. Unfamiliar or changing social or physical environments provide such challenges and the behavioural differences described in this thesis were observed in such situations. It should therefore not be expected that FE and SE show clear behavioural differences once an environment is very familiar or a hierarchy has stabilised and no changes occur.

Causes of behavioural differences

Physiological differences

One of Tinbergen's four questions is concerned with the causation of behaviour and most research on coping strategies has concentrated on this aspect. Especially physiological differences in stress responses are well studied and used as a basis for further research into the neuroendocrine mechanisms underlying the different strategies. In rodents and other vertebrates aggressive, active copers show a higher sympathetic reactivity to stress while non-aggressive, passive copers are presumed to show a higher parasympathetic reactivity (e.g. Bohus *et al.*, 1987; von Holst, 1986; Hessing *et al.*, 1994; van Raaij *et al.*, 1996). Koolhaas *et al.* (1997) suggest that the individual tendency to cope either actively or passively is determined by the detailed neurochemical state of limbic forebrain structures in terms of number of neurons, hormonal and neurotransmitter receptor binding capacity etc. These studies all show that that in an organism either one coping strategy or the other dominates, while hardly ever both strategies were found to occur simultaneously. Why can individuals only adopt one coping strategy, while in certain situations a switch to another strategy seems to be preferable? And why are two antagonistic systems, the sympathetic and the parasympathetic one, needed, which seems an unnecessary complex and inefficient mechanism? Why are they not combined in one, with differences in reactivity determining the coping strategy? It is quite conceivable that these phenomena are associated with neurological constraints, and perhaps in the future neurofysiologists will provide us with an answer to these intriguing questions.

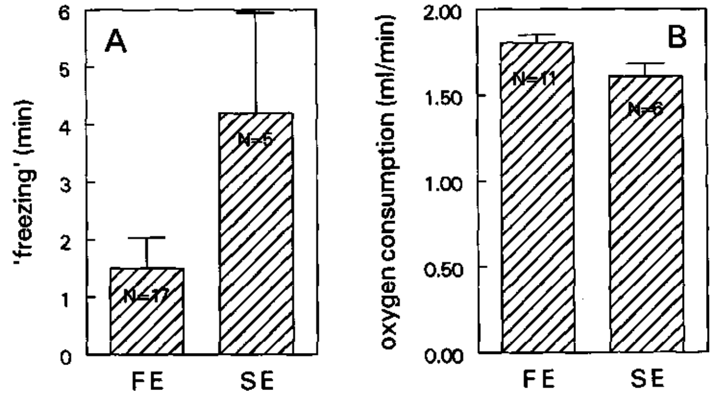


Figure 3. *Behavioural (A) and metabolic (B) reaction to an alarm call in FE and SE. Birds were weighed and put into a small metabolic chamber of plexiglass with a speaker from which the call was given. After 30-60 minutes in dimmed light and an ambient temperature of 18°C the birds sat down quietly; their oxygen consumption was low and stable and did not differ between FE and SE (Mann-Whitney U test: p=0.3). Then the alarm call was given. The duration of the behavioural reaction of 'freezing' was consistent for each individual in repeated measurements (Kruskal-Wallis statistic H=36.9, n=42, p=0.02). Figure A shows the mean 'freezing' time (+ s.e.) for FE and SE (MWU test: p=0.08). Figure B shows the mean (+ s.e.) elevated oxygen consumption during freezing for FE and SE (MWU test: p=0.04). After correction for weight the difference in oxygen consumption became less clear (FE: mean 0.12 ml O2/min/gr, SE: mean 0.10 ml O2/min/gr; MWU test: p=0.08), although FE and SE did not differ in weight (t-test: t=-0.11, df=15, p=0.9).*

The results of the studies on great tits suggest that the application of the coping concepts can be extended to birds. If the physiological basis is comparable, this application seems even more justified. A small pilot project provided preliminary data on physiological differences between FE and SE great tits. Both the behavioural and the metabolic reaction to an alarm call, that is normally used by great tits as a warning against predators, were recorded in FE and SE (for more details on methods and results see legend in figure 3). All tested birds crouched and remained immobile as a natural reaction to the call. The duration of this 'freezing' was consistent for each individual in repeated measurements. The data suggest that SE tended to 'freeze' for a longer period than FE (figure 3A). During this 'freezing', the oxygen consumption, indicator for the metabolic rate, was elevated on average by 44%. This elevated value of oxygen consumption was higher for FE than for SE (figure 3B).

In a recent study, blood samples were taken from selected FE and SE before and after they were put in a mixed aviary group with FE and SE in which a stable hierarchy developed. The preliminary results seem to indicate that the two selection lines differed in immunological parameters (the ratio of different types of leukocytes) as a reaction to the social experiences (Incagli and Drent, in progress). The results of both studies suggest that also in great tits behavioural differences in reaction to stress are accompanied by physiological differences. However, before any conclusion can be drawn, further tests of (para)sympathetic reactions in FE and SE are needed.

Nature - nurture

How do behavioural characteristics develop? This is another question that should be asked in analogy of Tinbergen's four questions. Besides a genetic basis, environmental factors may also influence the development of behavioural characteristics. Recent studies on rodents show that genetic differences, and in particular the Y-chromosome, play an important role in the development of aggression differences (Sluyter *et al.*, 1996). Testosterone, and especially the timing of testosterone releases in the perinatal period is important in the differentiation of coping styles (measured as differences in aggression; Compaan, 1993; de Ruiter *et al.*, 1992). Such perinatal testosterone levels are determined by genetic factors whereas environmental sources of variation like prenatal and postnatal maternal effects are of minor importance (Sluyter *et al.*, 1996).

There are several reasons why this low phenotypic plasticity in rodents can not simply be extrapolated to great tits. One is that Y-chromosomal effects on aggression in rodents cannot directly be translated to great tits, because birds do not have a Y-chromosome. They have a Z-chromosome which is only present in females who also have a W-chromosome; males have a double W-chromosome. Another reason is that in the rodent studies, selection lines are used and it can be expected that in a natural population in an unstable environment, plasticity is much larger. Recent findings indicate environmental influences on early and perinatal testosterone levels in birds. The amount of competition can influence testosterone production already in young chicks (Ros, 1997). In canaries and zebra finches, females have been found to transmit testosterone to the yolk of their eggs, and the amount of testosterone varied considerably in the same clutch (Schwabl, 1993). The social rank of juvenile sibling canaries was positively correlated with the concentration of yolk testosterone in the eggs from which they hatched, suggesting that the development of aggressive behaviour of offspring might be subject to modification by maternal testosterone.

There are some indications that plasticity in the development of the behavioural differences in great tits exists. Spring 1991 was very wet and cold and many great tit nestlings died of starvation. Although the nestlings collected that year weighed much less than usual at an age of eight to twelve days, they had normal weights after hand rearing, when they were four weeks old and could feed themselves. That year there were about three times more FE than SE (chapter 3), which was significantly more than in the other years when the ratio FE/SE was about 1 or 0.7 (figure 4). The different ratios are probably not caused by differences in population composition between areas, because in 1990 and 1991 most nestlings were collected in the same area. It seems more likely that they were caused by the bad circumstances in spring 1991. FE nestlings might have survived the lack of food and the cold better than SE nestlings or general retardation of growth during the first eight days might have stimulated the development of fast exploratory behaviour. The latter explanation implies plasticity. Such an effect of food shortage on later behaviour has been reported for mice (Tonkiss and Smart, 1982 cited in Huntingford and Turner, 1987). Mice that experienced a short period of undernourishment shortly after birth were more likely to initiate an attack on another mouse, which is characteristic behaviour of FE in great tits. Another indication for plasticity was found by Drent (unpubl.), who measured a correlation between growth rate of great tit nestlings between 5 and 10 days after hatching and approach time to a strange object. The young of FE that grew slowly had a longer approach time relative to their parents than faster growing young. Thus, retarded nestlings of FE became slower explorers than was expected based on the behaviour of their parents, although they were still faster than the young of SE. Such a correlation was not found in nestlings of SE, possibly because there was an upper limit to approach time preventing SE birds to become slower. The findings of Drent suggest that retardation of nestlings results in slower explorers, while the retardation of the nestlings in 1991 seemed to have resulted in faster explorers. Although the retardation Drent measured in nestlings was not extreme and all nestlings survived, in contrast to the nestlings of 1991, the suggested effects on the development of behavioural differences seem to be contradictory. The possible role of early retardation certainly needs further study.

