

# **Natural selection and avian personality in a fluctuating environment**

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Natural selection and avian personality in a fluctuating environment / Dingemanse, Niels Jeroen . – Utrecht: Universiteit van Utrecht, Faculteit Biologie. Thesis Utrecht University. – with ref. with a summary in Dutch.

ISBN 90-6464877-8

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Keywords: fitness / dispersal / dominance / personality / exploration / *Parus major*

Printed by Ponsen & Looijen BV, Wageningen, The Netherlands

# **Natural selection and avian personality in a fluctuating environment**

Natuurlijke selectie en persoonlijkheden van koolmezen  
in een veranderlijke leefomgeving

(met een samenvatting in het Nederlands)

Proefschrift ter verkrijging van de graad van doctor  
aan de Universiteit van Utrecht  
op gezag van de Rector Magnificus, Prof. Dr. W.H. Gispen,  
ingevolge het besluit van het College van Promoties  
in het openbaar te verdedigen  
op maandag 10 november 2003 des middags te 16:15 uur

door

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Geboren op 13 maart 1974 te Tholen

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Voor mijn familie en vrienden



## Contents

Chapter 1	General introduction	9
Chapter 2	Repeatability and heritability of exploratory behaviour in great tits from the wild	17
Chapter 3	Winter dominance and avian personality in the wild	33
Chapter 4	Natal dispersal and personalities in great tits ( <i>Parus major</i> )	47
Chapter 5	Reproductive success and great tit personalities	59
Chapter 6	Fitness consequences of avian personality in a fluctuating environment	71
Chapter 7	Summary and general discussion	83
	Samenvatting	95
	References	103
	Dankwoord	115
	Curriculum vitae	119





# **Chapter 1**

## **GENERAL INTRODUCTION**

## INTRODUCTION

The evolutionary origin and maintenance of variation within populations is a major topic in evolutionary biology. The ability to predict how environmental change affects the population dynamics and evolution of traits depends on knowledge about both the proximate (causation, development) and ultimate factors (function, evolutionary history) affecting phenotypic variation in natural populations. Integration of both factors – studying how phenotypes result from the interaction between genes and their environment during ontogeny and how the interaction between phenotypes and their environment affects individual fitness and population dynamics – is necessary to predict how traits can evolve.

In many vertebrates (e.g. humans, apes, rodents, fish, birds) and invertebrates (e.g. insects, octopi) individuals differ in their behaviour towards challenging situations (reviews: Wilson et al. 1994; Boissy 1995; Koolhaas et al. 1997; Gosling 2001). Some individuals are consistently more aggressive (e.g. towards competitors/mates/predators) and bold (e.g. towards unfamiliar objects/food/space), whereas others are less aggressive and more shy. The proximate factors underlying this individual variation in animal ‘personality’ (Gosling 2001) – comparable to the introversion/extroversion axis of human personality (Wilson et al. 1994; Gosling & Vazire 2002) – are relatively well-studied. No studies have, however, yet addressed both proximate and ultimate factors simultaneously or even in the same species. This is because such an approach requires a species that can be kept and bred under controlled conditions (i.e. to study proximate factors) and of which individual fitness can readily be measured in natural populations (i.e. to study ultimate factors). Furthermore, behavioural ecologists have long regarded variation in behaviour within populations as non-adaptive noise around an adaptive mean (Clark & Ehlinger 1987; Wilson 1998).

The recent finding of individual (Verbeek et al. 1994) and heritable (Drent et al. 2003) variation in behaviour towards novel or challenging situations (‘exploratory behaviour’, see below) of laboratory-bred great tits *Parus major* provided a unique possibility to study both the proximate basis and fitness consequences of personality in a single species. This is because the great tit is a model species for behavioural ecology, population dynamics, quantitative genetics in the field, and evolution (Kluyver 1951; Perrins 1965; van Balen 1973; van Noordwijk et al. 1980; Drent 1983; Tinbergen & Daan 1990). This thesis describes the results of a field study that aimed to quantify when, and how natural selection acts on this avian personality trait. This study was part of a program that aimed to investigate both the genetic structure (K. van Oers, PhD), plasticity (C. Carere, PhD), and fitness consequences of individual personality (C. Both, Post-doc; N.J. Dingemanse, this thesis) in a wild bird species. To study how natural selection acts on individual personality, our initial approach was to introduce eggs of selection lines for ‘slow’ and ‘fast’ early exploratory behaviour (see below) into a natural population and to study components of fitness for birds hatched from these eggs, allowing us to measure ‘gene survival’ *per se*. Because this challenging approach failed, we switched to an alternative approach. We measured the phenotype for exploratory behaviour of large numbers of wild-caught great tits (1342 individuals over 4 years) and measured all components of fitness, that is we studied the magnitude of natural selection acting on these behavioural phenotypes throughout the life cycle as a function of environmental conditions.

## AVIAN PERSONALITIES

Laboratory studies showed that hand-reared male and female great tits differ in their behaviour when confronted with novel environments, novel objects, and unknown conspecifics (Verbeek 1998; Drent & Marchetti 1999). When introduced into a novel environment (i.e. an unknown laboratory room), some birds quickly visited all artificial trees, whereas others took much more time. Birds that quickly moved between the trees in the novel environment, also took relatively little time to approach and explore novel objects introduced into their home cage, were routine-like in their foraging behaviour (i.e. took much time to adjust their behaviour to changes in feeding conditions), and were relatively aggressive (i.e. initiated many fights) when confronted with an unknown conspecific (Verbeek et al. 1994, 1996; Drent & Marchetti 1999; Marchetti & Drent 2000). These covarying behaviours did not simply result from differences in general activity: variation between individuals disappeared when the birds were confronted with the same behavioural test repeatedly, indicating that individuals differed in their behavioural response towards *novel or challenging situations* and not to the situation *per se* (Verbeek 1998).

In many other vertebrates, exploratory behaviour, boldness, and aggressiveness also covary in the same way (reviewed by Koolhaas et al. 1999). Individuals at the extremes of the trait distribution are generally regarded to employ alternative strategies to cope with environmental stress: 'Active copers' are relatively aggressive, bold or 'fast' in exploration, insensitive to external stimuli, quick in forming routines, and manipulative in stressful situations. 'Passive copers' have low levels of aggression, are shy or 'slow' in exploration, sensitive to external stimuli, and adjust their behaviour to changes in their environment (Bohus et al. 1987; Benus et al. 1991; Hessing et al. 1994; Verbeek et al. 1994; Koolhaas et al. 2001). In rodents these alternative coping strategies result from individual differences in reactivity of the sympatric nervous system (high in active copers) and the hypothalamic-pituitary-adrenal axis (high in passive copers) in response to stress (Koolhaas et al. 1997, 1999), and are mediated via neuroendocrine systems (Boissy 1995; Bucan & Abel 2001), indicating that fundamental differences in behavioural organisation underlie variation in animal personality (Bohus et al. 1987; Mendl & Paul 1990).

In laboratory-bred great tits, a large amount of the phenotypic variation in avian personality (54%) results from genetic variation among individuals (Drent et al. 2003). Behavioural genetics studies on personality-related traits (e.g. aggressiveness, boldness, reactivity) in both humans (Kagan et al. 1988; Bouchard & Loehlin 2001), fish (Bakker 1986; Magurran 1990), and laboratory rodents (van Oortmerssen & Bakker 1981; Henderson 1986) have reported similar findings: genetic sources of variation explain a major proportion of the phenotypic variation in animal personality under laboratory conditions (often 40-70%), although most evidence still only comes from few domesticated species (but see Palmer & Dingle 1989; Riechert & Maynard Smith 1989; Drent et al. 2003). Furthermore, artificial selection on single components of individual personality (e.g. aggressiveness) has been shown to result in evolutionary changes in other behaviours (e.g. exploration), indicating that suites of correlated behaviours are indeed genetically linked and may evolve as packages (Bakker & Sevenster 1989; Sluyter et al. 1995; Trut 1999; Bult & Lynch 2000).

## MEASURING SELECTION

The process of natural selection is most directly measured by the covariance between trait values and fitness (Endler 1986). This approach requires recognition of individual animals, the ability to measure individual phenotypes before selection acts, and the measurement of the major components of fitness (Brodie et al. 1995). Hence, natural selection is much easier studied for traits that show high individual consistency – like the great tit personalities – in a species where individuals can be marked individually, because such traits allow one to study selection throughout life once the individual phenotype has been determined. Given these requirements it is not surprising that very few studies have assessed whether natural selection acts on individual personality (Clark & Ehlinger 1987; Wilson et al. 1994), in particular because reliable measurements of individual behaviour are difficult to obtain in the wild and large sample sizes are usually required to detect selection in action (Endler 1986).

### Box 1 Natural selection and personality

The few studies on natural selection and individual behaviour suggest that personality traits can have important fitness consequences. Among the first pioneers in this field were Svendsen (1974) and Armitage (1986) who used mirror-image stimulation tests (MIS) in wild yellow-bellied marmots *Marmota flaviventris* to measure both individual variation in behaviour and its fitness consequences. Based on factor analysis, they recognized three independent axes of variation (approach, avoidance, sociability). Svendsen (1974) suggested that ‘aggressive females were most fit in small harems or at satellite sites, whereas social females were most fit in large social groups’, and Armitage (1986) further showed that females scoring high on sociability had highest reproductive success. More recently, studies on pumpkinseed sunfish *Lepomis gibbosus* (Wilson et al. 1993; Coleman & Wilson 1998) and bighorn sheep *Ovis canadensis* (Réale et al. 2000; Réale & Festa-Bianchet 2003) measured individual boldness (i.e. trappability) and its the ecological consequences in the wild. Bold fish had higher overall feeding rates and foraged in a riskier fashion than shy fish. Further work on other fish species showed that bold individuals were more vulnerable to predation (Dugatkin 1992), preferred by mates (Godin & Dugatkin 1996), had higher growth rates and dispersed further in the wild (Fraser et al. 2001). In bighorn sheep, bold ewes had higher weaning success than shy ewes (Réale et al. 2000), and during years of high predation pressure – but not in other years – bold ewes survived better (Réale & Festa-Bianchet 2003). Two studies further measured how natural selection acts on multiple behaviours simultaneously. First, in humans, two personality dimensions, extraversion and neurotism, did not predict the total number of biological children in postmenopausal females when considered in isolation but the interaction between the two traits did: selection favoured high neurotism in introverts and low neurotism in extroverts (Eaves et al. 1990). Second, in bighorn sheep adult survival related to both docility and boldness but not to the interaction between the two traits (Réale & Festa-Bianchet 2003). In summary, the few studies that have measured selection in the wild indicate that animal personality traits are under selection, potentially affecting dominance, survival, dispersal, and reproduction but most studies only measured single components of fitness (Svendsen 1974; Buirski et al. 1978; Armitage 1986; Eaves et al. 1990; Sapolsky 1993; Fraser et al. 2001; Réale & Festa-Bianchet 2003). Furthermore, in many of these study systems circumstantial evidence suggests that selection pressures fluctuate in space or time and may not favour a single optimal phenotype (Svendsen 1974; Wilson et al. 1993; Réale & Festa-Bianchet 2003).

The few fitness studies on animal personality have usually measured selection on individual behaviour only during a very limited part of the life-cycle and often measured single components of fitness only (Box 1). In age-structured populations, individual fitness – the rate of gene propagation in a population, however, depends both on (a) age-specific survival probabilities, (b) age-specific numbers of produced offspring and (c) the population growth rate (Fisher 1930). Thus, although often assumed, single components of fitness will not always predict the overall fitness of the individual. On the contrary, many examples of trade-offs between subsequent stages are known in theory and in empirical data. Hence, our ability to predict how selection can affect the composition of populations depends on our knowledge of the relation between the individual phenotype and the different components of fitness (i.e. survival, production of offspring) that affect the contribution of gene copies to future generations. In addition, a major problem when quantifying selection is that fitness estimates can be distorted by associations between phenotype and dispersal, because estimates are based on resightings of marked individuals in study plots of limited size (Clobert et al. 2001). Given these considerations, this thesis addresses the consequences of individual personality for survival, offspring production, offspring dispersal, and recruitment of offspring into the breeding population. Moreover, because selection pressures on single components of fitness often vary in space or time depending on fluctuations in environmental conditions (e.g. population density, predation regime, physical conditions, food availability), this thesis also addresses temporal variation in selection pressures by comparing selection pressures among different years. Almost by definition, selection relates to the combination of phenotype and environment. It is therefore essential to study selection in the relevant (=natural) environment and where possible to estimate selection as a function of environmental conditions that vary in space or time.

## OUTLINE OF THE THESIS

Our understanding of why animals have different personalities depends strongly on the knowledge and integration of the proximate (causation, development) and ultimate factors (function, evolutionary history) affecting the phenotypic variation. Laboratory studies on domesticated animals have already much improved our understanding of the proximate mechanisms underlying variation in personality (see above). The aim of this thesis was to take a logical next step in the study of the evolution of individual variation in personality traits: studying the fitness consequences of animal personality in a natural population. This thesis addresses the consequences of individual personality at different stages of the life-history of the model species, the great tit *Parus major* (Box 2), studying the relation between personality and dominance, dispersal, survival, reproduction, and offspring recruitment in the wild.

A first step in studying how natural selection acts on personalities is the measurement of individual behaviour of wild individuals. *Chapter 2* describes the method that we used to measure individual personality – exploratory behaviour in a novel laboratory environment – of great tits that were temporarily removed from the wild. In this chapter we further measured individual consistency of exploratory behaviour for recaptured individuals, and assessed whether exploratory behaviour is state-dependent. To understand whether phenotypic selection on this trait could result in evolutionary consequences (i.e. intergenerational change), we also estimated

### Box 2 The life-history of the model species

The great tit, a small songbird that occurs in forest areas in much of Eurasia, breeds in secondary nest holes and readily accepts artificial nest holes (i.e. nest boxes) for breeding (Kluyver 1951; Perrins 1965; Drent 1983b). Males defend territories throughout the year, whenever the environmental conditions allow. Non-territorial birds attempt to breed as 'guest pairs' in territories of others but nevertheless have very low reproductive success (Drent 1984). Territory defence is relaxed in much of late autumn and winter – when the birds aggregate in flocks – but territorial males remain dominant in and near their territories, enabling them to monopolize food when scarce (Saitou 1978; Drent 1983; de Laet 1984). In the winter flocks, males dominate females, and territorial males dominate non-territorial males. Female dominance rank is strongly influenced by the rank of her mate: territorial males provide their mates with prior access to food (Drent 1983).

Great tits have bi-parental care during the reproductive season. The amount of available caterpillars during chick-feeding positively affects breeding success, both in terms of numbers and quality (i.e. size, mass) of offspring (van Balen 1973). Parents that fledge high quality offspring have higher offspring recruitment (Tinbergen & Boerlijst 1990), probably because offspring condition is a predictor of competitive strength in interactions with other juveniles outside the breeding season (Both et al. 1999).