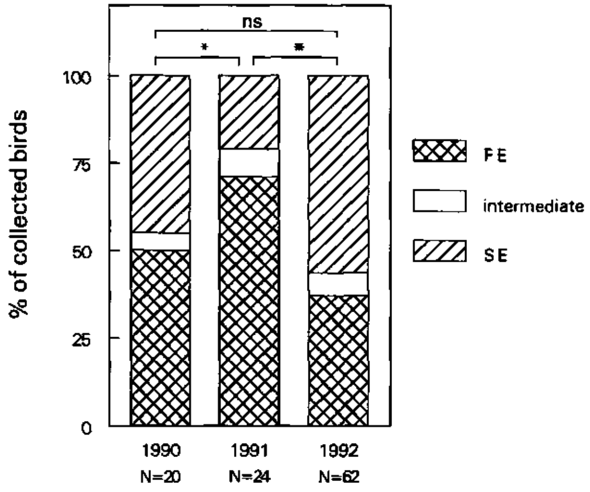


Figure 4. *Percentage of FE, intermediate explorers and SE collected in different years. The ratio of FE and SE differed between the years ($\chi^2=9.07$, df=2, p=0.01). Due to small numbers, intermediate explorers had to be excluded from the analyses. Further pair-wise χ^2-tests showed that this inter-year difference was caused by 1991: ** $p<0.01$; * $0.05<p<0.10$; ns $p>0.1$.*

It is clear that plasticity in the development of the behavioural differences cannot be ignored. This may also have implications for the findings presented in this thesis. All birds used in this study were hand-reared from day eight on after hatching with high quality and abundant food, which is not always the case under natural circumstances. Moreover, after four weeks, the juveniles were housed separately while under natural circumstances they would flock and feed together at that age (Drent, 1984; Verhulst and Hut, 1996). In several species, ranging from fish to monkeys, early isolation can influence later (social) behaviour (for an overview see Huntingford and Turner, 1987). Although the juveniles still had visual and auditory contact with other separately housed juveniles, their behaviour might have been affected by the artificial treatment. This possibility can be excluded by studies of the development of behavioural differences in genetically selected FE and SE growing up under natural circumstances.

Functional aspects of behavioural strategies

Why different strategies?

Why would different coping strategies exist? This question of Tinbergen considers the functional aspects of the behavioural characteristics. Let us assume that there is hardly any phenotypic plasticity but that coping strategies are genetically determined, with individuals being inflexible in the strategy they adopt and very consistent in their behaviour, as described by Jensen (1995). Since coping strategies coexist in populations, the different strategies must have equal pay-offs in terms of lifetime reproductive success under these assumptions.

There are two main hypotheses for the occurrence of alternative behavioural strategies with equal pay-off within a species (Huntingford and Turner, 1987; Krebs and Davies, 1987; Mendl and Deag, 1995). One hypothesis is that one strategy may be best in one particular physical (abiotic) environment while another strategy is favoured in another physical environment. In patchy habitats or frequently changing environments several strategies may persist because each does better in a different environment. It depends on the environment which individuals with a specific strategy are better off and therefore probably in higher numbers present in that particular environment. This hypothesis implies a fluctuating selection pressure in time and/or space. An example is the different colour morphs of the three spined stickleback (McPhail, 1969; Semler, 1971; Moodie, 1972; all cited in Krebs and Davies, 1987). Some males have bright red throats and others have dull throats. The red males are more attractive to females but also more susceptible to predation by trout, especially in bright light. In deep dark waters of the North American lakes most males are of the red type, while in shallow, brighter waters dull males do best since they are less predated.

The other hypothesis is that there may be different strategies whose pay-offs depend on what others in the population are doing. If most others are following one strategy, then following another strategy could be more advantageous. If the pay-offs of different strategies depend on their frequencies of occurrence in the population, game theory models show that there will be a stable balance in this population between the strategies (Maynard-Smith, 1982) at which frequencies the strategy pay-offs are equal. This hypothesis implies a frequency dependent selection.

The two hypotheses are not mutually exclusive, but concerned with either the physical or the social environment of the animal. An important aspect of different coping strategies is the degree to which behaviour is guided by environmental stimuli, both physical and social. This makes both hypotheses appropriate. Therefore coping strategies are likely in species that live in highly variable physical and social circumstances in time and/or space. If there is some degree of plasticity in the development of coping strategies, then strategies with different pay-offs can also coexist in a population. Even if for example passive copers would be better off than active copers and have a higher fitness, still phenotypically active copers could exist if circumstances like bad feeding conditions during the first weeks of their life stimulate the development of active coping behaviour in genetically passive copers. In that case fluctuating selection pressure in time and/or space and frequency dependent selection may not be sufficient to explain the existence of different coping strategies within one species. Still both hypotheses could offer at least part of the explanation, since there is a genetic basis for the strategies.

The case of the great tit

Why do FE and SE great tits both still exist in one population? To answer this question, it is necessary to assess the costs and benefits of the different behavioural strategies and their pay-offs in terms of fitness consequences under different circumstances. Lifetime reproductive success determines fitness (Daan and Tinbergen, 1997). During the annual cycle of the great tit there are several crucial moments in which the 'decisions' taken by individual birds are of prime importance for survival and reproduction, as discussed by Tinbergen *et al.* (1987). These are foraging and migration during the post-fledging period, social dominance in juvenile flocks and subsequent territory settlement in autumn, dispersal of non-territorial birds in winter, acquisition of territory and mate in spring, timing of breeding and clutch size, timing of weaning of the young of the first brood and a possible second brood. FE and SE may differ in these important 'decisions', since their behavioural characteristics may bring different cost and benefits under different circumstances. Based on the behavioural characteristics described in this thesis, I will try to predict qualitatively the possible costs and benefits of those important decisions for FE and SE. Since only differences in exploratory and agonistic behaviour in juveniles are described, and since one of the two main determinants of life time reproductive success is the chance that a fledgling survives to become a breeding bird (Tinbergen *et al.*, 1987), this attempt will only be made for the period between fledging and spring settlement.

Foraging in the post-fledging period

During the first weeks after fledging, juvenile great tits feed on insects only, mainly caterpillars (Betts, 1955; Gibb 1954). Caterpillars of most species are only available during a short time span in which their biomass peaks (van Balen, 1973). The different insect species live in different trees and peak at different times and foraging great tits shift from one species to the other with their changing abundances (Gibb, 1954). Young great tits become independent of their parents under these variable foraging conditions and many migrate to areas rich in food. Especially during the first period of independence marked reductions in body weight up to 10% of the fledging weight occur (Webber, 1975; cited in Drent, 1984). Findings by Gibb (1954) and Drent (1984) suggest that the mortality of on average 50-60% amongst these young in summer and early autumn is for a large part due to their inexperience and food availability. This implies that exploratory behaviour, a major activity in the post-fledging period, may be very important for survival. FE and SE differ in their attention to the environment and there may be a trade-off between the conflicting demands of sampling in a variable environment and the exploitation of the most profitable resources, as discussed in chapter 2. In a relatively good food situation with high insect biomass, differences in attention to the environment will not be crucial for survival. However, in a relatively bad food situation SE may be better off than FE under the variable foraging conditions, because SE pay more attention to the environment. SE may regularly sample other places or food types which will help finding food or shifting from insect species with their changing abundances. Especially in a critical food situation this may make the difference between life or death and SE may then survive better than FE. Experiments in which distribution and abundance of food are manipulated for juveniles in the post-fledging period are needed to test this hypothesis.

Dominance and territoriality

After a few weeks of independence, agonistic interactions over food and space increase and gradually a dominance hierarchy develops in the flock of juveniles. Juveniles with a low social rank show a higher tendency to leave the flock and migrate, especially in areas with low food availability (Drent, 1983; 1984). For those individuals chances to obtain a high rank in another flock will diminish quickly as hierarchies stabilise. Experiments show that a new bird that joins a stable hierarchy will almost always gain a low rank (Drent, 1983; Nilsson, 1989; Nilsson, 1990). Birds with a high rank in the resident flock have the best chance of occupying an empty territory in September after moulting (Drent, 1983). After removal of the top bird of a stable hierarchy in an aviary group, the second bird takes the top position and all others move up one place in the hierarchy. In the natural situation, a similar process takes place in a flock after settlement or disappearance of the top bird (Drent, 1983). We should therefore expect that after the settlement of juveniles with high ranks, subordinate individuals with middle ranks will be the first to settle if there are still vacancies.

This order of settlement may be of particular importance for SE who generally have middle ranks (chapters 4, 5, figure 1). FE and SE might have different strategies to become territorial in the autumn. The fighting behaviour of FE reaps high benefits if they win because they will be at the top of the hierarchy and thus have a very high chance of settling. FE have to bear considerate costs if they lose because they will obtain a rank at the bottom of the hierarchy. They will have a very low chance of settling because after the territorial strife in autumn there are usually flocks of unsuccessful birds left. The behaviour of SE brings low costs if they lose: they will be in the lower middle regions of the hierarchy, but still have a higher chance of settling than the fast explorers that lost and obtained the bottom ranks. If SE win they will be in the higher middle regions of the hierarchy and have relatively low benefits, since they have a lower chance of settling than top ranking FE.

The chances of obtaining a territory may therefore differ for FE and SE and depend on their frequencies of occurrence in the flock as illustrated in figure 5. If there are many SE, fast attacking FE have a high chance to gain a high rank and become territorial. In a flock with a high proportion of FE, only some FE will obtain a high rank. Most FE lose from other FE; they have difficulties in coping with severe defeat which will be used by the SE, and eventually FE will fall to a low rank and have low chances of obtaining a territory. The average chance for all FE to obtain a territory is then relatively low. If it is assumed that such a simple model can be applied to the FE and SE and their chances of territoriality in the autumn, then the relative frequencies of FE and SE at equilibrium, when chances to obtain a territory are equal for FE and SE, will depend on the costs and benefits in that process. These will be density-dependent because at a high density of adults a lower proportion of juveniles will eventually settle (Drent, 1983), and hence it becomes more important to have a high rank. A decrease of the proportion of juveniles that becomes territorial will therefore especially diminish chances of becoming territorial for the middle-ranking SE (figure 5). Experiments in which the composition of the juvenile flocks or the density of resident birds (and thus the number of vacant territories) is manipulated and measurements of hierarchy in juvenile flocks before territory settlement and identification of territory owners after settlement are needed to validate such a model.

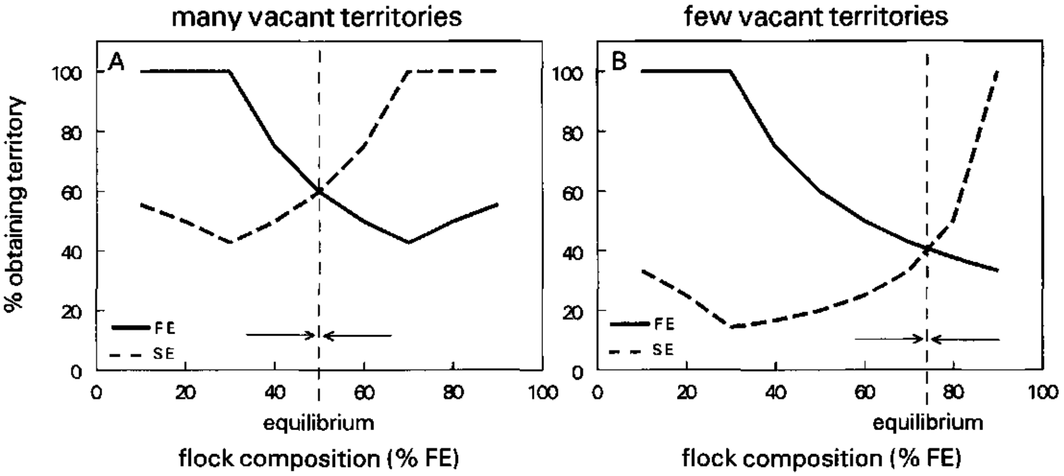


Figure 5. *Frequency dependent model of chances for FE and SE to obtain a territory in autumn. Figures are derived by assuming: 1) social rank determines settlement order (Drent 1983); 2) a maximum of 30% FE will obtain top ranks, all extra FE have bottom ranks; 3) the birds do not disperse; 4) there are no interactions with (adult) birds other than flock mates. At the intersection of the curves chances are equal for both strategies. In a flock with a higher frequency of FE (right of the equilibrium flock composition), SE have a better chance than FE; with a lower frequency of FE, FE have a better chance. If having a territory determines fitness, an increase in frequency of FE above equilibrium will result in a higher fitness of SE and more SE will return in the next generation. Due to this frequency dependent selection pressure (arrows), the flock composition will eventually adjust to the equilibrium point. The equilibrium flock composition depends on the number of vacant territories which is influenced by population density. Curves are given for many vacant territories (A) when a high proportion (set at 60%) of the flock will obtain a territory, and for few vacant territories (B) when a low proportion (set at 40%) will obtain a territory. The number of vacancies changes the point of equilibrium mainly by affecting the curve for SE.*

Winter dispersal and foraging

After the autumn territory settlement, non-territorial birds have the choice of staying put in the local flock of non-territorial birds and waiting until vacancy occurs (even under favourable conditions 30-40% of the territory owners dies during the winter, Drent 1979) or disperse in the hope of finding less populated areas. Especially for FE at the bottom of the hierarchy the benefits of being in a flock may be low since they have little access to food or vacant territories. The costs to stay may be high for them because they will be defeated often by territorial and dominant non-territorial birds and FE have difficulties to cope with defeat (chapters 4, 5). Therefore FE at the bottom of the hierarchy can be expected to disperse, especially in areas with high density and low food supply, where competition is severe. SE are better able to cope with defeat and might have a higher tendency to stay as a permanent member of a flock and wait for a vacancy.

Winter flocks of non-territorial great tits roam over large areas searching for food. Within such a flock, detection of food sources by some can be exploited by others, as has been reported in many species (Barnard, 1984). A system may exist of producers, specialised in finding food, and scroungers, specialised in exploiting the food discovery of producers by stealing it from the producer or monopolising the discovered food patch. Since SE pay more attention to the environment, they may be good at finding food and thus be producers. Aggressive, dominant FE may be scroungers and monopolise most of the food in the discovered patch, displacing other foragers, mainly other aggressive scroungers.

Barnard and Sibly (1981) show that the amount of food obtained by individual producers and scroungers depends on their frequencies in the flock. The amount of food obtained by scroungers will increase when there are more producers present. The pay-off to producers decreases with increasing numbers of scroungers. At a certain composition of the flock an equilibrium will exist with equal pay-off to both, and this equilibrium is influenced by the amount and distribution of food (Koops and Giraldeau, 1996). If food is spread over large areas then it is hard to monopolise and SE may then do better and thus be with a higher frequency in the flock at equilibrium. Food densely clumped in patches enhances competition and then FE may do better. Experiments in large aviaries in which flock composition of FE and SE are manipulated, as well as food supply and distribution, will help to understand the possible processes in winter flocks better. Measurements of local winter survival of FE and SE in flocks with different composition in different circumstances regarding population density or flock size and food supply and distribution are also needed.