After fledging, juveniles aggregate in flocks that have linearly structured dominance hierarchies at or shortly after independence (*ca.* 35 days after hatching). The position in the dominance hierarchy is negatively related to fledging date and positively related to prior residence in the local area (e.g. Drent 1983; Sandell & Smith 1991). During this period of the year (July/August), competition for food and space causes many low-ranking juveniles to disperse to other areas (Goodbody 1952; Dhondt 1979; Drent 1984). From September onwards, high-ranking juveniles become territorial either by filling vacancies that occur when territorial adults die or by settling at the edges of existing territories, particularly in low quality habitat (Drent 1983). The amount of autumn settlement relates positively to the density of juvenile candidates and negatively to the density of surviving (i.e. territorial) adults (Drent 1984; Tinbergen et al. 1987). Whereas few juveniles settle in autumn, most juveniles settle in early spring, again depending both on the density and winter mortality of territorial great tits. Early territory ownership and high dominance ranks decrease winter mortality in most winters (Drent 1983, 1984). In years with abundant winter food caused by masting of beeches *Fagus sylvaticus*, both juvenile and adult survival is high, resulting in increased competition for territory space (van Balen 1980; Perdeck et al. 2000).

narrow-sense heritability of exploratory behaviour (see also *chapter 6*). Another parallel study indicated that the behaviour of these wild-caught individuals resembled the behaviours studied in earlier laboratory experiments by showing a correlation between exploratory behaviour of wild-caught great tits and their laboratory-raised offspring (Drent et al. 2003).

Earlier laboratory studies showed a link between dominance in aviary flocks of juvenile great tits and individual personality (Verbeek et al. 1999). Such differences in competitive ability provide a functional explanation for potential differences in juvenile dispersal, survival, and recruitment (see Box 2). In *chapter 3* we study whether position in the dominance hierarchy – measured on feeding tables in winter – correlates with individual personality in the wild. In *chapter 4* we assessed whether natal dispersal – the movement between the place of birth and first reproduction – is related to avian personality by measuring both the relation between

natal dispersal distance and parental personality as well as differences in behaviour between immigrants and locally born juveniles.

In *chapter 5* and *6* we study components of fitness and their relation with avian personality in a fluctuating environment. In *chapter 5* we describe how breeding performance (i.e. timing of breeding, clutch size, offspring condition, number of fledglings) correlates with male and female personality of the breeding pair. In *chapter 6* we measure the two major fitness components, annual adult survival and number of recruiting offspring, to study how they relate to individual personality of male and female great tits, and evaluate potential evolutionary consequences of the observed patterns of selection.

*Chapter 7* summarizes and integrates the main results presented in this thesis, and discusses the evolutionary consequences of selection on avian personality in a fluctuating natural environment.





## Chapter 2

### **REPEATABILITY AND HERITABILITY OF EXPLORATORY BEHAVIOUR IN GREAT TITS FROM THE WILD**

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& Arie van Noordwijk

*Animal Behaviour* (2002) 64, 929-937

**ABSTRACT**

We investigated whether individual great tits, *Parus major*, vary consistently in their exploratory behaviour in a novel environment and measured the repeatability and heritability of this trait. Wild birds were caught in their natural habitat, tested in the laboratory in an open field test on the following morning, then released at the capture site. We measured individual consistency of exploratory behaviour for recaptured individuals (repeatability) and estimated the heritability with parent–offspring regressions and sibling analyses. Measures of exploratory behaviour of individuals at repeated captures were consistent in both sexes and study areas (repeatabilities ranged from 0.27 to 0.48). Exploration scores did not differ between the sexes, and were unrelated to age, condition at fledging or condition during measurement. Heritability estimates were 0.22–0.41 (parent–offspring regressions) and 0.37–0.40 (sibling analyses). We conclude that (1) consistent individual variation in open field behaviour exists in individuals from the wild, and (2) this behavioural variation is heritable. This is one of the first studies showing heritable variation in a behavioural trait in animals from the wild, and poses the question how of this variation is maintained under natural conditions.

## INTRODUCTION

In a wide range of vertebrates, individuals show consistent behavioural differences in how they respond to novel situations (Wilson et al. 1994; Gosling 2001). These behavioural responses have been arranged along axes such as shyness/boldness (Clark & Ehlinger 1987; Wilson et al. 1994), aggression (Benus et al. 1992), neophobia (Greenberg & Mettke-Hofmann 2001) or exploration (Winkler & Leisler 1999). Many laboratory studies have shown heritable variation in such behaviour towards novel social or nonsocial situations in mammals (e.g. van Oortmerssen & Bakker 1981; Simmel & Bagwell 1983; Kagan et al. 1988; Magurran 1990; Benus et al. 1991; Sluyter et al. 1996).

Behavioural variation in reaction to novel situations may be adaptive and be maintained by natural selection (Clark & Ehlinger 1987; Wilson 1998), rather than reflecting nonadaptive variation around an adaptive mean. However, the processes responsible for maintaining this genetic variation in the wild are largely unexplored, in part because most study species have a long history of domestication.

If we want to understand the existence and maintenance of this behavioural variation in the wild, we need to know both its repeatability and heritability in wild-living animals. Phenotypic selection will have evolutionary consequences only when the phenotypic variation is heritable (Fisher 1930; Endler 1986). Some studies have demonstrated repeatable differences in reaction to novel situations in wild-caught animals (Armitage 1986; Wilson et al. 1993; Réale et al. 2000; Fraser et al. 2001) or wild-caught animals reared under standardized conditions (Greenberg 1992; Verbeek et al. 1994, 1996). However, despite the considerable evidence for heritable variation in animals reared under laboratory conditions, heritability estimates have, to our knowledge, not yet been published for wild populations. Heritability estimates may be substantial when measured for laboratory populations, but insignificant in the wild because of large effects of environmental factors (Falconer & Mackay 1996). For instance, behaviour towards novel situations can be strongly affected by experiences during early stages of ontogeny (e.g. Winkler & Leisler 1999). Such potential sources of environmental variation are usually controlled in laboratory studies, but are present in wild-caught individuals. Therefore, field heritabilities are more reliable indicators of the potential response to natural selection on behaviour towards novel situations.

Verbeek et al. (1994) showed consistent individual differences in exploratory behaviour in hand-reared great tits, *Parus major*. They studied behavioural reactions towards novel objects and novel environments, defining exploration as any behaviour that provides the animal with information about its environment (Birke & Archer 1983). These behavioural differences covaried: birds that quickly explored novel environments also quickly explored novel objects in their home cage, readily formed routines and were aggressive in pairwise confrontations (Verbeek et al. 1996; Drent & Marchetti 1999; Marchetti & Drent 2000). Furthermore, a five-generation artificial selection experiment yielded a significant response to both downward ('slow') and upward ('fast') selection for a combined measure of behaviour towards both novel objects and environments (Drent et al. 2003). These heritable and covarying behaviours towards novel situations can be viewed as evidence for the concept of temperament (Boissy 1995; Segal & MacDonald 1998), personality (Buss 1991) or coping strategies (Jensen 1995). Furthermore, these individual strategies may have major fitness consequences, particularly since they relate to foraging, exploration and aggression.

We measured phenotypic variation in exploratory behaviour in a novel laboratory environment in wild-caught great tits to estimate the repeatability and heritability of exploratory behaviour. The repeatability of exploratory behaviour was measured for recaptured individuals in two study populations. The heritability of exploratory behaviour was estimated in one population, using parent–offspring regressions and sibling analyses. We further tested whether an aspect of rearing conditions, fledging weight, or body weight at testing influenced exploratory behaviour.

## METHODS

### *Study sites*

We measured exploratory behaviour of great tits captured from two study areas between May 1998 and March 2001. The Westerheide (WH) study area near Arnhem, the Netherlands, covers 250 ha of mixed wood, with patches of predominantly birch, *Betula pendula*, pedunculate oak, *Quercus robur*, red oak, *Q. rubra*, pine, *Pinus sylvestris*, larch, *Larix decidua* and beech, *Fagus sylvatica*. Approximately 600 nestboxes were provided from 1995 onwards. The Oosterhout (OH) study area near Nijmegen, the Netherlands, covers about 12 ha of isolated deciduous wood with pedunculate oak as the predominant tree species. Here, about 150 nestboxes were provided from 1956 onwards as part of a long-term study on the population dynamics of the great tit (van Balen 1973). All data were analysed separately for Oosterhout and Westerheide, because both catching intensity and methodology differed between the two study areas (see below). Heritabilities were calculated for Westerheide only, because sample sizes to do so were insufficient for Oosterhout.

### *Catching methods*

In the breeding season of 1998 (May–June) we captured 61 individuals from both study areas and used them to develop a suitable behavioural test in the laboratory (their offspring were removed and hand-reared for another experiment). To take birds from the two study areas into the laboratory and score their behaviour, we inspected nestboxes twice a year during winter nights in November/December and February/March. In Westerheide individuals were also captured in mistnets at feeding stations baited with sunflower seeds (about twice a week from July to April). To exclude juveniles that were still dependent on their parents, only individuals older than 50 days of age or with fully grown tail feathers were taken to the laboratory for testing (Drent 1984; Verhulst & Hut 1996). All the adult birds captured at feeding stations had stopped breeding, and their offspring had already been independent for over 3 weeks in all cases.

Within 1.5 h of catching, we transported the selected birds to the laboratory in darkened boxes, weighed them and housed them individually. The following morning, we measured individual exploratory behaviour in a novel environment test (see below), except in the breeding season of 1998, when few birds were measured 10 days after catching (61 of 1070 individuals). After the last bird had been tested, all birds were weighed to the nearest 0.1 g and released in the field near their individual place of capture. We measured exploratory behaviour in the laboratory for 878 (WH)

and 192 (OH) individuals. Between November 1998 and December 1999, some birds were recaptured ( $n_{WH}=185$ ,  $n_{OH}=33$ ) to score their behaviour in the laboratory for a second time. Another experiment on Westerheide between March 2000 and April 2001 provided another opportunity to enlarge this sample of recaptured birds. Birds were never tested twice within a week.

The age of the birds not ringed as nestlings was determined by the colour of their greater wing coverts, allowing distinction between juvenile and older birds (Jenni & Winkler 1994). Juveniles caught in July and August were sexed with molecular markers (Griffiths et al. 1998) and adult birds were sexed by plumage characteristics (Jenni & Winkler 1994). Blood samples (5–15  $\mu$ l) used for sexing were taken from the brachial vein in the wing. This procedure has been shown to have no adverse effects (Hoysak & Weatherhead 1991; Lubjuhn et al. 1998). Blood samples were always taken after the measurement of exploration behaviour to prevent any effect of the sampling procedure on the behaviour of the bird.

### *Housing*

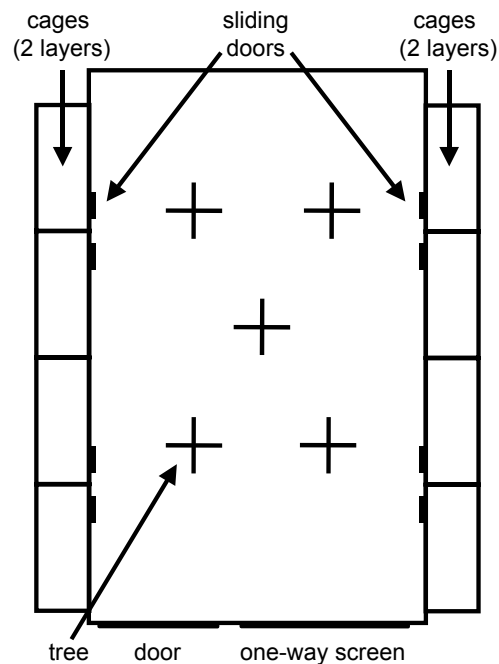
In the laboratory, we housed the birds individually under normal daylight in cages of 0.9×0.4 m and 0.5 m high, with a solid bottom and top, side and rear walls, a wire mesh front and three perches. Each cage was connected to an observation room via a 20×20-cm sliding door in the rear wall. The birds received mealworms and unrestricted access to water, sunflower seeds and commercial seed mixture (Verbeek et al. 1994). Human exposure was kept to a minimum.

### *Novel environment test*

We used the novel environment test (Verbeek et al. 1994), which is a variant of the classical open field test of animal psychologists (Walsh & Cummins 1976). Each bird was tested alone between 0800 and 1400 hours in a sealed room under artificial light. Trials began at least 1 h after sunrise, allowing the birds to eat before the first trials started. The room contained five artificial wooden trees (figure 1). We introduced each bird into the room without handling by darkening the cage with a curtain, opening the sliding door, turning on the light in the test room and briefly lifting the curtain, after which all birds flew into the room. We observed the behaviour of the birds in the observation room for the first 2 min after arrival. If the bird had not visited all five trees within this period, the observation time was extended until it had reached all trees, or up to a maximum of after 10 minutes, after which observation was stopped.

Besides the trees, birds could land on the edges of sliding doors, the main door and the one-way observation screen, and most birds explored the environment by flying between these and the trees, hopping between branches within the trees and/or actively scanning the room from a perch. During the observation period, we noted where a bird was at each second in time, and we noted details of movements, including whether the bird flew or hopped between locations.

We used the total number of flights and hops within the first 2 min as an index of exploratory behaviour ('exploration score'). Earlier laboratory studies of hand-reared great tits used the time of first arrival on the fourth (Drent et al. 2003) or fifth tree (Verbeek et al. 1994) as a measure of exploratory behaviour. We did not use these variables, because in our study many individuals (48%) did not reach the fifth tree



**Figure 1** Plan of the observation room (4.0×2.4×2.3 m) in which we tested the exploratory behaviour of wild-caught great tits. Along each 4.0-m wall were eight sliding doors (in two rows of four above each other), connecting the holding cages to the room. The front 2.4-m wall had a 0.9×2.0-m door at the left side and a 1.1×0.16-m one-way screen through which the birds could be observed. The room contained five artificial trees made of wood with a trunk of 4×4 cm and a height of 1.5 m. Each tree had four cylindrical branches 20 cm long. The upper two branches (5 cm below the top) were on opposite sides of the trunk, perpendicular to the lower branches (25 cm below the top). Birds entered the room through one of the sliding doors.

within the 10-min observation period, and thus had identical censored scores, masking the behavioural variation in which we were interested. However, our measure of exploratory behaviour was highly correlated with first arrival time in our data (fourth tree:  $r_s=0.78$ ; fifth tree:  $r_s=0.72$ ;  $n=1070$  individuals, both  $p<0.0001$ ).

### *Statistical analyses*

#### Within-individual sources of variation

Since part of the phenotypic variation may be due to factors with non-permanent effects (e.g. seasonality), which will lower our ability to compare the behaviour of different individuals, especially when individuals are measured consistently under different conditions (Falconer & Mackay 1996; Griffiths & Sheldon 2001), we tested whether within-individual variation in exploration score was related to within-individual variation in a number of explanatory variables with potentially non-permanent effects (table 1), to correct for them. We used a General Linear Model (GLM) and type III sums of squares to evaluate the within-individual relationship between exploration score and a range of explanatory variables. Only data for those individuals measured twice were included in this analysis. ‘Individual’ was entered as a factor in each model, treating the repeated exploration scores within subjects as independent cases. We constructed a model with all explanatory variables and all two-

**Table 1** Within-individual sources of variation in exploratory behaviour in repeated tests of wild-caught great tits for the study areas Westerheide and Oosterhout. The results are from a GLM with normal errors and type III sums of squares with individual as a factor after backward elimination of nonsignificant terms. *F* values given are for the inclusion of the variable in the final model.