Spring settlement

A new wave of attempts to occupy a territory occurs in spring, when winter flocks break up and all non-territorial birds roam alone or accompanied by a mate. The situation differs from the autumn settlement, because it is not the dominance hierarchy, but outcomes of short fights between two roaming birds that will determine settlement (Drent, 1983). If the competitors arrive simultaneously in the vacant area, FE may win from SE by giving the first blow (chapters 3, 4, 5). This will however depend on the previous experiences of the birds. The outcome of the fight may be different if the FE previously lost many fights, which will be the case if he was at the bottom of the hierarchy in the winter flock. Simultaneous arrival of two competitors may mainly occur in areas with low density of candidates for a territory, where all residents already occupied a territory in autumn or winter. In high density areas, the outcome of fights over spring territories is difficult to predict. Besides immigrants, there may be many resident non-territorial birds left from the local winter flock who were not able to occupy a territory during winter. Birds that are already present in the area have a higher chance of winning than newcomers (Drent, 1983; Sandell and Smith, 1991). The effect of prior residence on the outcome may be stronger than the effect of behavioural characteristics. Besides, in high density areas, chances of losing are also higher, which may be a disadvantage for FE that have difficulties to cope with defeat. The relative effects of prior residence and behavioural characteristics can be tested in aviary experiments, or in experiments in the natural situation by introducing FE and SE either simultaneously or one after the other in an area in which many territory owners were removed, thus creating enough vacancies for spring settlement.

Conclusions of predictions

Based on the above predictions, both of the discussed hypotheses for the occurrence of alternative behavioural strategies with equal pay-off seem to apply to the great tit. The proposed different strategies of FE and SE to become territory owner in autumn are frequency dependent, as are the suggested different foraging strategies in winter flocks. In both situations, FE and SE will do equally well when the population is at equilibrium and the balance between FE and SE stable. In the postfledging period, SE may be better at finding food when there is little food available, and thus have a higher chance of surviving, assuming that a system of producers and scroungers is formed only later, when agonistic behaviour is fully developed. With enough food available, chances of surviving may be equal for FE and SE. During spring settlement, FE may be better at winning fights for vacant territories and hence have a higher chance to produce off-spring, provided that population density is low and the FE did not lose many fights previously. When there are many resident rivals for spring territories due to high population density, such differences between FE and SE may be overruled by prior residence and previous experience. These processes could be interpreted as a fluctuating selection pressure in time with (under certain conditions) SE having a higher fitness in the post-fledging period and FE in spring.

This effort to predict qualitatively the possible costs and benefits for FE and SE of several important decisions in the different phases of the first half year of their life is clearly speculative. It is also too simple, since it does not take into account factors like predation chance or mate choice which may differ for FE and SE. It does clarify, however, which kind of experiments should be done before any statement can be made on relative chances of FE and SE fledglings to survive and become a breeding bird. Even then it will be very difficult since not only factors like density and food availability have to be taken into account, but also the effect of the experiences and outcome in a preceding phase on the decisions in the next. To make a model that predicts the chances to become breeding bird of FE and SE under different conditions therefore is a true and most complicated challenge. Still it is worth trying, since such a model will enhance the understanding of the consequences of the different strategies for population dynamics and evolution. A model with the great tit can then more generally be applied to other species with different coping strategies.

Recently fledged

SUMMARY

Summary

Social dominance affects territory acquisition, reproduction and survival in many species. It plays a major role in the life of an individual, and has important consequences for its fitness. Several factors that can influence dominance relationships between individuals have been well studied, such as differences between rivals in size, weight, fighting experience, prior residence, and resource value. Individual behavioural characteristics can also influence dominance. Studies of domesticated and laboratory animals show that individual animals can be characterised by their aggressiveness, as measured in standardised tests, and that aggressive individuals are generally dominant over non-aggressive ones. These behavioural characteristics have a genetic basis, and are not only reflected in aggressiveness but also in a whole range of other behaviours, such as exploration or nest building. Based on these behavioural characteristics, different types of animals can be distinguished. So far, behavioural characteristics have mainly been studied in mammals, not in birds. Moreover, the effect of such behavioural characteristics on social dominance has received little attention in studies of natural populations. This thesis aims to take a first step by studying the existence of consistent individual behavioural characteristics and their effect on social dominance in the great tit (*Parus major*).

If behavioural characteristics are really individual traits, or in other words 'consistent', they should already exist early in life, before any dominance relationship develops. In that phase of life, exploration and foraging are the main activities of great tits. Indeed, during the first 18 weeks of their life, hand-reared young male great tits, collected from a natural population, could be characterised by their exploratory behaviour (chapter 2). In repeated tests, they showed consistent reactions to a strange object in their home cage, even with different objects and after an interval of some weeks. This extended to other exploratory behaviour. Birds that approached a strange object quickly, were also fast to explore an aviary with which they were unfamiliar. Accordingly, birds that approached a strange object more slowly, took more time to explore thoroughly the unfamiliar aviary. These behavioural differences were also reflected in the strength of foraging habits, built up during a training in which food was always offered in the same place. After a change in the location of food, the fast and superficial explorers (FE) would stick to their habit, and keep going to the place where the food used to be. The slow and thorough explorers (SE) soon changed their behaviour and stopped going to the usual feeding place. They seemed to remain alert and to pay more attention to stimuli in the known environment than the fast, superficial explorers.

The juveniles could also be characterised by their aggressive behaviour in experimental pair-wise confrontations (chapter 3). FE started more fights and won more often than SE, also when possible effects on dominance of other factors such as weight and size were taken into account. For FE clearly the first blow was half the battle. For natural populations, the relevance of these findings could still be small, since dominance relationships normally develop in a flock of juveniles, resulting in a more complex social hierarchy. Therefore groups of birds were observed in aviaries, which probably better resemble natural conditions (chapter 4). In all observed groups, a stable hierarchy only established after a dynamic phase of several days, in which many reversals in dominance relations occurred. During the first day in the aviary, the situation was similar to that observed in the tests with pair-wise confrontations. FE initiated more fights than SE and won more often, again after correction for factors such as weight and size. Surprisingly though, once the hierarchy had stabilised, SE were on average dominant over FE; SE had higher ranks than FE in the hierarchy.

Apparently, the same behavioural characteristics result in different dominance relationships under different circumstances. Further observations supported and specified this conclusion. Other studies have shown that familiarity with the environment increases chances of becoming dominant. The birds in the groups had been unfamiliar with the aviary before being put together. The SE initiated fewer fights than FE and initiated their first fight more often in the place where they had spent most time. This suggested that SE made more use of their knowledge of the environment than FE, who were more focused on fights. Their more thorough manner of exploring may gradually have led to a better, or more detailed, knowledge of the environment in SE, which in turn may increase their chances of winning. In this way, the initial advantage that FE had by giving the first blow, could be reversed by the alertness and increasing spatial knowledge of SE. Such a gradual process could not happen in groups of birds that were first separately familiarised with the aviary before being put together (chapter 5). In those groups, all birds had a good knowledge of the environment and FE and SE did not show the differences in their behaviour which they showed in the unfamiliar aviaries. In these familiar aviaries, FE won on average over SE, both on the first day and after stabilisation of the hierarchy. These results suggest that SE may be best adapted to new or unstable and changing environments, while FE may do better in familiar and stable ones.