Variable	Westerheide			Oosterhout		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Age*	1,181	0.09	0.76	1,29	0.37	0.55
Body weight	1,181	0.55	0.46	1,29	1.14	0.30
Catching method†	2,180	0.20	0.82	-	-	-
Season	1,182	14.00	0.0002	1,29	2.99	0.095
Time of day	1,181	0.15	0.70	<i>na</i> ‡		
Sequence‡	1,182	50.20	<0.0001	1,30	5.62	0.024
Interval	1,182	14.01	0.0002	1,29	3.50	0.072
Time of day × sex	1,180	3.12	0.08	1,30	5.55	0.025

\*Juvenile or older.

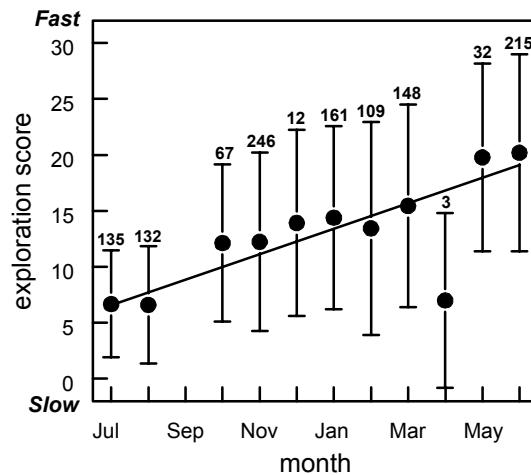
†Breeding season 1998, net, roost.

‡First or second measurement.

§Not applicable; higher order interaction is significant.

way interactions with sex separately for each study area, using backward elimination of nonsignificant terms. Explanatory variables included the following factors (f) and covariates (c): individual (f), catching method (f; caught in (1) nestbox during breeding season 1998, (2) nestbox during roosting inspection, or (3) mistnet), time of the start of the novel room test (c; in minutes after sunrise), age (f; juvenile versus older), body weight (c; at the time of entering the laboratory), sequence (f; first or second measurement), and between-test interval (c; tested by entering exact age in days as a continuous variable; mean  $x \pm SD$  interval =  $131.2 \pm 130.3$  days,  $n_{WH} = 185$  and  $168.6 \pm 120.0$  days,  $n_{OH} = 33$ ). We also included an explanatory variable for season, because exploration score was significantly related to month in first tests (ANOVA:  $F_{10,1059} = 24.04$ ,  $p < 0.00001$ ,  $r^2 = 0.18$ ), with exploration score increasing from July to the following June (figure 2). Season was defined as the number of days from 30 June (range 1–365), because the coefficient of determination between exploration score and season ( $r^2_{1068} = 0.17$ ,  $p < 0.00001$ ) was not significantly different from that derived from the model with month as a factor ( $Z = 0.39$ ,  $p = 0.70$ ).

Based on the analyses described above, a corrected exploration score ( $Y$ ) was calculated as  $Y = \text{measured exploration score} - \sum b_i \times x_i + 10$  with  $b_i$  = parameter estimate of explanatory variable  $i$  and  $x_i$  = value of explanatory variable (categorical variables were transformed into dummy variables, and parameter estimates were calculated separately for each category). For both study areas, the data were corrected for explanatory variables that were significant ( $p < 0.05$ ) in the final model (table 1) and used for all other analyses.



**Figure 2** The relation between mean±SD exploration score and month for first captures of wild-caught great tits ( $n=1070$  individuals; Westerheide and Oosterhout study areas combined). The solid line depicts the slope of the regression coefficient for season, defined as the number of days from 30 June (see Methods). Numbers represent sample sizes per month.

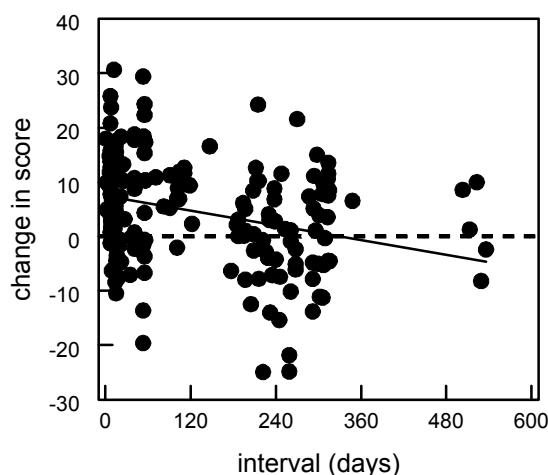
#### Repeatability and heritability

We calculated repeatability of exploration score for the recaptured individuals for which we obtained multiple measurements. Repeatability, the proportion of the phenotypic variance explained by the individual (Falconer & Mackay 1996), was calculated following Lessells & Boag (1987) and its standard errors following Becker (1984). The repeatability of exploration score was analysed separately for each combination of sex and area, because repeatabilities could differ between subgroups owing to differences in gene frequencies, large-scale environmental effects or sex-specific expression (Falconer & Mackay 1996).

We estimated narrow-sense heritabilities ( $h^2$ ) of exploratory behaviour using parent–offspring regressions, where heritability is the proportion of total variance that is attributable to the additive effect of genes (Falconer & Mackay 1996). Because exploration scores of the male and female parent were not correlated ( $r^2_{40}=0.03$ ,  $p=0.30$ ), we did not correct the estimates for assortative mating. Unequal sample sizes in the number of offspring measured were taken into account by weighting by the square root of the number of offspring in the nest (Sokal & Rohlf 1995). Relatedness between offspring and parents was determined where the chicks were ringed in the nest and their parents were captured during the breeding cycle. Females were identified while incubating eggs, and both parents were caught when their young were 8–10 days old (see van Balen 1973 for a full description of nest box inspection methods). An alternative heritability estimate was derived from a one–way ANOVA with nest as a factor and calculated as twice the intraclass correlation coefficient, assuming that all nestlings are full siblings (sibling analysis, Falconer & Mackay 1996). Both heritability estimates include common environment effects and may be inflated when those effects explain significant variation, in particular sibling analyses (Falconer & Mackay 1996).

To test for ontogenetic effects on exploration score, we weighed nestlings 15 days after hatching (van Balen 1973), and tested whether fledging weight explained





**Figure 3** Within individual change in exploration score (second minus first measure, corrected for season) in wild-caught great tits in relation to the interval between the two measures in the Westerheide study area. The dotted line depicts equal scores for both measures. The slope of the solid line is the regression coefficient for interval from the model in table 1.

significant within- and between-brood variation in nests with sampled offspring of known origin.

The data were analysed using with SPSS v.10.1. Kolmogorov–Smirnov tests for normality confirmed that the assumptions underlying analyses of variance were fulfilled in all cases. *P* values are two tailed throughout.

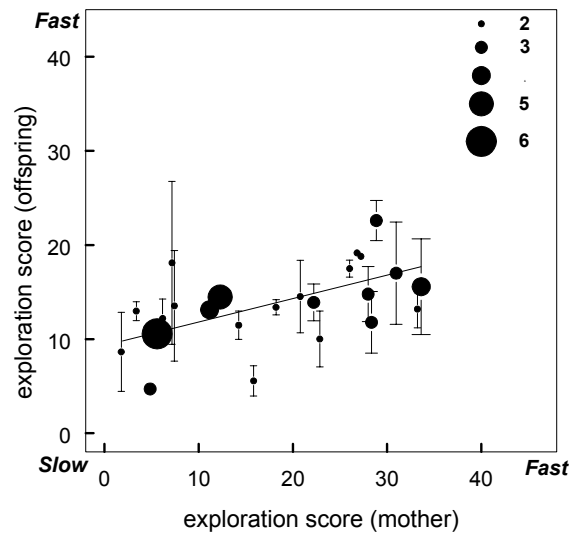
#### *Ethical note*

Apart from the 61 individuals kept in the laboratory for 10 days to develop a suitable behavioural test, our test procedure involved a 14–24-h period in which birds were removed from their natural environment. Our data showed no adverse effect of the test procedure. First, changes in body weight between arrival and departure from the laboratory (males: mean±*SE* change = -0.87±0.38 g; females: -0.96±0.39 g) were well within the natural range of overnight weight loss (of about 1 g; van Balen 1967). Second, only one of 1070 individuals died between capture and release from the laboratory, which is well within the natural range of this species (annual mortality rates are ca. 0.5; Bauchau & van Noordwijk 1995). Third, male great tits usually do not lose their territory when removed for less than 48 hours (Krebs 1982; N.J. Dingemans, unpublished data). Permission for short-term transport of great tits to the laboratory was granted by KNAW Dierexperimenten Commissie.

## RESULTS

### *Within-individual sources of variation*

In Westerheide, within-individual variation in exploration score was significantly related to season but was not related to age, catching method or time of start of the



**Figure 4** The relationship between mean $\pm$ SE exploration score of offspring and mother in wild-caught great tits in the Westerheide study area, for broods with more than one offspring sampled. Heritability estimates are  $h^2 \pm SE = 0.40 \pm 0.20$  (sibling analysis) and  $0.41 \pm 0.14$  (mother–offspring regression; see Results). The line is the fitted regression equation weighted for the square root of the number of offspring sampled per mother ( $0.21 \times \text{mother's score} + 1.93$ ). Dot sizes increase with the number of offspring sampled per mother.

novel room test (table 1). Within-individual variation in exploration score was unrelated to within-individual variation in body weight, indicating that the exploration score was not affected by changes in body condition. The birds explored the room significantly faster during their second measurement, but the effect diminished as the interval between subsequent measurements increased (table 1; figure 3). The analysis for Oosterhout confirmed that within-individual variation in exploratory behaviour was unrelated to age or body weight (table 1). Explanatory variables that were significant in the Westerheide model were either also significant or showed similar nonsignificant trends in the Oosterhout model, with qualitatively similar parameter estimates. The much smaller sample sizes for Oosterhout probably accounted for the lack of significance in some analyses.

### *Repeatability*

Exploratory behaviour was repeatable for males and females in both study areas (range  $r=0.27$ – $0.66$ ; table 2) and the estimates did not differ significantly from each other ( $F_{3,432}=1.09$ ,  $p=0.35$ ; calculation of the  $F$  statistic after D.L. Thomson, N.J. Dingemanse & A.J. van Noordwijk, unpublished data). Furthermore, the effect of individual remained significant when all other (nonsignificant) variables in table 1 were also controlled for (Westerheide:  $F_{184,177}=2.08$ ,  $n=185$ ,  $p<0.0001$ ; Oosterhout:  $F_{32,27}=2.41$ ,  $n=33$ ,  $p=0.01$ ).

**Table 2** Repeatability estimates ( $r$ ) of exploratory behaviour in two populations of wild-caught great tits for study area and sex. Repeatability was calculated after Lessells & Boag (1987) from a one-way ANOVA with individual as a factor ( $n$  = number of individuals).

Study area/Sex	$n$	Mean score	$V_p$	$r \pm SE$	$df$	$F$	$p$
Westerheide							
Male	111	17.74	55.21	0.48±0.07	110,111	2.84	<0.0001
Female	74	17.50	56.27	0.27±0.11	73,74	1.72	0.010
Oosterhout							
Male	22	20.37	69.83	0.46±0.17	22,23	2.73	0.012
Female	11	24.01	107.58	0.66±0.17	10,11	4.95	0.007

**Table 3** Heritability estimates of exploratory behaviour of wild-caught great tits in the Westerheide study area. Heritability estimates were calculated as (1) the slope (midparent–midoffspring) or twice the slope (single parent–midoffspring) of the regression for offspring and parents after weighing for the square root of offspring number per nest; (2) twice the intraclass correlation coefficient from a one-way ANOVA with nest as a factor (sibling analysis);  $n$  = number of nests,  $n_{off}$  = mean number of offspring per nest.

Method	$n$	$n_{off}$	Mean Score	$V_p$	$h^2 \pm SE$	$df$	$F$	$p$
Midparent–offspring	42	1.67	20.06	86.76	0.22±0.14	1,40	2.52	0.120
Father–offspring	59	1.78	20.96	72.52	0.31±0.19	1,57	2.53	0.117
Mother–offspring	63	1.65	18.96	95.41	0.34±0.16	1,61	4.30	0.042
Sibling analysis	50	2.64	15.13	90.72	0.61±0.20	49,82	2.16	0.001
Sibling analysis*	33	2.75	13.84	67.18	0.37±0.24	32,58	1.62	0.055

\*Broods with parent(s) of known exploratory score.

### Heritability

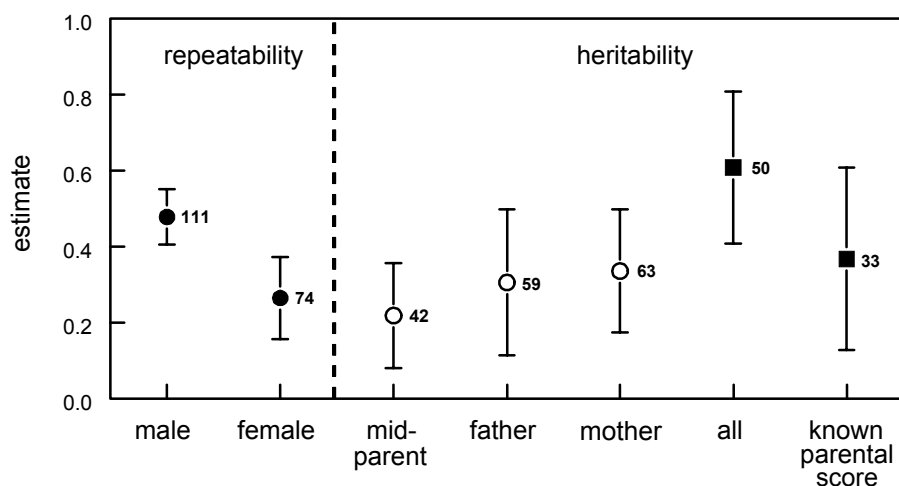
The heritability estimates of exploratory behaviour derived from parent–offspring regressions ranged from 0.22 to 0.34 (table 3) and did not differ significantly from each other ( $Z$  tests; all  $p > 0.36$ ). Furthermore, based on the data from nests where more than one offspring was sampled, a sibling analysis confirmed that exploration scores differed significantly between nests (table 3). The heritability estimate derived from this sibling analysis was higher ( $h^2 = 0.61$ ) but not significantly different from the estimates derived from parent–offspring regressions ( $Z$  tests: all  $p > 0.11$ ). However, in 34% (11 of 50) of nests included in the sibling analysis, the parents' behaviour had not been scored. The parent–offspring estimate may be derived from a biased sample if parents of known and unknown score differ in their exploratory behaviour. To check this, we excluded nests from parents with unknown exploration score and reran

the sibling analysis. This indeed gave a heritability estimate that was much closer to that derived from parent–offspring regressions ( $h^2=0.37$ ; table 3).