The presence and behaviour of flock mates in the groups also modified dominance relations of FE and SE (chapters 4, 5). Several studies have shown that previous experience in a fight influences the outcome of a subsequent fight. FE and SE differed in their fighting behaviour and reaction to previous fights. FE

seemed to take more risks in their fighting behaviour. In all groups, they attacked quickly and won from SE on the first day. But if FE lost severely, they needed more time to recover before starting a new fight, which strongly suggests that they had problems in coping with the defeat. The more cautious SE needed less time to recover and seemed not only to make more use in their fights of information about their physical, but also about their social, environment. They would take advantage of the vulnerability of a FE that had just lost from a third bird, by starting a fight with that loser. In this way, a FE with a high rank that lost severely from a FE with an even higher rank, could subsequently also lose from SE and fall in hierarchy to the lowest positions. This resulted in a stable hierarchy in which fast explorers had either high or low ranks, while slow explorers had middle ranks. This characteristic dominance pattern was found in all observed groups. In the groups in unfamiliar aviaries, only a small proportion of the FE had extreme high ranks, while a large proportion had extreme low ranks. In the groups in familiar aviaries it was the other way round. Hence, familiarity with the environment only influenced the proportion of FE in highest or lowest places, resulting in different *average* ranks of FE and SE in the two experimental situations. Such average ranks are therefore not the most sensitive way to describe dominance relations in a stable hierarchy.

The last chapter (6) discusses whether the behavioural characteristics reflect two different, but equally successful, behavioural strategies to cope with environmental challenges, and what their consequences could be for foraging success, territoriality and survival in different natural situations. This could be the starting point for future studies.

In conclusion, the results of this study show that juvenile male great tits show consistent individual differences in exploratory behaviour. These differences extend to fighting behaviour, which is consistent over different social situations. These behavioural characteristics predict dominance, the outcome depending on familiarity with the environment and behaviour of possible flock mates.

SAMENVATTING

Samenvatting

Sociale dominantie is het verschijnsel waarbij van twee dieren die herhaaldelijk met elkaar vechten, er steeds één, de dominante, als winnaar uit de bus komt. Sociale dominantie beïnvloedt in veel diersoorten de kansen op een territorium, op nageslacht en op overleving. Het speelt dan ook een grote rol in het leven van een individu en heeft bovendien gevolgen voor de hoeveelheid nageslacht dat een individu voortbrengt, waardoor de samenstelling van de populatie in de volgende generatie wordt beïnvloedt. Een aantal factoren die dominantieverhoudingen tussen dieren kunnen beïnvloeden zijn grondig bestudeerd, zoals de verschillen tussen rivalen in grootte, gewicht, ervaring in eerdere gevechten, bekendheid met de omgeving en ook het belang van de zaken waarom wordt gevochten. Ook verschillen in individueel gedrag kunnen invloed hebben op dominantie. Onderzoeken aan (landbouw)huis- en laboratoriumdieren laten zien dat individuele dieren gekenmerkt kunnen worden door hun agressiviteit, gemeten in standaard testen, en dat agressieve dieren in het algemeen dominant zijn over niet-agressieve dieren. Deze gedragskenmerken hebben een genetische basis en komen behalve in agressiviteit ook tot uiting in een reeks andere gedragingen, zoals exploratief gedrag en nestbouw. Op basis van deze gedragskenmerken zijn er verschillende typen dieren te onderscheiden. Tot nog toe zijn gedragskenmerken voornamelijk onderzocht bij zoogdieren maar niet bij vogels. Bovendien heeft het effect van gedragskenmerken op sociale dominantie weinig aandacht gekregen in onderzoek aan natuurlijke populaties, terwijl toch juist in de natuurlijke situatie dominantie zoveel gevolgen heeft. Deze dissertatie heeft als doel hier een begin mee te maken, door zowel het bestaan van individuele gedragskenmerken als hun invloed op sociale dominantie te onderzoeken in de koolmees (*Parus major*).

Als gedragskenmerken werkelijk individuele eigenschappen zijn, in andere woorden 'consistent', dan moeten ze al vroeg in het leven van een dier aanwezig zijn. Eigenlijk nog voordat zich enige dominantieverhouding met een soortgenoot kan ontwikkelen. In die levensfase van de koolmees zijn exploratie en voedsel zoeken de belangrijkste activiteiten. Inderdaad konden met de hand opgevoede jonge mannelijke koolmezen, afkomstig uit een natuurlijke populatie, gedurende de eerste 18 levensweken onderscheiden worden op basis van hun exploratief gedrag (hoofdstuk 2). In herhaalde testen bleken zij consistent te reageren op een vreemd voorwerp in hun kooi. Ook bij wisselende vreemde voorwerpen en na een tussenpoos van enkele weken reageerden zij consistent. Dit gold ook voor ander exploratief gedrag. Vogels die een vreemd voorwerp snel naderden, waren ook snel in het onderzoeken van een onbekende volière. Evenzo namen vogels die een vreemd voorwerp langzamer naderden meer tijd om de onbekende volière grondig te onderzoeken. Deze gedragsverschillen kwamen ook tot uiting in het volharden in gewoontes bij voedsel zoeken. Deze gewoontes waren opgebouwd in een training waarbij telkens op dezelfde plaats voedsel werd aangeboden. Na een verandering van de voerplaats bleven de snelle en oppervlakkige exploreerders lang vasthouden aan hun gewoonte en zochten zij voedsel op de plaats waar altijd gevoerd werd. De langzame en grondige exploreerders veranderden al snel hun gedrag en lieten de vroegere voerplaats eerder links liggen. Zij leken alerter te zijn en meer aandacht te hebben voor hun omgeving dan de snelle en oppervlakkige exploreerders.

De jonge vogels werden ook gekenmerkt door hun vechtgedrag in experimentele paarsgewijze confrontaties (hoofdstuk 3). Snelle exploreerders begonnen meer als eerste te vechten en wonnen vaker dan langzame exploreerders, ook als er rekening werd gehouden met mogelijke effecten van andere factoren op dominantie, zoals gewicht en grootte. Voor snelle exploreerders was de eerste klap duidelijk een daalder waard. Voor natuurlijke populaties zou de relevantie van deze bevindingen bij tweetallen echter laag kunnen zijn, aangezien dominantieverhoudingen zich normaal gesproken ontwikkelen in een groep jongen met een complexe hiërarchie als gevolg. Daarom werden de vogels in groepen bij elkaar gezet in een volière, wat de natuurlijke situatie waarschijnlijk beter benaderde (hoofdstuk 4). In alle bekeken groepen ontwikkelde zich pas een stabiele hiërarchie na een dynamische fase van enkele dagen, waarin vele omkeringen in dominantieverhoudingen optraden. Tijdens de eerste dag in de volière was de situatie vergelijkbaar met die in de experimentele paarsgewijze confrontaties. Snelle exploreerders begonnen meer gevechten dan langzame exploreerders en wonnen ook vaker, ook weer na correctie voor factoren als gewicht en grootte. Verrassend genoeg bleek echter dat na stabilisatie van de hiërarchie, de langzame exploreerders gemiddeld genomen dominant waren over de snellen; veel langzamen bezetten hoge rangen en veel snellen lage. Blijkbaar leiden dezelfde gedragskenmerken in verschillende situaties tot verschillende dominantieverhoudingen.

Deze conclusie kon beter worden onderbouwd en uitgewerkt door verdere waarnemingen. Andere onderzoekers hebben aangetoond dat bekendheid met de omgeving de kans op dominant worden vergroot. De vogels in de groepen waren onbekend met de volière voordat ze daar samen in werden gezet. De langzame exploreerders begonnen minder gevechten dan snelle exploreerders en begonnen hun eerste gevecht ook vaker op de plaats waar zij tot dan toe de meeste tijd hadden doorgebracht. Dit suggereert dat langzame exploreerders meer gebruik maakten van hun kennis van de omgeving dan snelle exploreerders, die meer op vechten gericht waren. De meer grondige manier van exploreren van de langzame exploreerders kan geleidelijk tot een betere of meer gedetailleerde kennis van de omgeving geleid hebben, wat weer een hogere kans op winst kon geven. Op deze manier zou het voordeel dat de snellen in het begin hadden door de eerste klap te geven, teniet kunnen worden gedaan door de alertheid en van de langzamen. Een dergelijk geleidelijk proces hoefde niet plaats te vinden bij vogels die eerst ieder apart de volière hadden kunnen onderzoeken voordat ze in groepen er in werden geplaatst (hoofdstuk 5). In die groepen waren alle vogels bekend met de omgeving en vertoonden snelle en langzame exploreerders niet de verschillen in gedrag die ze in de onbekende volière wel lieten zien. In deze bekende volières wonnen snelle exploreerders gemiddeld genomen van de langzamen, zowel op de eerste dag als na stabilisatie van de hiërarchie. Deze resultaten suggereren dat langzame exploreerders goed toegerust zijn voor een nieuwe of instabiele en veranderende omgeving, terwijl snelle exploreerders het het beste doen in een bekende en stabiele omgeving.

De aanwezigheid en het gedrag van groepsgenoten was ook van invloed op de dominantieverhoudingen van snelle en langzame exploreerders (hoofdstuk 4, 5). Uit enige onderzoeken is bekend dat de ervaring in een eerder gevecht de uitkomst van een daarop volgend gevecht beïnvloedt. Snelle en langzame exploreerders verschilden in hun vechtgedrag en hun reactie op zo'n eerder gevecht. In alle groepen vielen snelle exploreerders snel aan en wonnen zij op de eerste dag van langzame exploreerders. Wanneer snelle exploreerders echter flink verloren, hadden zij meer tijd nodig om te herstellen voordat zij een volgend gevecht begonnen, wat suggereert dat zij meer moeite hadden om verlies te verwerken. De meer voorzichtige langzame exploreerders hadden minder tijd nodig om te herstellen en leken in hun gevechten niet alleen meer gebruik te maken van informatie over hun fysieke maar ook over hun sociale omgeving. Zij deden vaak hun voordeel met de kwetsbaarheid van een snelle exploreerder die net van een derde vogel verloren had, door juist dan een gevecht met deze verliezer te beginnen. Op deze manier kon een snelle exploreerder met een hoge rang die flink verloren had van een nog hogere snelle exploreerder, vervolgens ook van langzame exploreerders verliezen en in de hiërarchie naar de onderste regionen vallen. Dit resulteerde in een stabiele hiërarchie waarin snelle exploreerders of hoge of lage rangen bezetten, terwijl de langzame exploreerders de middenposities innamen. Dit karakteristieke dominantie patroon werd in alle groepen gevonden. In de groepen in onbekende volières bezette slechts een klein aantal van de snelle exploreerders extreem hoge rangen en een groot deel extreem lage rangen. In bekende volières was dit net andersom. Bekendheid met de omgeving beïnvloedde dus alleen de proportie van snelle exploreerders in de hoogste en laagste rangen, waardoor de gemiddelde rang van snelle en langzame exploreerders verschilden in beide experimentele situaties. Dergelijke gemiddelde rangen zijn dan ook niet de meest directe manier om dominantieverhoudingen in een stabiele hiërarchie te beschrijven.

In het laatste hoofdstuk (6) wordt besproken of de consistente gedragsverschillen uitingen zijn van twee verschillende maar even succesvolle gedragsstrategieën voor het omgaan met uitdagingen of problemen, opgelegd door de omgeving. En ook wat de gevolgen van die gedragsverschillen zouden kunnen zijn voor fourageersucces, territorialiteit en overleving in verschillende natuurlijke situaties. Dit markeert een beginpunt voor verder onderzoek.

Concluderend blijkt uit deze studie dat jonge mannelijke koolmezen consistente individuele verschillen tonen in exploratief gedrag. Deze verschillen komen ook tot uiting in vechtgedrag, en zijn consistent in verschillende sociale situaties. Deze gedragskenmerken voorspellen dominantie, waarbij de uitkomst afhangt van bekendheid met de omgeving en het gedrag van eventuele groepsgenoten.

REFERENCES

REFERENCES

Arcese P and **Smith JNM**,1985. Phenotypic correlates and ecological consequences of dominance in song sparrows. J Anim Ecol 54: 817-830.

Assenmacher I, 1973. The peripheral endocrine glands. In: Avian Biology, volume 3 (eds. DS Farner and JR King). pp 183-286. Academic Press, New York.

Baker RR, 1993. The function of post-fledging exploration: a pilot study of three species of passerines ringed in Britain. Ornis Scand 24: 71-79.

Balen JH van, 1973. A comparative study on the breeding ecology of the Great Tit *Parus major* in different habitats. Ardea 61: 1-92.

Balen JH van, 1980. Population fluctuations of the Great Tit and feeding conditions in winter. Ardea 68: 143-164.

Balthazart J, 1983. Hormonal correlates of behavior. In: Avian Biology, volume 7 (eds. DS Farner, JR King and KC Parkes). pp 221-336. Academic Press, New York.

Barnard CJ, 1984. The evolution of food-scrounging strategies within and between species. In: Producers and Scroungers: strategies of exploitation and parasitism (ed. CJ Barnard). pp 95-126. Croom Helm, London & Sidney.

Barnard CJ and **Sibly RM**, 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. Anim Behav 29: 543-550.

Bekoff M and **Scott AC**, 1989. Aggression, dominance and social organization in evening grosbeaks. Ethology 83: 177-194.

Benus RF, 1988. Aggression and coping: differences in behavioural strategies between aggressive and non-aggressive male mice. PhD thesis, University of Groningen, Netherlands.

Benus RF, Koolhaas JM and Oortmerssen GA van, 1987. Individual differences in behavioral reaction to a changing environment in mice and rats. Behaviour 100: 105-122.

Benus RF, Bohus B, Koolhaas JM and Oortmerssen GA van, 1989. Behavioral strategies of aggressive and non-aggressive male mice in active shock avoidance. Behav Process 20: 1-12.

Benus RF, Den Daas S, Koolhaas JM and Oortmerssen GA van, 1990. Routine formation and flexibility in social and non-social behaviour of aggressive and non-aggressive male mice. Behaviour 112: 176-193.

Benus RF, Bohus B, Koolhaas JM and Oortmerssen GA van, 1991. Heritable variation in aggression as a reflection of individual coping strategies. Experientia 47: 1008-1019.

Bernstein IS, 1981. Dominance: The baby and the bathwater. Behav Brain Sc 4: 419-457.

Bertram BCR, 1978. Living in groups: predators and prey. In: Behavioural Ecology (eds. JR Krebs and NB Davies). pp 64-96. Blackwell Scientific Publications, Oxford.

Betts MM, 1955. The food of titmice in oak woodland. J Anim Ecol 24: 282-323.

Blanchard RJ, Hori K, Tom P and Blanchard DC, 1988. Social dominance and individual aggressiveness. Aggr Behav 14: 195-203.

Blurton Jones NG, 1968. Observations and experiments on causation of threat displays of the great tit (*Parus major*). Anim Behav Monogr 1: 74-158.

Bohus B, Benus RF, Fokkema DS, Koolhaas JM, Nyakas CA, van Oortmerssen GA, Prins AJA, de Ruiter AJH, Scheurink AJW and Steffens AB, 1987. Neuroendocrine states and behavioural and physiological stress responses. In: Progress in brain research, volume 72: Neuropeptides and brain function (eds de Kloet ER, Wiegant VM and de Wied D.). pp 57-70. Elsevier, Amsterdam.

Clark AB and Ehlinger TJ, 1987. Pattern and adaptation in individual behavioural differences. In: Perspectives in ethology, volume 7: Alternatives (eds. PPG Bateson and PH Klopfer). pp 1-47. Plenum Press, New York.