Heritability estimates derived from sibling analyses may be inflated by common environment effects (Falconer & Mackay 1996). However, the heritability estimates based on a sibling analysis and a mother–offspring regression for all nests with known maternal exploration score were very similar (respectively  $h^2 \pm SE = 0.40 \pm 0.20$ ,  $F_{23,41} = 1.67$ ,  $p = 0.074$  and  $h^2 = 0.41 \pm 0.14$ ,  $F_{1,22} = 8.73$ ,  $p = 0.007$ ; figure 4), suggesting that this estimate was not strongly determined by ontogenetic effects. Furthermore, fledging weight did not explain significant between-brood variation (linear regression:  $F_{1,97} = 0.002$ ,  $n = 37$  nests,  $p = 0.97$ ) or within-brood variation (ANCOVA:  $F_{1,61} = 0.80$ ,  $n = 37$  nests,  $p = 0.37$ ) in exploration score, although fledging weight differed significantly between broods (ANCOVA:  $F_{36,62} = 3.95$ ,  $n = 37$  nests,  $p < 0.0001$ ). This latter result, combined with the similarity between heritabilities calculated from parent–offspring regression and sibling analyses, indicates that ontogenetic effects on exploration behaviour are relatively small.

## DISCUSSION

This is one of the first studies showing heritable variation in a behavioural reaction towards a novel situation in nonhuman animals from the wild. Our heritability estimates of exploration score ranged from 0.22 to 0.61 and confirm the moderate heritabilities of comparable psychological traits in humans (e.g. Kagan et al. 1988; Bouchard 1994; Segal & MacDonald 1998) and other mammals (van Oortmerssen & Bakker 1981; Simmel & Bagwell 1983; Magurran 1990; Benus et al. 1991; Sluyter et al. 1996; Weiss et al. 2000). Furthermore, our results support the findings of two earlier studies in hand-reared great tits that showed (1) resemblance between siblings (Verbeek et al. 1994) and (2) a significant response to both upward and downward



**Figure 5** Repeatability (●) and heritability (○,■) estimates  $\pm SE$  of exploration score in wild-caught great tits in the Westerheide study area. Heritability estimates are for parent–offspring regressions (○) and sibling analyses (■). Numbers represent sample sizes for each analysis.

selection for a composite measure of exploratory behaviour (broad-sense heritability = 0.54; Drent et al. 2003). These hand-reared birds were originally derived from natural populations, thus supporting our evidence for the existence of heritable variation in this trait in wild-caught birds.

The heritability estimates derived from parent–offspring regressions were not significantly different from each other, although regressions that included the father’s exploration score showed nonsignificant trends (table 3, figure 5). However, in these analyses the heritability estimate might have been underestimated and its standard error and *P* value inflated, because paternity of the offspring was uncertain owing to the occurrence of extrapair paternity in this species (3–18%; Gullberg et al. 1992; Lubjuhn et al. 1993; Blakey 1994; Verboven & Mateman 1997). Furthermore, in great tits, maternity of the offspring is certain, because brood parasitism has not been reported and is likely to be very rare (Kempnaers et al. 1995; references cited above).

We showed consistent individual differences in exploratory behaviour in a novel environment in males and females in two populations of wild-caught great tits. Since repeatability normally sets an upper limit to the heritability (Lessells & Boag 1987; Falconer & Mackay 1996), our repeatability estimates ( $r=0.27$ – $0.66$ ) confirm the moderate field heritabilities for this behaviour. Significant repeatabilities could be related to other differences between individuals, for instance in body size, age or body condition (Boake 1989; Falconer & Mackay 1996). However, within-individual variation in exploratory behaviour was not related to age or changes in body weight (table 1). Furthermore, there was significant between-individual variation in exploration score when controlling for all other explanatory variables in table 1. Thus, individual variation in exploratory behaviour cuts across categories of sex, size, age and state, confirming results from earlier laboratory studies (Verbeek et al. 1994; Drent & Marchetti 1999).

We have no evidence that exploratory behaviour was influenced by rearing condition. First, the heritability estimate based on sibling analysis was not inflated compared to the estimate derived from parent–offspring regressions (figure 5), which suggests that common environment effects were relatively unimportant (Falconer & Mackay 1996). Second, rearing condition (i.e. fledging weight) did not affect within- or between-brood variation in exploratory behaviour, in agreement with earlier results (Verbeek et al. 1994, 1996). However, we might have been unable to detect effects of rearing conditions if exploratory behaviour is affected by fledging weight only in individuals of extremely poor quality: the offspring included in our analyses were most probably individuals of higher quality, because survival is positively related to fledging weight in great tits (Tinbergen & Boerlijst 1990; Both et al. 1999).

#### *Locomotor exploration*

The assumption behind novel environment studies is that the amount of movement is an index of exploration, since animals have to move around to explore the environment (Russell 1983). The use of novel environment tests has been criticized, because locomotion in forced tests may also reflect behaviour that is unrelated to exploration (Barnett & Cowan 1976; Renner 1990; Hughes 1997). For instance, the effect of sequence and interval (figure 3) may indicate that the birds experienced less fear (Maier et al. 1988; Budaev 1997) when recaptured shortly after the first capture, and that stress affected the behaviour during the first measurements. Despite these limitations, the behaviour in novel environments is likely to result in

information acquisition and therefore reflects some aspects of exploration (Russell 1983).

Earlier studies on hand-reared great tits showed that activity in the home cage was unrelated to measures of exploration in novel object and novel environment tests (Verbeek et al. 1994, 1998). In concordance with our study (table 1), hand-reared birds also explored novel situations more quickly when confronted with the same challenge a second time (Verbeek et al. 1994). These results imply that the birds used information acquired during the first tests (Welker 1961; Renner 1990), and strongly suggest that the individual differences in behaviour of great tits reflect differences in aspects of exploration. Furthermore, the behaviour in the novel environment of hand-reared offspring and wild-caught parents is significantly correlated (Drent et al. 2003), providing direct evidence for a link between the behaviours measured in hand-reared and wild-caught great tits. Exploration tests in the field would provide an interesting new step to evaluate whether the behaviour in wild-caught great tits in the laboratory also extends to the wild.

#### *Adaptive variation in behavioural traits*

We now have three independent samples showing that heritable variation in exploratory behaviour exists in great tits (Verbeek et al. 1994; Drent et al. 2003; this study). Apparently these genotypes coexist. From an evolutionary perspective, genetic variation in behavioural traits may be adaptive and be maintained by natural selection (Wilson 1998; Foster & Endler 1999; Mousseau et al. 2000). The mechanisms responsible for the maintenance of variation in psychological traits that are related to how animals cope with novel situations are largely unstudied (Wilson et al. 1994; Wilson 1994), partly because of the difficulty in determining both fitness and behavioural phenotypes in the same species (but see Armitage 1986; Eaves et al. 1990; Mealey & Segal 1993; Réale et al. 2000). The few studies that have measured the consequences of these behavioural traits for survival, dispersal or reproduction either lack evidence for a genetic basis (Wilson et al. 1993; Réale et al. 2000; Fraser et al. 2001) or suffer from insufficient statistical power (Armitage 1986). Only studies on personality traits in humans have aimed to integrate both the genetic background (e.g. Kagan et al. 1988; Bouchard 1994) and fitness consequences (Eaves et al. 1990; Mealey & Segal 1993) of traits related to how individuals respond to novelty. The great tit is one of the few wild-living species for which we now have substantial evidence for a heritable basis of a behavioural trait both from a laboratory (Verbeek et al. 1994; Drent et al. 2003) and a wild population (this study). Because individual life histories are relatively easily obtained in wild populations of great tits, these findings provide a unique opportunity to study the consequences of individual behavioural strategies for major life history traits, including survival, dispersal and reproduction. In addition, such field studies are necessary to identify the processes responsible for the maintenance of heritable variation in temperament traits in natural populations (Wilson 1994, 1998).

## ACKNOWLEDGEMENTS

We thank Piet de Goede for general assistance. Henri Bouwmeester, Leontien Witjes, Anna den Held, Kathelijne de Meijer, Maarten Hageman, Michel Geven and Dirk Zoetebier for help in the field and laboratory, Kate Lessells and Christa Mateman for sex determination using molecular markers, Bart van IJmeren, Mary-Lou Aaldering and Tanja Thomas for taking care of the birds in the laboratory and Jan Visser for managing the great tit databases. We are grateful to 'Het Gelders Landschap' and Mrs van Boetzelaer for permission to work in their properties. Helpful suggestions on the manuscript were made by Ton Groothuis, Jaap Koolhaas, Kate Lessells, David Thomson, Joost Tinbergen, Marcel Visser and two anonymous referees. N.D., C.B. and K.v.O. are supported by the Life Sciences Foundation (ALW grants 805-33-321, -324, and -323), which is subsidized by the Netherlands Organisation for Scientific Research (NWO).





## **Chapter 3**

# **WINTER DOMINANCE AND AVIAN PERSONALITY IN THE WILD**

Niels J. Dingemanse & Piet de Goede

### ABSTRACT

Individual differences in personality affect behaviour in novel or challenging situations. Personality traits may be subject to selection because they affect the ability to dominate others. We investigated whether winter dominance rank at feeding tables correlated with a heritable personality trait (exploratory behaviour in a novel environment) in a natural population of great tits, *Parus major*. We provided clumped resources at feeding tables and calculated linear dominance hierarchies on the basis of observations between dyads of colour-ringed individuals, and we used an experimental procedure to measure individual exploratory behaviour of these birds. We show that fast-exploring territorial males had higher dominance ranks than slow-exploring territorial males in two out of three samples, and that males were more dominant near their territory. In contrast, fast-exploring non-territorial juveniles had lower dominance ranks than slow-exploring non-territorial juveniles, implying that the relation between dominance and personality is state-dependent. Our findings suggest that this personality trait may be subject to selection in situations when food is clumped and scarce, because it affects the ability to dominate others. Our results further imply that fast and slow explorers should employ different settlement strategies, enabling them to avoid social environments where they perform poorly.

## INTRODUCTION

In a wide range of animals, individuals differ in their behaviour towards novel or challenging situations (Wilson et al. 1994; Boissy 1995; Gosling 2001; Greenberg & Mettke-Hofmann 2001). These individual differences in behaviour are expressed across many different situations (Huntingford 1976; Koolhaas et al. 1999) and can be regarded as general personality traits (Budaev 1997; Gosling 2001), comparable with variation in human personality (Gosling & Vazire 2002). The proximate basis of variation in personality has received considerable attention, and one general finding is that this variation has a substantial genetic component in humans (Bouchard & Loehlin 2001), laboratory rodents (Henderson 1986; Koolhaas et al. 1999), and a bird (Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003).

Recent studies indicate that personality traits are subject to selection, with individual behaviour affecting survival (Dugatkin 1992; Réale & Festa-Bianchet 2003; *chapter 6*), dispersal (Fraser et al. 2001; Dingemanse et al. 2003, *chapter 4*), and reproduction (Armitage 1986; Eaves et al. 1990; *chapter 6*). The reason why personality affects components of fitness is poorly understood (Clark & Ehlinger 1987; Wilson 1998), but likely to relate to differences in foraging behaviour (Benus et al. 1990; Verbeek et al. 1994; Drent & Marchetti 1999; Marchetti & Drent 2000) or the ability to become and remain dominant in highly competitive situations (van Oortmerssen et al. 1985; Benus et al. 1991; Verbeek et al. 1996, 1999; Drent & Marchetti 1999). In this study, we evaluate the relationship between dominance and an avian personality trait in a natural population of great tits, *Parus major*.

Individual great tits differ in the way they explore novel environments (ranging from extremely 'slow' to 'fast'), both in captive-bred (Verbeek et al. 1994; Drent et al. 2003; van Oers et al. 2003) and wild-caught birds (Dingemanse et al. 2002, *chapter 2*), and this behaviour is strongly correlated with behaviour towards novel objects (Verbeek et al. 1994), aggression in pair-wise confrontations (Verbeek et al. 1996; Drent & Marchetti 1999), and foraging behaviour (Drent & Marchetti 1999; Marchetti & Drent 2000). The extremes of the trait distribution have been described as alternative strategies to cope with novel or challenging situations (Verbeek et al. 1994; Koolhaas et al. 1999): 'Active copers' are relatively aggressive, bold or fast in exploration, insensitive to external stimuli, quick in forming routines, and manipulative in stressful situations. 'Passive copers' have low levels of aggression, are shy or slow in exploration, sensitive to external stimuli, and adjust their behaviour to changes in their environment (Bohus et al. 1987; Benus et al. 1991; Hesting et al. 1994; Verbeek et al. 1994; Koolhaas et al. 2001). This personality trait has a substantial heritable component ( $h^2$  estimates of 0.3-0.6) in wild-caught great tits (Dingemanse et al. 2002, *chapter 2*). In laboratory-bred great tits, a major proportion of the phenotypic variation is explained by additive and nonadditive genetic variation based on a two-way artificial selection experiment (Drent et al. 2003) and reciprocal backcrosses of selection lines for exploratory behaviour (van Oers et al. In Press a). Exploratory behaviour is unrelated to condition during the nestling phase or at the time of measurement, age, sex or body size (Verbeek et al. 1994; Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003).

Laboratory experiments with captive-bred great tits showed that the relationship between dominance and exploratory behaviour depends on familiarity with the physical environment, because fast and slow explorers differ in their reaction to novel or challenging situations. Whereas fast explorers quickly initiate aggressive

interactions in unfamiliar physical environments, slow explorers first explore the environment before engaging in social interactions, resulting in fast explorers dominating slow explorers in unfamiliar space (Verbeek et al. 1996, 1999; Verbeek 1998; Drent & Marchetti 1999; Carere et al. 2001). Nevertheless, slow explorers eventually obtain higher dominance ranks than fast explorers (Verbeek et al. 1996), because slow explorers manage to increase in rank by preferentially attacking dominant birds that were recovering from severe loss. At the same time, fast explorers drop in rank because they take more time to recover from severe defeats than slow explorers (Verbeek 1998)

Verbeek et al. (1998, 1999) suggested that fast explorers had lowest ranks in aviary groups because they were physically forced to stay in the group and were therefore unable to recover from severe losses. Because fast explorers have an active coping strategy, we expect them to flee from the stressful situation when unable to actively remove the stressor (see Benus et al. 1992; Koolhaas et al. 1997). In the wild, fast explorers may thus escape cascading effects of their inability to cope with social stress by resorting to sites where they are not dominated by others. We therefore expect that the relationship between dominance and exploratory behaviour differs between territorial and non-territorial birds, with fast explorers dominating slow explorers in territorial birds but slow explorers dominating fast explorers in non-territorial birds. This is because territorial birds can resort to their territory, where they can dominate others (Saitou 1979; Drent 1983; de Laet 1984) and thus recover from social stress, whereas non-territorial birds cannot. Moreover, non-territorial birds could be 'forced' to stay in winter flocks, because the benefits of group living outweigh the costs (Krebs et al. 1972; Bertram 1978).

We examined whether dominance correlates with exploratory behaviour in a nest-box population of great tits in two successive winters, using an experimental procedure to measure individual exploratory behaviour of these birds (Dingemanse et al. 2002, *chapter 2*). We also examine whether territorial birds have highest dominance ranks nearby their territory, and further examine the correlation between dominance status and exploratory behaviour for territorial and non-territorial birds.