Cole DD and Shafer JN, 1965. A study of social dominance in cats. Behaviour 27: 39-53.

Compaan JC, Buijs RM, Pool CW, de Ruiter AJH and Koolhaas JM, 1993. Differential lateral septal vasopressin innervation in aggressive and non-aggressive male mice. Brain Res Bull, 30: 1-6.

Corson SA and **Corson EO**, 1976. Constitutional differences in physiologic adaptation to stress and distress. In: Psychopathology of human adaptation (ed. G Serbum). pp 77-94. Plenum Press, New York.

Crawley MJ, 1993. - GLIM for ecologists. Blackwell Scientific Publications, Oxford.

Daan S and **Tinbergen JM**, 1997. Adaptation of life histories. In: Behavioural Ecology (eds. JR Krebs and NB Davies). pp 311-333. Blackwell Scientific Publications, Oxford.

Dhondt AA, 1979. Summer dispersal and survival of juvenile great tits in southern Sweden. Oecologia 42: 139-157.

Dhondt AA and **Schillemans R**, 1983. Reproductive success of the great tit in relation to its territorial status. Anim Behav 31: 902-912.

Drent PJ, 1979. Territory occupancy in the autumn, seed food supply in the winter, and local survival during the annual cycle. Verh Kon Ned Akad Wetensch 2e Reeks 72: 310-316.

Drent PJ, 1983. The functional ethology of territoriality in the great tit (*Parus major L.*). Ph.D. thesis, University of Groningen, Netherlands.

Drent PJ, 1984. Mortality and dispersal in summer and its consequences for the density of great tits (*Parus major*) at the onset of autumn. Ardea 72: 127-162.

Drent PJ, 1995. Individuality and dominance during the year cycle of the great tit. Progress Report 1993-1994 of the Netherlands Institute of Ecology. pp 37-39.

Drent PJ, 1997. Realised heritability of a behavioural syndrome in the great tit. Progress Report 1996 of the Netherlands Institute of Ecology. pp 44-47.

Drews C, 1993. The concept and definition of dominance in animal behaviour. Behaviour 125: 283-311.

Ekman J, 1984. Density dependent mortality and population fluctuations of the temperate zone willow tit (*Parus montanus*). J Anim Ecol 53: 119-134.

Ekman J, 1990. Alliances in winter flocks of willow tits; effect of rank on survival and reproductive success in male-female associations. Behav Ecol Sociobiol 26: 239-245.

FitzGerald GJ and **Kedney GI**, 1987. Aggression, fighting, and territoriality in sticklebacks: three different phenomena? Biol Behav 12: 186-195.

Fels D, Rhisiart AA, Vollrath F, 1995. The selfish crouton. Behaviour 132: 49-55.
Fokkema DS, 1985. Social behaviour and blood pressure: a study of rats. Ph.D. thesis, University of Groningen, Netherlands.

Garnett MC, 1976. Some aspects of body size in the great tit. Ph.D. thesis, University of Oxford.

Garnett MC, 1981. Body size, its heritability and influence on juvenile survival among Great tits, *Parus major.* Ibis 123: 31-41.

Gibb J, 1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. Ibis 96: 513-543.

Goede P de , 1982. The survival of juvenile great tits in the first two weeks after fledging. Verh Ned Akad Wetensch Afd Natuurkunde 79, 2e reeks: 7-9.

Hansen SW and **Damgaard BM**, 1993. Behavioural and adrenocortical coping strategies and the effect on eosinophil leucocyte level and heterophil/lymphocyte-ratio in beech marten (*Martes foina*). Appl Anim Behav Sci 35: 369-388.

Hegner R, 1985. Dominance and anti-predator behaviour in blue tits (*Parus caeruleus*). Anim Behav 33: 762-776.

Hessing MJC, 1994. Individual behavioural characteristics in pigs and their consequences for pig husbandry. Ph.D. thesis, Agricultural University Wageningen.

Hessing MJC, Hagelsø AM, van Beek JAM, Wiepkema PR, Schouten WPG and Krukow R, 1993. Individual behavioural characteristics in pigs. Appl Anim Behav Sci, 37: 285-295.

Hessing MJC, Hagelsø AM, van Beek JAM, Wiepkema PR, and Schouten, WPG, 1994. Individual behavioral and physiological strategies in pigs. Physiol Behav 55: 39-46.

Hinde RA, 1952. The behaviour of the great tit (*Parus major*) and some other related species. Behaviour 2: 1-201.

Holst D von, 1986. Vegetative and somatic components of tree shrew behavior. J Autonom Nerv Sys (suppl): 657-670.

Hosmer DW and **Lemeshow S**, 1989. Applied logistic regression. John Wiley & sons, New York.

Houston AI and **Davies NB**, 1985. The evolution of cooperation and life histories in the dunnock, *Prunella modularis*. In: Behavioural ecology (eds RM Sibley and RH Smith). pp 471-487. Blackwell Scientific Publications, Oxford.

Houston AI and **McNamara J**, 1985. The variability of behaviour and constrained optimization. J Theor Biol 112: 265-273.

Huntingford F and **Turner A**, 1987. Animal Conflict. Chapman & Hall, London.
Jackson WM,1988. Can individual differences in history of dominance explain the development of linear dominance hierarchies? Ethology 79: 71-77.

Jackson WM, 1991. Why do winners keep winning? Behav Ecol Sociobiol 28: 271-276

Järvi T and **Bakken M**, 1984. The function of the variation in the breast stripe of the great tit, *Parus major*. Anim Behav 32: 590-596.

Järvi T, Walsø Ø and Bakken M, 1987. Status signalling by *Parus major:* an experiment in deception. Ethology 76: 334-342.

Jensen P, 1995. Individual variation in the behaviour of pigs - noise or functional coping strategies? Appl Anim Behav Sc 44: 245-255.

Kacelnik A, Houston AI and Krebs JR, 1981. Optimal foraging and territorial defence in the great tit (*Parus major*). Behav Ecol Sociobiol 8: 35-40.

Kleinbaum DG, Kupper LL and Muller KE, 1988. Applied Regression Analysis and Other Multivariable Methods. PWS-KENT publishing Company, Boston.

Kluyver HN, 1951. The population ecology of the great tit, *Parus major*. Ardea 39: 1-135.

Koolhaas JM, Boer SF de, Bohus B, 1997. Motivational systems or motivational states: behavioural and physiological evidence. Appl Anim Behav Sc 53: 131-143.

Koops MA and **Giraldeau L**, 1996. Producer-scrounger foraging games in starlings: a test of rate-maximizing and risk-sensitive models. Anim Behav 51: 773-783.

Krebs JR, 1971. Territory and breeding density in the great tit, *Parus major* L. Ecology 52: 1-22.

Krebs JR, MacRoberts MH and Cullen JM, 1972. Flocking and feeding in the great tit *Parus major* - an experimental study. Ibis 114: 507-530.

Krebs JR, Erichsen JT, Webber MI and Charnov EL, 1977. Optimal prey selection in the great tit (*Parus major*). Anim Behav 25: 30-38.

Krebs JR, 1982. Territorial defence in the great tit (*Parus major*): do residents always win? Behav Ecol Sociobiol 11: 185-194.

Krebs JR and **Davies NB**, 1987. An introduction to behavioural ecology. Blackwell Scientific Publications, Oxford.

Laet JV de, 1985. Dominance and aggression in juvenile great tits, *Parus major L.* in relation to dispersal. In: Behavioural ecology (eds. RM Sibley and RH Smith). pp 375-380. Blackwell Scientific Publications, Oxford.

Lagerspetz KMJ, 1964. Studies on the aggressive behaviour in mice. Ann Acad Sci Fenn B 131: 1-131.

Lemel J, 1989. Habitat distribution in the Great Tit, *Parus major*, in relation to reproductive success, dominance and biometry. Ornis Scand 20: 226-233.