## MATERIAL AND METHODS

### *Study area and field methodology*

We collected data from a nest box population of great tits in the southern Veluwe area (study areas 'Westerheide' and 'Warnsborn-West') near Arnhem, the Netherlands, to study winter dominance. The study area consists of a mixed pine–deciduous wood of about 250 ha (10.000 m<sup>2</sup>) with about 600 nest boxes where we supplied additional winter food (sunflower seeds) at 7 permanent feeding stations between July and April (for further details see Dingemanse et al. 2002, *chapter 2*).

To measure properties of the individual (age, sex, territorial status, exploratory behaviour) we captured birds in mistnets at the feeding stations (about twice a week from July to April) and captured birds roosting in the nest boxes at night (twice a year, in November and February/March). We also captured birds breeding in the nest boxes between April and July. We used molecular markers to sex juvenile birds captured at the feeding stations in July or August (see Griffiths et al. 1998), and used plumage

characteristics to sex all other birds (Jenni & Winkler 1994). Birds not ringed as nestlings were aged and sexed according to Jenni & Winkler (1994).

Birds captured from November 1998 onwards were transported to the laboratory, where they were individually housed. The following morning, we measured exploratory behaviour of each bird individually, before we released them near their individual place of capture within 14–24 hours of capture. Each bird was taken to the laboratory only once, for further details on housing and field methodology see Dingemanse *et al.* (2002, *chapter 2*).

#### *Measuring exploratory behaviour*

We measured exploratory behaviour using the ‘novel environment test’ (Verbeek *et al.* 1994), a variant of the classical open field test of animal psychologists (Walsh & Cummins 1976). We recognize that this single test may reflect the total effect of several behavioural traits (e.g. exploration, fear, curiosity; see Barnett & Cowan 1976). Our earlier results indicate that birds acquire information in the novel environment, and the behaviour thus reflects exploratory behaviour (Drent & Marchetti 1999; Dingemanse *et al.* 2002, *chapter 2*). Moreover, the behaviour of captive-bred offspring and wild-caught parents is significantly correlated (Drent *et al.* 2003), providing a direct link between the behaviour of captive-bred and wild-caught great tits, and between exploratory behaviour and other measures of exploration measured for the captive population (e.g. behaviour towards of novel objects and unfamiliar conspecifics; see introduction).

Each bird was tested individually between 0800 and 1400 hours in a sealed room (4.0×2.4×2.3 m) under artificial light, containing five artificial wooden trees. Trials began at least one hour after sunrise, allowing the birds to eat before the first trials started. We introduced each bird into the room without handling by manipulating the light in the observation room. We observed their behaviour in the observation room for the first two minutes after arrival and used the total number of movements (hops between branches within the trees, and flights among trees or other perches) as an index of exploratory behaviour (‘exploration score’). We corrected the scores for date of capture, based on within-individual changes in behaviour with capture date. For further details see Dingemanse *et al.* (2002, *chapter 2*).

#### *Measuring dominance rank*

To measure dominance in the wild, we observed aggressive interactions at feeding tables baited with clumped food (balls of fat and sunflower seeds) that were placed near permanent feeding stations in two following winters (1998/1999, 1999/2000; observations were between November and February). We observed the birds from a car between 0900 and 1300 hours (10–15 metres from the feeding table). In each winter we measured dominance at two of the seven feeding stations, using those that were visited most regularly by many birds to increase the number of interactions (winter 1998/1999: sites A & B; 1999/2000: sites A & C).

Because great tits use highly ritualised behaviour to express their dominance or subordination to others (Hinde 1952; Blurton Jones 1968), winner and losers of interactions between dyads of colour-ringed individuals were easily identified. Great tits have linear (Saitou 1979; Drent 1983; de Laet 1984) and sex-specific dominance hierarchies (Drent 1983). During our study, most interactions between males and

females were indeed won by males (winter 1998/1999: 91.5 % of 481 interactions; winter 1999/2000: 94.2% of 851 interactions), confirming that males dominated females (Saitou 1979; Drent 1983; de Laet 1985; Sandell & Smith 1991; Krams 1998). We therefore calculated linear dominance hierarchies at each feeding table for males and females separately (for methodology see de Vries 1995, 1998), including only individuals that interacted with at least two colour-ringed conspecifics. Hence, we defined dominance as ‘an attribute of the pattern of repeated agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and default yielding response of its opponent rather than escalation’ (Drews 1993). We calculated 2 dominance hierarchies on the basis of 372 (47 males, site A) and 167 (39 males, site B) interactions in winter 1998/1999 (we did not have enough data to calculate hierarchies for females), and calculated 4 dominance hierarchies on the basis of 116 (32 males, site A), 336 (47 males, site C), 13 interactions (8 females, site A), and 15 (7 females, site C) interactions in winter 1999/2000. Tests of linearity using Landau’s linearity index corrected for unknown relationships ( $h'$ ; calculated after de Vries 1995) confirmed that none of the 6 dominance hierarchies was significantly non-linear (all  $p > 0.741$ ).

To compare dominance ranks between the sites, we scaled the dominance ranks between 0 (lowest rank, subordinate) and 1 (highest rank, dominant). Dominance rank correlated positively with both the proportion of all fights an individual had won ( $r = 0.733-0.960$ , all  $p < 0.022$ ) and the number of individuals it dominated (calculated after de Vries 1995, 1998;  $r = 0.703-0.939$ , all  $p < 0.002$ ) for all 6 calculated dominance hierarchies.

#### *Defining territorial status*

To evaluate whether dominance of great tits decreased with the distance from the territory or ‘domicile’ – the location where high-ranking non-territorial birds aim to settle (Kluyver 1957; Drent 1983a), we estimated its approximate position. Because territorial male great tits (Kluyver 1957; Saitou 1979; Drent 1983a) and their mates (Drent, unpublished Data) roost and breed at this location, we calculated the mean co-ordinate of all the nest boxes that an individual used for roosting and/or breeding between 1995 and 2001 and further used this mean co-ordinate to calculate the distance in metres between the territory and the feeding table. Most individuals in our study area indeed used very few neighbouring nest boxes for roosting or breeding throughout their lives: the distance between the mean position of all nest boxes used for roosting and the mean position of all nest boxes used for breeding was very small ( $47.4 \pm 65.88$  m,  $n = 567$  individuals; using 7 years of data, 1995-2001) compared to the size of the study area (about  $1200 \times 1800$  m). Furthermore, for birds that were captured more than once, the average distance between the nest boxes of capture (roosting/breeding) and the mean co-ordinate was very small (mean  $\pm$  SD =  $64.4 \pm 69.2$  m,  $n = 716$  individuals). As a result of this high site fidelity, the estimated distance between nest boxes of capture and the feeding table was highly repeatable (repeatability ( $r$ ) calculated after Lessells & Boag 1987) for birds that were captured more than once (for all 3 feeding stations:  $r = 0.954-0.971$  (roosting,  $n = 406$  individuals) and  $0.951-0.969$  (breeding,  $n = 318$  individuals), all  $p < 0.0001$ ). Because territorial birds prevent non-territorial or low-ranking juveniles from roosting in nest boxes (Drent, 1983a,b), we assumed that individuals caught in nest boxes were territorial and that all other birds were not, although we recognize that we may have

**Table 1** Sources of variation in dominance ranks of territorial male great tits for winters 1998/1999 (final model:  $r^2=0.565$ ) and 1999/2000 (final model:  $r^2=0.500$ ). The results are from a GLM with normal errors and type III sums of squares after backward elimination of nonsignificant terms ( $p>0.05$ ).  $F$  values given are for the inclusion of the variable in the final model. We scaled the dominance ranks between 0 (lowest rank, subordinate) and 1 (highest rank, dominant). Note that we have not listed all effects that were included in the full model.

Variable	Winter 1998/1999			Winter 1999/2000		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Final model	2,29	21.172	<0.001	6,39	8.502	<0.001
Age	1,28	0.637	0.432	<i>na</i> §		
Distance	1,29	34.528	<0.001	<i>na</i> §		
Behaviour	1,29	7.660	0.010	<i>na</i> §		
Site	-	-	-	<i>na</i> §		
Age × distance	1,27	0.008	0.931	1,39	8.757	0.005
Age × behaviour	1,27	0.409	0.528	1,38	1.034	0.316
Behaviour × distance	1,28	0.003	0.959	1,38	0.202	0.655
Behaviour × site	-	-	-	1,39	10.903	0.002
Age × behaviour × distance	1,24	0.205	0.654	1,37	1.674	0.204
Age × behaviour × site	-	-	-	1,36	4.529	0.099

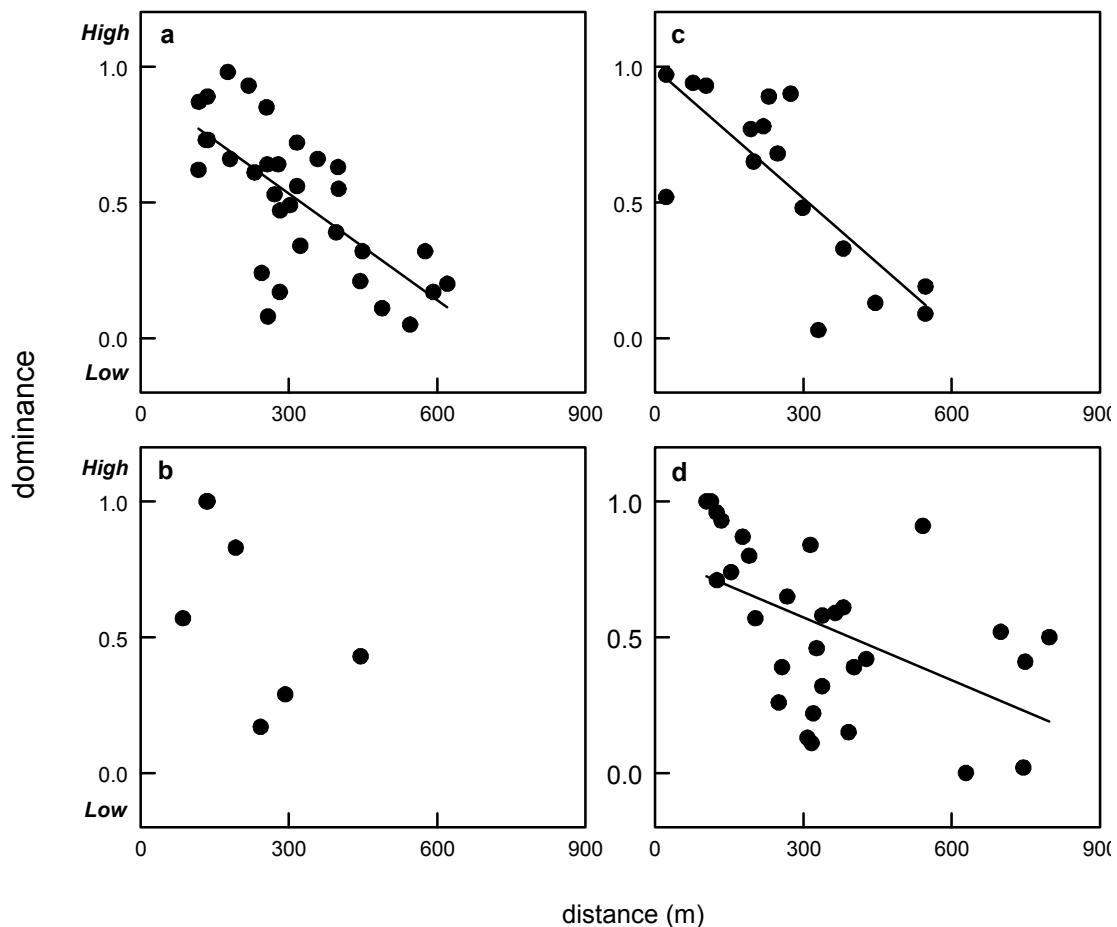
§Not applicable; higher order interaction is significant.

misjudged the status of individuals that were territorial but roosted or bred outside our study area, particularly for adult birds.

### Statistical analyses

We used General Linear Models (GLMs) with normal errors and type III sums of squares to evaluate the relationship between dominance and a range of explanatory variables, omitting all birds of which we had not measured exploratory behaviour. For each analysis, we fitted all main effects and their interactions, (i.e. the full model) and removed non-significant terms in inverse order of significance until removing further terms significantly changed the model (i.e. the final model).  $F$  values given are for the inclusion of the variable in the final model.

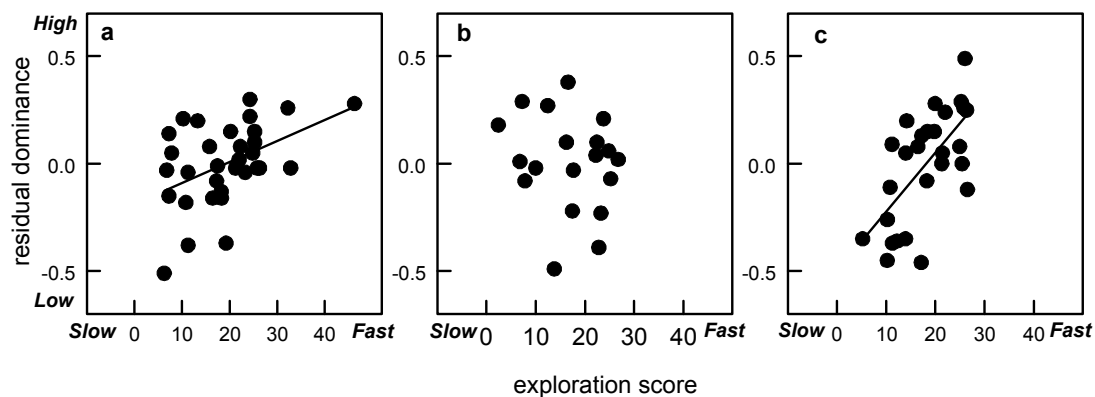
In winter 1998/1999, we only used the roosting inspections to capture birds for behavioural scoring, thus confining our analyses to territorial birds only. For many birds of known exploratory behaviour we obtained a dominance rank at both the sites (19 of 32 males), most likely because the distance between the sites used for the observations was relatively small (225 metres). To avoid pseudoreplication, we calculated an average dominance rank (mean of both sites) and analysed the relationship between dominance rank and age (juvenile versus older), distance (mean of the distance from the territory to each site), and exploratory behaviour (including both linear and quadratic terms). Dominance ranks were not related to the number of sites visited (all *NS*, results not shown) and distance from the territory to the site was not correlated with exploratory behaviour ( $r=-0.160$ ,  $p=0.569$ ).



**Figure 1** The relationship between dominance rank of great tits and distance (in metres) between the site of observation and the territory in (a) winter 1998/1999 and (b-d) winter 1999/2000 for (a) all males, (b) all females, (c) juvenile males, (d) and adult males. Dominance ranks were scaled between 0 (subordinate) and 1 (dominant). The lines are fitted regression lines ( $p < 0.01$ ).

From July 1999 onwards we used both mist-nets and roosting inspections to capture birds for behavioural scoring, enabling us to analyse data for both territorial and non-territorial birds. For very few birds of known exploratory behaviour we obtained a dominance rank at both sites (2 of 67 males; 0 of 13 females), most likely because in this year the distance between the sites used for the observations was relatively large (560 metres). For each individual, we only used the data for further analyses of the site where it had most interactions. For this winter, we present three analyses. First, for the territorial males we analyse the relationship between dominance rank and age, distance (from the territory to the site), exploratory behaviour, and site (A or C). Distance from the territory to the site was not correlated with exploratory behaviour ( $r = -0.012$ ,  $p = 0.937$ ). Second, for non-territorial males we analyse the relationship between dominance and age, exploratory behaviour, and site. Third, for all females we analyse the relationship between dominance and distance (from the territory to the site), and exploratory behaviour (for each site separately) only, because we had very few data. To avoid misleading results due to the strong effects of distance for territorial birds (see results), we do not present a combined





**Figure 2** The relationship between dominance rank and exploration score of territorial male great tits in (a) winter 1998/1999 and (b-c) winter 1999/2000 for (a) sites A & B combined (see Methods), (b) site A and (c) site C. Dominance ranks were scaled between 0 (subordinate) and 1 (dominant) and corrected for distance (a; see results) or age-specific effects of distance between the site of observation and the territory (b-c; see results). The lines are fitted regression lines ( $p < 0.01$ ).

analysis for both classes of territorial status. Nevertheless, territorial males tended to have higher dominance ranks than non-territorial males (ANOVA, both years combined: territorial status:  $F_{1,127}=2.982$ ,  $p=0.087$ ) when we used all the data – irrespective of whether we had measured individual exploratory behaviour. Kolmogorov-Smirnov tests and Levene’s tests for equality of error variances confirmed that the assumptions underlying analyses of variance were fulfilled in all cases. We used SPSS v. 10.1 software. Values of  $p$  are two-tailed throughout.

## RESULTS

### *Territorial males*

In winter 1998/1999, males from nearby territories had highest dominance ranks, with dominance decreasing with distance from the territory (figure 1a; table 1). Fast-exploring males had higher dominance ranks than slow-exploring males (figure 2a; table 1). We found the same result when we removed a single male with an extremely high exploration score from the analysis (score > 45, see figure 2a; distance:  $F_{1,28}=31.582$ ,  $p < 0.001$ ; exploratory behaviour:  $F_{1,28}=4.743$ ,  $p < 0.038$ ;  $r^2=0.516$ ). Dominance rank did not differ between the age-classes (table 1).

In winter 1999/2000, again males from nearby territories had highest dominance ranks, though the effect of distance from the territory differed between juveniles and older birds (table 1; figure 1c,d), with dominance rank decreasing more steeply with distance in juveniles. Fast-exploring males had higher dominance ranks than slow-exploring males at one site (figure 2c) but not at the other (figure 2b), the effect of exploratory behaviour differed between the sites (table 1).

### *Non-territorial males*

For non-territorial birds, the correlation between dominance and exploratory behaviour did not differ between the two sites (table 2). Dominance rank correlated with exploratory behaviour, but the effect differed between the age-classes (table 2). Separate analyses for the two age-classes showed that fast-exploring juveniles had lower ranks than slow-exploring juveniles (figure 3a;  $F_{1,13}=5.284$ ,  $p=0.039$ ,  $r^2=0.234$ ) but fast-exploring adults tended to have higher ranks than slow-exploring adults (figure 3b;  $F_{1,4}=6.604$ ,  $p=0.062$ ,  $r^2=0.528$ ). Most of the adults included in this analysis were observed at site C (figure 3b), where fast-exploring territorial males dominated slow-exploring territorial males (figure 2c). Given the similarity of these two patterns, we think that those non-territorial adults were in fact birds that had their territory outside our study area. Moreover, almost all adult great tits hold territories, whereas many juveniles do not (Drent 1983).

### *Females*

Although many females visited the feeding tables in both years we only had sufficient data to calculate dominance ranks in winter 1999/2000, because most interactions were between the sexes and not among females (see Methods). Nevertheless, the analyses for females yielded results that were qualitatively very similar to those obtained for males. Females from nearby territories probably had highest dominance ranks (figure 1b), although we have insufficient data to show this statistically ( $F_{1,5}=2.422$ ,  $p=0.180$ ). Also fast-exploring females tended to have highest ranks at one location (figure 4b;  $F_{1,5}=5.328$ ,  $p=0.069$ ) but not at the other (figure 4a;  $F_{1,4}=0.091$ ,  $p=0.778$ ).

## DISCUSSION

We examined the correlation between dominance and an avian personality trait in a natural population of great tits. We showed that fast-exploring birds had higher dominance ranks than slow-exploring birds for territorial males in two out of three samples. We found the opposite result for non-territorial juvenile males in two samples available. The opposite effects of personality according to territorial status seems to contradict the findings in laboratory-bred great tits where fast-exploring birds dominated slow explorers in pair-wise confrontations (Verbeek et al. 1996; Drent & Marchetti 1999). The low dominance ranks of non-territorial fast explorers is however consistent with the observation that fast-exploring males that lose a fight have difficulties to cope with social defeat and therefore easily lose dominance (Verbeek 1998; Verbeek et al. 1999). For fast-exploring individuals it is therefore more important to be dominant, and consequently the relation between dominance and avian personality is state-dependent. Hence, our results imply that dominance should not be regarded as a measure of individual personality (contra Buirski et al. 1978; Gosling & John 1999; Réale et al. 2000) but rather depends on the characteristics of both the individual and its social or physical environment (Francis 1988; Drews 1993; Verbeek et al. 1996; Earley et al. 2000).

We expected the relation between dominance and personality to differ between territorial and non-territorial birds, because in the wild territorial fast

**Table 2** Sources of variation in dominance ranks of non-territorial male great tits for winter 1999/2000 (final model:  $r^2=0.256$ ). The results are from a GLM with normal errors and type III sums of squares after backward elimination of nonsignificant terms ( $p>0.05$ ).  $F$  values given are for the inclusion of the variable in the final model. We scaled the dominance ranks between 0 (lowest rank, subordinate) and 1 (highest rank, dominant).

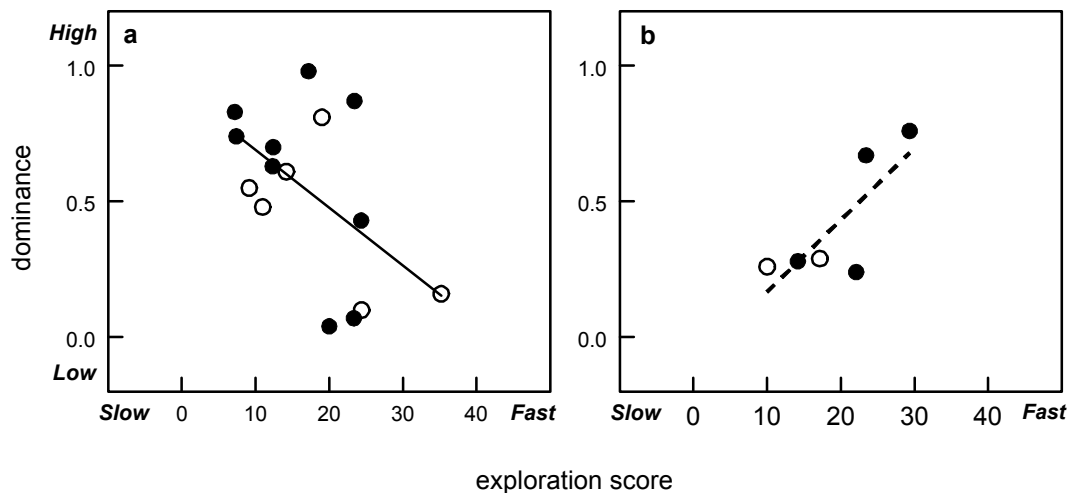
Variable	Non-territorial males		
	$df$	$F$	$p$
Final model	3,17	3.291	0.046
Age	na§		
Behaviour	na§		
Site	1,16	0.282	0.603
Age × behaviour	1,17	6.905	0.018
Age × site	1,15	0.116	0.738
Behaviour × site	1,15	0.006	0.937
Age × behaviour × site	1,13	0.274	0.609

§Not applicable; higher order interaction is significant.

explorers may be able to escape cascading effects of their inability to cope with social defeat by temporarily resorting to sites where they could dominated others – unlike non-territorial birds (Verbeek et al. 1999). The negative correlation between dominance and distance from the territory confirmed that territorial birds were indeed more dominant nearby their territory (Drent 1983; for similar findings see de Laet 1985).

Drent (1983a) indicated that this site-dependence is a consequence of the territorial system (see also Brown 1963; Wilson 1975), with dominance ranks decreasing not with distance *per se* but with the amount of territories birds pass from their own territory to the feeding site. Whereas territorial males win almost all fights at their own territory, they are likely to lose fights when passing through areas defended by other males. Hence, the amount of losses birds experience before arriving at the feeding site may negatively affect their resource-holding power elsewhere, because prior social experiences affect dominance relations through so-called loser effects (Francis 1983; Beaucham & Newman 1987).

Dominance status decreased more steeply with distance in territorial juveniles, in agreement with the findings from an earlier study (Drent 1983). This age-dependent relation between dominance and distance has been shown to disappear in the early spring (Drent 1983) and may therefore have resulted from the dominance relations prior to the settlement of the juvenile males. The effect of distance did not vary among territorial males with different personalities, suggesting that fast explorers were relatively more dominant than slow explorers that had their territories at equal distances from the feeding table but not more dominant at larger distances from their territories.



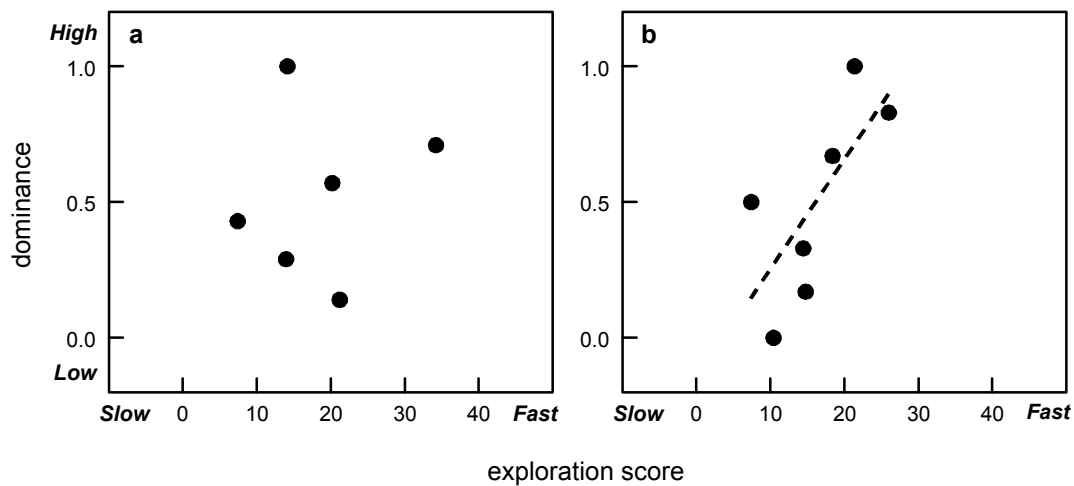
**Figure 3** The relationship between dominance rank and exploration score of (a) non-territorial juvenile and (b) non-territorial adult males great tits in winter 1999/2000 for site A (open symbols) and site C (closed symbols). Dominance ranks were scaled between 0 (subordinate) and 1 (dominant). The lines are fitted regression lines (solid lines:  $p < 0.05$ , broken line,  $p < 0.1$ ). Note that the adults may have been territorial birds that had their territory outside our study area (see results).

### *Settlement strategies*

The effect of territorial status on the relation between dominance and avian personality implies that fast and slow explorers should employ different settlement strategies. Earlier we suggested that exploratory behaviour could be traded off against the ability to cope with social stress, resulting in phenotypes differing in their optimal dispersal strategy (Dingemanse et al. 2003, *chapter 4*). Similarly, we expect that fast explorers start defending territories early in autumn because they benefit from early settlement given their inability to cope with subordinate dominance ranks (Koolhaas et al. 1999; Verbeek et al. 1999). Fast explorers may therefore actively search for vacancies in a larger area than slow explorers as early as possible (i.e. in autumn), resulting in increased natal dispersal distances (Dingemanse et al. 2003, *chapter 4*), whereas slow explorers may 'queue' for territories of high quality that are not yet available and settle later in the year (i.e. in early spring). Thus, individuals may reduce the costs linked to their personality (i.e. aggressive individuals are ill-adapted to subordinate ranks) by avoiding environments where they perform relatively poorly (Wilson & Yoshimura 1994; Zhivotovsky et al. 1996). Individual variation in settlement strategies (Ens et al. 1995; Badyaev et al. 1996) may thus be explained by variation in personality (Stamps 2001).

### *Consequences for survival and dispersal*

The reason why personalities affect components of fitness is poorly understood (Clark & Ehlinger 1987; Wilson 1998). Avian personalities may be subject to selection in situations of intense competition for food, because it affects the ability to monopolise clumped resources. Unfortunately, we had too few data to directly test the relationship between survival and dominance rank. Based on our results, however, we expect that in non-territorial juveniles fast explorers would be the first to suffer in situations of



**Figure 4** The relationship between dominance rank and exploration score of females at (a) site A and (b) site C in winter 1999/2000. Dominance ranks were scaled between 0 (subordinate) and 1 (dominant). The line is a fitted regression line ( $p < 0.1$ ).

food shortage because dominance in great tits affects feeding success (de Laet 1985; Pöysä 1988; Carrascal et al. 1998) and survival (Ekman 1989), potentially resulting in the movement of fast explorers to other feeding areas (Dingemanse et al. 2003, chapter 4).

For territorial males, the relationship between dominance and exploratory behaviour differed among sites in the same study area: fast-exploring birds were dominant over slow-exploring birds at one site but not at the other, implying that dominance depends partly on the characteristics of the social or physical environment. Spatial variation in predation regime could explain the site-dependent relation between dominance and personality: fast explorers are likely to be more vulnerable to predation than slow explorers, because they are insensitive to external stimuli (Koolhaas et al. 1997), take more risks during foraging and fighting (see Brick & Jakobson 2002), and spend less time in exploring unfamiliar social environments (see Verbeek 1998). Animals with an active coping strategy (i.e. fast explorers), in addition, allocate more time to aggression particularly when they are dominant (Ruis et al. 2002; see also Brick & Jakobsson, 2002). Although dominant great tits on average spend more time in scanning for predators than subordinates (Krams 1998), the trade-off between time spent in aggression and vigilance could result in increased mortality of dominant fast explorers under high predation pressures (Jakobson et al. 1995; Brick 1998; Lange & Leimar 2001; Sih et al. 2003). In our study, the site-dependent correlation between dominance and personality may therefore have been caused by differential mortality induced by sparrowhawks, *Accipiter nisus*, a major predator of great tits. Our observations do, however, not suggest spatial variation in predation risk, because in this winter we observed equal numbers of attacks by sparrowhawks at both sites (6 in total, one of which resulted in predation of a blue tit *Parus caeruleus*). Moreover, the properties of the surrounding habitat (including vegetation, breeding density and frequencies of different personalities) appear to be very similar. Thus, we do not yet know the cause of this site-dependence.

Identification of the factors underlying such spatial variation may allow us to better understand why different personalities can coexist in natural populations (Foster 1995; Wilson 1998; Foster & Endler 1999).