Lemel J and **Wallin K**, 1993. Status signalling, motivational condition and dominance: an experimental study in the great tit, *Parus major L.* - Anim Behav 45: 549-558.

MacDonald K, 1983. Stability of individual differences in behavior in a litter of wolf cubs (*Canis Lupus*). Journ Comp Psych 97 (2): 107-119.

Magurran AE, 1986. Individual differences in fish behaviour. In: The behaviour of teleost fishes (ed. TJ Pitcher). pp 338-365. John Hopkins University press, Baltimore, Maryland.

Marchetti C and **Drent PJ** (submitted). Individual differences in the use of social information in foraging by captive great tits.

Maynard Smith J and **Parker GA**, 1976. The logic of asymmetrical contests. Anim Behav 24: 159-175.

Maynard-Smith J, 1982. Evolution and the theory of games. Cambridge university press, Cambridge.

Mendl M and **Deag JM**, 1995. How useful are the concepts of alternative strategy and coping strategy in applied studies of social behaviour? Appl Anim Behav Sci 119-137.

Nilsson JÅ, 1989. Establishment of juvenile marsh tits in winter flocks: an experimental study. Anim Behav 38: 586-595.

Nilsson JÅ, 1990. Establishment success of experimentally delayed juvenile marsh tits *Parus palustris*. Ethology 85: 73-79.

Oakeshott JG, 1974. Social dominance, aggressiveness and mating success among male house mice (*Mus musculus*). Oecologia 15: 143-158.

Oortmerssen GA van and **Bakker TCM**, 1981. Artificial selection for short and long attack latencies in wild *Mus musculus domesticus*. Behav genet 11: 115-126.

Oortmerssen GA van, Benus I and Dijk DJ, 1985. Studies in wild house mice: genotype-environment interactions for attack latency. Neth J Zool 35: 155-169.

Oortmerssen GA van and **Busser, J.**, 1989. Studies in wild house mice. III. Disruptive selection on aggression as a possible force in evolution. In: House Mouse Aggression: A Model for Understanding the Evolution of Social Behavior. (eds. PF Brain, D Mainardi and S Parmigiani). pp 87-117. Harwood Academic, Chur.

Partridge L, 1976. Individual differences in feeding efficiencies and feeding preferences of captive great tits. Anim Behav 24: 230-240.

Pöysä H, 1988. Feeding consequences of the dominance status in Great Tit *Parus major* groups. Ornis Fennica 65: 69-75.

Pusey AE and **Packer C**, 1997. The ecology of relationships. In: Behavioural Ecology (eds JR Krebs and NB Davies). pp 254-283. Blackwell Scientific Publications, Oxford

Raaij MTM van, Pit DSS, Balm PHM, Steffens AB, van den Thillart GEEJM, 1996. Behavioral strategy and the physiological stress response in rainbow trout exposed to severe hypoxia. Hormones and Behavior 30: 85-92.

Röhss M and **Silverin B**, 1983. Seasonal variations in the ultrastructure of the Leydig cells and plasma levels of luteinizing hormone and steroid hormones in juvenile and adult male great tits *Parus major*. Ornis Scand 14: 202-212.

Ros AFH, 1997 Role of sensitisation to testosterone in the early development of aggression in black-headed gull, chapter II. Ph.D. thesis, University of Groningen, Netherlands.

Ruiter JH de, Koolhaas JM, Keijser JN, Oortmerssen GAvan, Bohus B, 1992. Differential testosterone secretory capacity of the testes of aggressive and non-aggressive house mice during ontogeny. Aggr Beh 18: 149-157.

Sandell M and **Smith HG**, 1991. Dominance, prior occupancy, and winter residency in the great tit (*Parus major*). Behav Ecol Sociobiol 29: 147-152.

Sapolsky RM, 1990. Stress in the wild. Scientific American, Jan.: 106-113.

Schouten WGP and **Wiepkema PR**, 1991. Coping styles of tethered sows. Beh Proc 25: 125-132

Schwabl H, 1993. Yolk is a source of maternal testosterone for developing birds. Proc Natl Acad Sci USA 90: 11446-11450.

Slater PJB, 1981. Individual differences in animal behavior. In: Perspectives in ethology. Volume 4 (eds PP Bateson and PH Klopfer). pp 35-49. Plenum Press, New York.

Sluyter F, Bult A, Lynch CB, Oortmerssen GA van and Koolhaas JM, 1995. A comparison between house mouse lines selected for attack latency or nest-building: Evidence for a genetic basis for alternative behavioral strategies. Behav Genet 25: 247-252.

Sluyter F, Oortmerssen GA van, Ruiter AJH de and Koolhaas JM, 1996. Aggression in wild house mice: current state of affairs. Behav Genet 26: 489-496.

Smith JNM and **Sweatman HPA**, 1974. Food-searching behavior of titmice in patchy environments. Ecology 55: 1216-1232.

Sokal RR and **Rohlf FJ**, 1969. Biometry. Freeman, New York.

Stamps JA, 1987. The effect of familiarity with a neighbourhood on territory acquisition. Behav Ecol Sociobiol 21: 273-277.

Tinbergen JM, Balen JH van, Drent PJ, Cave AJ, Mertens JAL, den Boer-Hazewinkel J, 1987. Population dynamics and cost-benefit analysis: an attempt to relate population dynamics via lifetime reproductive success to short-term decisions. Neth J Zool 37: 180-213.

Verhulst S and **Hut RA**, 1996. Post-fledging care, multiple breeding and the cost of reproduction in the great tit. Anim Behav 51: 957-966.

Verhulst S, Perrins CM, Riddington R, 1997. Natal dispersal of great tits in a patchy environment. Ecology 78(3): 864-872.

Wiepkema PR, van Hellemond KK, Roessingh P and Romberg H, 1987. Behaviour and abosamal damage in individual veal calves. Appl Anim Behav Sci 18: 257-268.

Wiepkema PR and **Schouten WGP**, 1988. Mechanisms of coping in social situations. In: Social stress in domestic animals (eds. R Zayan and R Dantzer). pp 8-24. Kluwer Academic Publishers, Dordrecht.

Wilson JD, 1992a. A re-assessment of the significance of status signalling in populations of wild great tits, *Parus major*. Anim Behav 43: 999-1009.

Wilson JD, 1992b. Correlates of agonistic display by great tits *Parus major*. Behaviour 121: 168-214.

Zwickel FC, 1980. Surplus yearlings and the regulation of breeding density in blue grouse. Can J Zool 58: 896-902.

Curriculum Vitae

Monica Elisabeth Maria Verbeek was born in Nijmegen, the Netherlands, on 9 September 1963. In 1981 she completed her secondary education (gymnasium ß) at the Jacobus College in Enschede. In the same year she started her study biology at the Agricultural University of Wageningen. For her Masters degree, she carried out a physiological study at the Utrecht University on the (in)ability of homing pigeons to see polarised light. She also obtained her secondary school and university teaching qualification, and completed several courses in communication sciences and scientific journalism. At the Department of Fisheries and Oceans in Canada, she participated in a study on narwhals, a whale species. With surveys from a helicopter and underwater-recordings of narwhal sounds, the population size was estimated of narwhals that migrate past Baffin Island, north of the polar circle, during summer. To conclude her Masters degree, she studied abnormal (stereotypic) behaviour of tethered sows, as held in intensive husbandry. In 1988 she graduated with honours (cum laude). In that same year she started her PhD research on dominance in the great tit at the Netherlands Institute of Ecology in Heteren, which eventually resulted in the present thesis. In 1993 she started at Greenpeace Netherlands as an ocean ecology campaigner, being responsible for the development and execution of the campaign against whaling. In 1995 as campaign leader biodiversity, she became also responsible for the fisheries campaign and co-ordinated a team of campaigners. Since the beginning of 1997 she is living in Lisbon where she works as an international environmental consultant.

1998