### **ACKNOWLEDGEMENTS**

We thank Christiaan Both, Kees van Oers, Piet Drent, Marloes van Anker, Leontien Witjes, Henri Bouwmeester, Maarten Hageman, Michel Geven and Dirk Zoetebier for help in the field and laboratory, Bart van IJmeren for taking care of the birds in the laboratory, Anne Rutten and Han de Vries for help in calculating linear(ity of) dominance hierarchies, Jan Visser for managing the great tit database, and Christiaan Both, Piet Drent, Kees van Oers, Arie van Noordwijk, Joost Tinbergen, Claudio Carere, Jaap Koolhaas and Ton Groothuis for discussing ideas and/or commenting on an earlier draft. We are grateful to ‘Het Gelders Landschap’ for permission to work in their properties. N.D. is supported by the Life Sciences Foundation (ALW grant 805-33-321), which is subsidized by the Netherlands Organisation for Scientific Research (NWO). Permission for short-term transport of great tits to the laboratory was granted by KNAW Dierexperimenten Commissie.

## **Chapter 4**

### **NATAL DISPERSAL AND PERSONALITIES IN GREAT TITS (*PARUS MAJOR*)**

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Anne L. Rutten & Piet J. Drent

*Proceedings of the Royal Society London B* (2003) 270, 741-747

### ABSTRACT

Dispersal is a major determinant of the dynamics and genetic structure of populations, and its consequences depend not only on average dispersal rates or distances, but also on the characteristics of dispersing and philopatric individuals. We investigated whether natal dispersal correlated with a pre-disposed behavioural trait: exploratory behaviour in novel environments. Wild great tits were caught in their natural habitat, tested the following morning in the laboratory using an open field test and released at the capture site. Natal dispersal correlated positively with parental and individual exploratory behaviour, using three independent data sets. First, fast exploring parents had offspring that dispersed furthest. Second, immigrants were faster explorers than locally born birds. Third, post-fledging movements, comprising a major proportion of the variation in natal dispersal distances, were larger for fast females than for slow females. These findings suggest that parental behaviour influenced offspring natal dispersal either via parental behaviour *per se* (e.g. via post-fledging care) or by affecting the phenotype of their offspring (e.g. via their genes). Because this personality trait has a genetic basis, our results imply that genotypes differ in their dispersal distances. Therefore, the described patterns have profound consequences for the genetic composition of populations.



## INTRODUCTION

Natal dispersal – the movement between the place of birth and first breeding – is a major determinant of the dynamics and genetic structure of populations (Hamilton & May 1977; Johnson & Gaines 1990; Whitlock 2001). Dispersal rates and distances have been shown to correlate with properties of the individual – like body mass or wing shape – or properties of its parents (Swingland 1983; Lidicker & Stenseth 1992; Clobert et al. 2001), many of which have a substantial heritability (reviewed by Roff & Fairbairn 2001). To predict the consequences of dispersal for the genetic structure of populations, we need to know both the phenotypic correlates of dispersal and their heritability. Furthermore, most theoretical models are based on population mean values and ignore individual variation (Johnson & Gaines 1990; Clobert et al. 2001).

Most studies of dispersal involved attempts to relate dispersal rates and distances to traits that are known to be important in understanding life histories (see Clobert et al. 2001). Avian dispersal has, for instance, been related to parental clutch size (Pärt 1990), date of birth (Dhondt & Hublé 1968; Nilsson 1989; van de Castele 2002) and fledgling mass (Greenwood et al. 1979; Drent 1984; Nilsson 1989; Verhulst et al. 1997; Altwegg et al. 2000; van der Jeugd 2001; but see Dhondt 1979). Behavioural traits – like aggression, sociability, or boldness – may also explain variation in dispersal behaviour (Svendsen 1974; Brandt 1992; Fraser et al. 2001). For example, the Chitty–Krebs hypothesis (Chitty 1967; Krebs 1978) predicts that aggressive individuals force docile individuals to disperse when population densities are high. The relationship between dispersal and behavioural traits has received little attention so far (Wilson et al. 1994; Fraser et al. 2001).

The aim of this study was to examine whether natal dispersal correlates with individual exploratory behaviour. We used an experimental procedure to measure individual differences in behaviour towards novel environments ('exploratory behaviour') of great tits (Dingemanse et al. 2002, *chapter 2*). Our measure of exploratory behaviour has a substantial heritable component in both captive-bred and wild-caught great tits ( $h^2$  estimates between 0.3–0.6), and is unrelated to condition during the nestling phase or at the time of measurement, age, sex or body size (Verbeek et al. 1994, 1996; Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003). Exploratory behaviour correlates with other types behaviours, including boldness towards novel objects, aggression in pair-wise confrontations, and foraging behaviour in social and non-social situations (Verbeek et al. 1994, 1996; Drent & Marchetti 1999; Marchetti & Drent 2000). These co-varying behaviours reflect general strategies that individuals use to cope with novel social and non-social situations (Benus et al. 1991; Verbeek et al. 1994; Koolhaas et al. 1999) and can be viewed as evidence for the concept of coping strategies (Koolhaas et al. 1999), personality (Buss 1991), or temperament (Boissy 1995; Segal & MacDonald 1998).

We have studied natal dispersal in a nest box population of great tits. We first showed that in our study population natal dispersal distance is not correlated with date of birth or individual morphology, i.e. traits previously shown to affect natal dispersal in great tits (Dhondt & Hublé 1968; Greenwood et al. 1979; Drent 1984; Verhulst et al. 1997; van de Castele 2002). We then used three independent data sets to examine the correlation between natal dispersal and exploratory behaviour. Because exploratory behaviour has a substantial heritability (Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003) and we cannot measure exploratory behaviour in nestlings, we first examine the correlation between natal dispersal of juveniles and the exploratory

**Table 1** The relation between natal dispersal distance and nestling traits for great tits hatched from first broods. The results are from a GLM with normal errors after backward elimination for females ( $n=80$ ) and males ( $n=84$ ). Dispersal distances were transformed as  $\log_{10}(x+1)$  and year of birth was forced in the model irrespective of significance.  $F$  values are for the inclusion of the variable in the final model.

Variable	Females			Males		
	$df$	$F$	$p$	$df$	$F$	$p$
Fledgling mass	1,73	0.90	0.35	1,77	0.31	0.58
Tarsus	1,73	0.00	0.98	1,77	0.06	0.81
Hatching date	1,73	0.02	0.89	1,77	1.21	0.27
Year of birth	5,74	1.54	0.19	5,78	1.19	0.10

behaviour of their parents. Parents can influence natal dispersal of their offspring either via their behaviour *per se* or by affecting the phenotype of their offspring, and we discuss both possible causes. Second, we compared individual exploration scores of immigrants and locally born birds captured in their first year of life. Third, we show that great tits disperse at or shortly after independence and we examine the correlation between individual post-fledging movement and individual exploratory behaviour.

## MATERIALS AND METHODS

### *Study area and field methodology*

We used 7 years of data (1995-2001) from a nest box population of great tits in the southern Veluwe area (study areas ‘Westerheide’ and ‘Warnsborn-West’) near Arnhem, the Netherlands, to study phenotypic correlates of natal dispersal. The study area consists of a mixed pine-deciduous wood of 250 ha with about 600 nest boxes (for further details see Dingemanse et al. 2002, *chapter 2*). We checked the nest boxes weekly during the breeding season, and daily before the day of expected egg hatching to determine hatching date of the chicks (measured as the day the first egg in a brood hatched, in days from 1 April). We captured both parents when their chicks were 8–10 days old. Parents were ringed and released immediately afterwards. The chicks were ringed and measured (i.e. body weight to the nearest 0.1 g, tarsus to the nearest 0.1 mm) 14–16 days after hatching. We measured natal dispersal as the distance in metres between the nest box of birth and first breeding (Greenwood 1980). We located *ca.* 5% of all fledged chicks as breeding adults.

Outside the breeding season, we used two methods to capture immigrants and locally born birds. First, we captured individuals in mist nets at 6–8 feeding stations baited with sunflower seeds (about twice a week). Second, we captured birds roosting in the nest boxes at night (twice a year, in November and February/March). We used molecular markers to sex juvenile birds captured in July or August (see Griffiths et al. 1998), and used plumage characteristics to sex all other birds (Jenni & Winkler 1994).

Birds not ringed as nestlings were aged and sexed according to Jenni & Winkler (1994). We used the captures in July and August to calculate individual post-fledging movement, defined as the distance in metres between the nest box of birth and the feeding station of first capture in the summer of birth.

Birds captured between November 1998 and March 2001 were transported to the laboratory, where they were individually housed and provided with food and water. The following morning, we measured exploratory behaviour of each bird individually, before we released them near their individual place of capture within 14–24 hours of capture. Each bird was taken to the laboratory only once. For further details on housing and field methodology see Dingemanse et al. (2002, *chapter 2*).

### *Measuring exploratory behaviour*

We measured exploratory behaviour using the ‘novel environment test’ (Verbeek et al. 1994), a variant of the classical open field test of animal psychologists (Walsh & Cummins 1976). We recognize that this single test may reflect the total effect of several behavioural traits (e.g. exploration, fear, curiosity; see Barnett & Cowan 1976). Results from previous studies, however, suggest that birds acquire information in a novel environment, and their behaviour thus reflects exploratory behaviour (Drent & Marchetti 1999; Dingemanse et al. 2002, *chapter 2*).

Each bird was tested individually between 0800 and 1400 hours in a sealed room (4.0×2.4×2.3 m) under artificial light, containing five artificial wooden trees. Trials began at least one h after sunrise, allowing the birds to eat before the first trials started. We introduced each bird into the room without handling. We observed their behaviour in the observation room for the first two minutes after arrival and used the total number of movements (hops between branches within the trees, and flights among trees or other perches) as an index of exploratory behaviour (‘exploration score’). For further details see Dingemanse et al. (2002, *chapter 2*). We corrected the scores for date of capture, based on within-individual changes in behaviour with capture date (Dingemanse et al. 2002, *chapter 2*).

### *Statistical analyses*

We used General Linear Models (GLMs) with normal errors to evaluate the relationship between natal dispersal distance and sex (104 females, 123 males) and between natal dispersal distance and morphological traits at fledging (listed in table 1; 80 females, 84 males). We fitted all main effects in the model and removed non-significant terms in inverse order of significance. For a smaller data set, we tested the relation between natal dispersal distance and mid-parent exploration score (mean of paternal and maternal scores), using the mean dispersal distance of all offspring per nest as the unit of analysis to avoid pseudoreplication (16 nests for females, 20 nests for males). Unequal sample sizes in the number of offspring measured were taken into account by weighting by the square root of the number of offspring in the nest (Sokal & Rohlf 1995). To investigate whether natal dispersal distance was equally affected by the behaviour of both parents, we re-ran this model and included both maternal and paternal scores – instead of mid-parent score – as independent effects and tested each effect after simultaneously controlling for the other, using type III sums of squares. We did not, however, have sufficient data to also test the relation between natal dispersal distance and individual exploratory behaviour of nestlings that were later

scored for exploratory behaviour. Year of birth was fitted in each model irrespective of significance, to avoid misleading results due to variation between years in natal dispersal distances. We analysed data for females and males separately, because dispersal patterns in great tits have previously been shown to differ between the sexes (Greenwood 1980; Clarke et al. 1997). In the analyses, we included only birds that hatched from first broods, thus omitting 8 (2.6%) of 233 birds with known dispersal distance. Dispersal distances were transformed as  $\log_{10}(x+1)$ . Kolmogorov–Smirnov tests confirmed that the transformed distances were normally distributed.

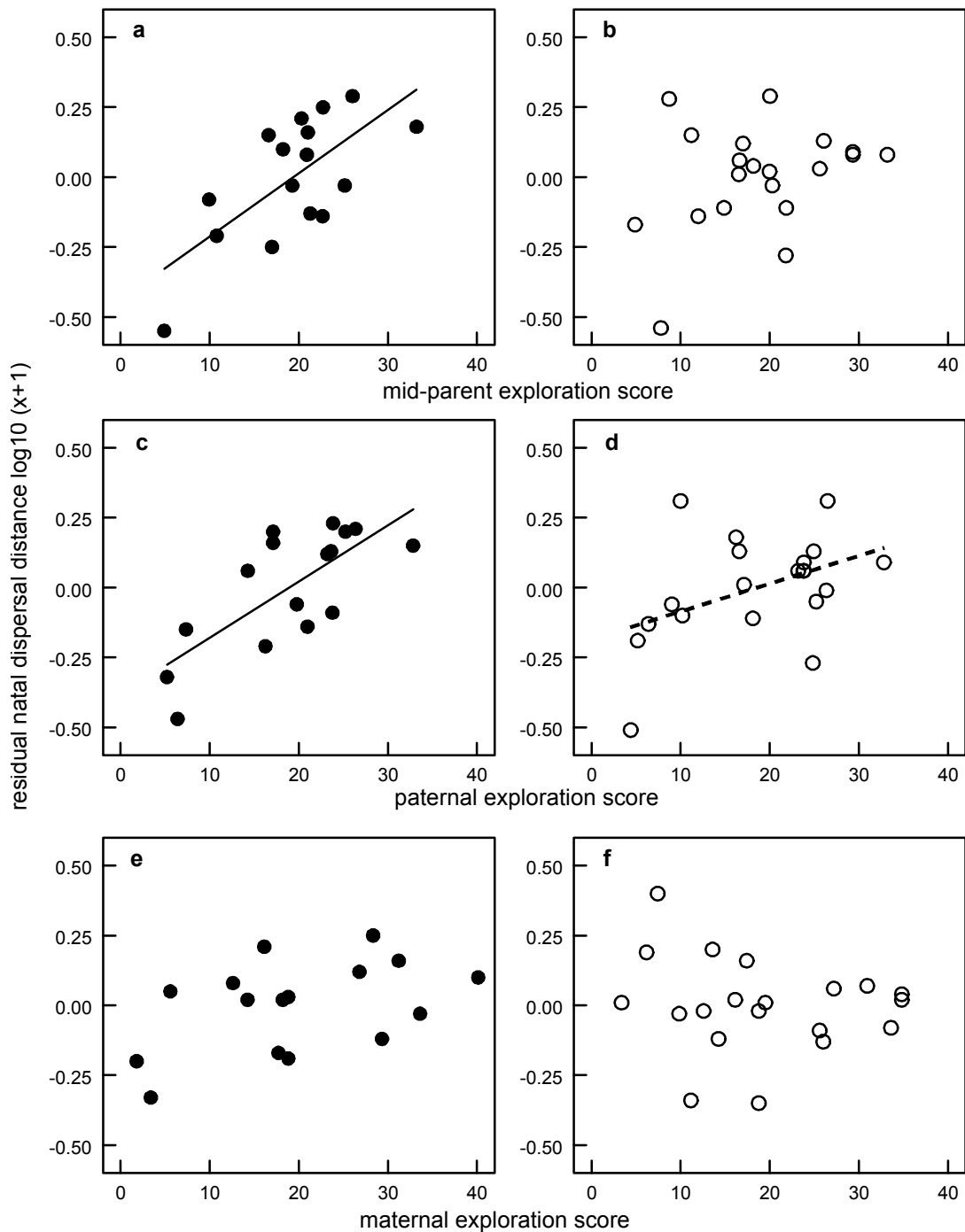
Earlier studies on great tits have suggested that natal dispersal starts at or shortly after independence (Dhondt & Hublé 1968; Dhondt 1979; Drent 1984). To evaluate whether individual post-fledging movements comprised most of the variation in natal dispersal distances, we calculated Pearson's correlations between post-fledging care movement and natal dispersal distance. We used GLMs with normal errors to evaluate the relationship between post-fledging movement, transformed as  $\log_{10}(x+1)$ , and properties of the individual (individual exploration score, body mass during capture, fledging mass, tarsus length, hatching date) for individuals captured in July/August 2000 (25 females, 24 males).

We used randomization tests to check whether significant relationships between dispersal distance and explanatory variables were caused by a non-random distribution of phenotypes over natal nest boxes (van Noordwijk 1984, 1995). In each test we calculated the distance between the natal nest box and a random nest box. We then calculated  $F$  values by following simple or multiple regression procedures outlined in Sokal & Rohlf (1995; page 626-629) and took the proportion of 1000 tests on randomized data giving a  $F$  value larger than the observed value as an approximate  $p$  value. The approximate  $p$  value derived from the 1000 randomization tests was very similar to the observed  $p$  value in all analyses ( $r^2=0.996$ , results not shown, number of tests=8). Hence, the position of the natal nest box did not affect our results and therefore we present the parametric statistics. The data were analysed with SPSS v.10.1 software. Values of  $p$  are two-tailed throughout.

## RESULTS

### *Correlates of natal dispersal distance*

Females dispersed further than males (females:  $643\pm 376$  (mean $\pm$ SD) m, males:  $498\pm 310$  m; ANCOVA: year:  $F_{1,220}=1.71$ ,  $p=0.13$ ; sex:  $F_{1,220}=7.33$ ,  $p=0.007$ ), and the effect of sex did not differ between years (interaction sex  $\times$  year:  $F_{5,215}=0.54$ ,  $p=0.74$ ). Females also dispersed further than males in a comparison of nest mates (ANCOVA controlling for nest and year:  $F_{1,39}=5.42$ ,  $p=0.025$ ,  $n=31$  nests), implying that the observed sex-bias in dispersal was not caused by a non-random distribution of offspring sexes among natal nest boxes (van Noordwijk 1984, 1995). Natal dispersal distance was not related to hatching date, tarsus length or fledging mass in either females or males (table 1). Moreover, quadratic terms were all non-significant (all  $p>0.43$ ), confirming that these results were not caused by a poor fit of linear terms.



**Figure 1** The relation between natal dispersal distance and mid–parent exploration score (a,b), paternal exploration score (c,d) and maternal exploration score (e,f) for female (filled circles) and male great tits (open circles). Dispersal distances were transformed as  $\log_{10}(x+1)$  and corrected for the effect of year (a–f), maternal score (c,d) and/or paternal score (e,f). The lines are the fitted regression equations (solid lines:  $p < 0.05$ , broken line:  $p < 0.1$ ) weighted for the square root of the number of offspring sampled per nest (females:  $n = 16$  nests, males:  $n = 20$  nests).

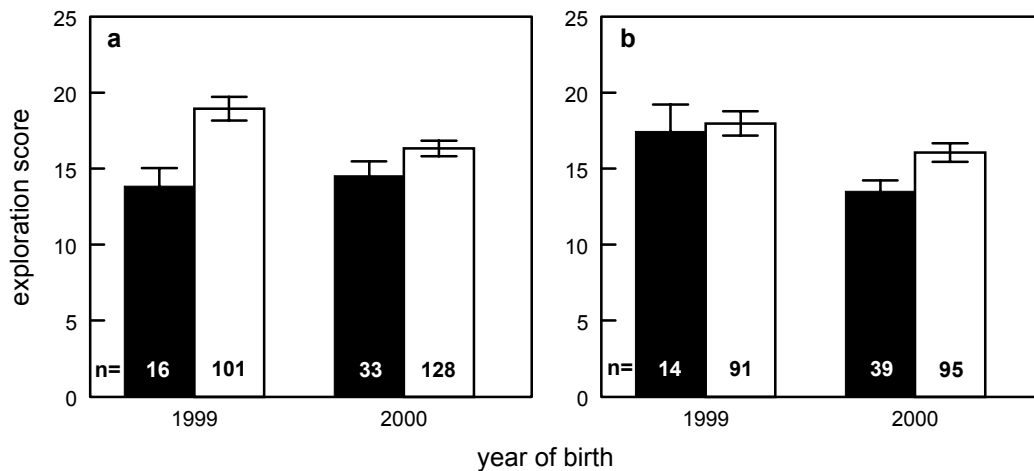
Female natal dispersal distance was related to mid-parent exploration score: females with fast parents (i.e. high mid-parent scores) moved over larger distances than females with slow parents ( $F_{1,11}=7.48$ ,  $p=0.019$ ; figure 1a). Female natal dispersal distance increased with paternal score ( $F_{1,10}=8.58$ ,  $p=0.015$ ; figure 1c) but not with maternal score ( $F_{1,10}=2.15$ ,  $p=0.17$ ; figure 1e). Although these results seem to suggest that female natal dispersal distance was not equally affected by the behaviour of both parents, we cannot show that the effect of paternal and maternal score differed ( $F$  test for difference between two regression coefficients, Sokal & Rohlf 1995:  $F_{1,28}=0.17$ ,  $p=0.68$ ). Male natal dispersal distance was not related to mid-parent exploratory behaviour ( $F_{1,15}=1.81$ ,  $p=0.20$ ; figure 1b). Male natal dispersal distance tended to increase with paternal score ( $F_{1,14}=3.89$ ,  $p=0.069$ , figure 1d) but not with maternal score ( $F_{1,14}=0.11$ ,  $p=0.74$ ; figure 1f). However, our ability to detect phenotypic correlates of male natal dispersal distance may have been limited, because natal dispersal distances tended to be less variable in males compared to females (Levene's test for equal variances:  $F_{1,34}=3.15$ ,  $p=0.085$ ). Moreover, the effect of mid-parent exploration score did not differ between the sexes when both sexes were fitted in the same model (interaction, sex  $\times$  parental score:  $F_{1,29}=2.45$ ,  $p=0.13$ ), and only the main effect of mid-parent exploration score remained in the final model ( $F_{1,30}=5.32$ ,  $p=0.028$ ). There was also no effect of the interaction between sex and paternal ( $F_{1,27}=0.83$ ,  $p=0.37$ ) or maternal score ( $F_{1,27}=2.11$ ,  $p=0.16$ ), and the main effect of paternal ( $F_{1,29}=8.34$ ,  $p=0.007$ ) but not maternal score ( $F_{1,29}=0.33$ ,  $p=0.57$ ) affected natal dispersal distance when both terms were fitted in the same model. These results therefore suggest that the correlation between natal dispersal distance and mid-parent or paternal behaviour did not differ between the sexes.

#### *Behaviour of immigrants versus locals*

Immigrants had higher exploration scores (i.e. were faster explorers) than locally born birds among juvenile birds captured before first reproduction (year:  $F_{1,514}=13.43$ ,  $p<0.0001$ ; Immigration status (local/immigrant):  $F_{1,514}=11.43$ ,  $p=0.001$ ), and the effect of immigration status did not vary between either years (interaction, year  $\times$  immigration status:  $F_{1,513}=0.21$ ,  $p=0.65$ ) or the sexes (interaction, sex  $\times$  immigration status:  $F_{1,512}=0.84$ ,  $p=0.36$ ; figure 2).

#### *Timing of dispersal*

Post-fledging movement comprised a major proportion of the variation in natal dispersal distance in both females ( $r=0.79$ ,  $n=14$ ,  $p<0.001$ ; average proportion of total distance = 0.86) and males ( $r=0.80$ ,  $n=10$ ,  $p=0.005$ ; average proportion of total distance = 0.95). The distance covered after post-fledging movement (defined as distance between site of first capture in summer and site of first breeding) was relatively small and did not explain significant variation in natal dispersal distance in either females ( $r=0.32$ ,  $n=14$ ,  $p=0.26$ ) or males ( $r=0.07$ ,  $n=10$ ,  $p=0.85$ ). These results strongly suggest that dispersing juveniles move to their new neighbourhood at or shortly after independence. Female post-fledging movement was correlated with individual exploration score: fast females moved over larger distances than slow females ( $F_{1,24}=6.01$ ,  $p=0.022$ ; slope:  $3.35 \cdot 10^{-2} \pm 0.014$  (SE)  $\log_{10}$  m/unit of score). Post-fledging movement of males was not correlated with individual exploration score ( $F_{1,23}=0.49$ ,  $p=0.49$ , slope:  $-1.24 \cdot 10^{-2} \pm 0.018$  (SE)  $\log_{10}$  m/unit of score), and



**Figure 2** Exploration scores (+SE) and immigration status (filled bars: locals, open bars: immigrants) for (a) female and (b) male great tits that were scored during their first year of life.

the effect of individual exploration score differed between the sexes (interaction, sex  $\times$  individual score:  $F_{1,47}=4.25$ ,  $p=0.045$ ). Post-fledging movement neither related to fledgling traits (fledgling mass, tarsus length, hatching date) nor to body mass at capture (all  $p>0.36$ ), confirming our results presented in table 1.

## DISCUSSION

We showed that natal dispersal distance correlated positively with a personality trait, phenotypic exploratory behaviour, using three largely independent data sets. First, natal dispersal distances were largest for individuals with fast parents. Second, immigrants were faster explorers than locally born birds. Third, post-fledging movements, comprising a major proportion of the variation in natal dispersal distances, were largest for fast females. Our results are qualitatively similar to findings of Fraser et al. (2001) who showed that fast or 'bold' (in their terminology) Trinidad killifish, *Rivulus hartii*, moved over larger distances than slow or 'shy' fish.

Individual differences in morphology, physiology, or behaviour may either be the cause or consequence of dispersal (Dufty & Belthoff 2001; Ims & Hjermann 2001). Most investigators who have reported correlations between dispersal and individual behaviour have only measured individual behaviour during or after dispersal (e.g. Myers & Krebs 1971; Svendsen 1974; Ims 1990), making it difficult to separate cause and effect (Brandt 1992; Ims & Hjermann 2001). Because individual differences in exploratory behaviour arise early in life (Verbeek et al. 1994; Drent et al. 2003), before the onset of dispersal, our data suggest that differences in exploratory behaviour are the cause and not the consequence of dispersal. This suggestion is further confirmed by the correlation between mid-parent exploration score and offspring natal dispersal distance.

Parents may have affected natal dispersal of their offspring via parental behaviour *per se* (e.g. via post-fledging care or aggression directed towards offspring) or by influencing the phenotype of their offspring (e.g. via their genes, egg steroids, or parental investment), which in turn affected offspring dispersal strategy. Effects of

parental behaviour *per se* are likely to occur during the period of post-fledging care, when the male great tit parent guides the brood to good foraging sites (Drent 1984; Verhulst & Hut 1996). Furthermore, fast-exploring fathers (and mothers) may not only be more aggressive to conspecific competitors (Verbeek et al. 1996; Drent & Marchetti 1999) but also towards their fledged offspring than slow exploring fathers, and as a consequence force their offspring to disperse further. We think, however, that the patterns described are not caused by parental behaviour *per se*, because we would have expected that paternal behaviour differed in its effects from maternal behaviour. Moreover, movements during post-fledging care do not predict natal dispersal distances in great tits (van de Castele 2002). We therefore think it is more likely that parents influenced the phenotype of their offspring which in turn affected natal dispersal.

Effects of parental behaviour on the phenotype of their offspring may be mediated via variation among females in egg steroids (Schwabl 1993), thus indirectly affecting offspring natal dispersal (Dufty & Belthoff 2001). If so, we would have expected a correlation between natal dispersal distance and maternal – not paternal – exploratory behaviour, unless male behaviour affected female breeding condition (Schwabl 1997; Gil et al. 1999). We therefore favour the idea that parents influenced natal dispersal by genes passed to their offspring and that the substantial heritability of exploratory behaviour (Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003) explains the correlation between parental exploratory behaviour and offspring natal dispersal.

Our results may seem to suggest that natal dispersal is relatively inflexible and inherited (Howard 1960). However, field studies have failed to show a significant heritability of natal dispersal (Greenwood et al. 1979; van Noordwijk 1984; Waser & Jones 1989; van de Castele 2002). It is therefore usually assumed that dispersal behaviour is flexible and depending on prevailing environmental conditions (Howard 1960; Ims & Hjermann 2001). This notion of environmental dependence is not incompatible with our result of phenotype-dependent dispersal, because environmental effects may differentially affect these behavioural phenotypes. In our study system we have evidence that slow exploring individuals are better in coping with social defeat (Verbeek 1998; Verbeek et al. 1999), which may enable them to remain in highly competitive situations. The slower exploratory behaviour may thus be traded-off against the ability to cope with social stress, resulting in phenotypes differing in their optimal dispersal strategy. The sex difference in the relationship between post-fledging dispersal and individual exploratory behaviour further illustrates that patterns of phenotype-dependent dispersal may also differ between the sexes (Greenwood 1980; Clarke et al. 1997), although we could not detect sex differences in the relationship between natal dispersal and phenotypic exploratory behaviour. A next step would be to understand how phenotype-dependent dispersal depends on the environmental conditions (see also Drent et al. 2003). For instance, conflicting evidence for a relationship between dispersal and aggressiveness in rodents, or dispersal and nestling traits (e.g. fledging mass, tarsus length) in birds, is likely to result from variation in the amount and distribution of resources, levels of competition, and social structure of the population (Brandt 1992; Verhulst et al. 1997).

Because exploratory behaviour has a substantial heritable component (Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003), differential dispersal with respect to exploratory behaviour may have profound consequences for the genetic composition of metapopulations (Bohonak 1999; Roff & Fairbairn 2001; Whitlock



2001). In rodents, for instance, genetically docile individuals may be more likely become founders of new populations (Chitty 1967; Krebs 1978), potentially affecting the composition of behavioural phenotypes in source and sink populations (Pulliam 1996). Moreover, dispersal may allow a certain genotype to persist that has a lower fitness in general, but is better adapted to new and changing circumstances.

### ACKNOWLEDGEMENTS

We thank Piet de Goede for general assistance. Henri Bouwmeester, Leontien Witjes, Kathelijne de Maijer and Kees van Oers for help in the field and laboratory, Christa Mateman for sex determination using molecular markers, Bart van IJmeren, Mary-Lou Aaldering and Tanja Thomas for taking care of the birds in the laboratory and Jan Visser for managing the great tit databases. We are grateful to 'Het Gelders Landschap' for permission to work on their properties, and Ani Kazem, Kate Lessells, Judy Stamps, Joost Tinbergen, Kees van Oers, Marcel Visser and Jon Wright, and two anonymous referees for comments on the manuscript. N.D., C.B. and A.R. are supported by the Life Sciences Foundation (ALW grants 805-33-321, 805-33-324, STW grant GBI4804), which is funded by the Netherlands Organization for Scientific Research (NWO). Permission for short-term transport of great tits to the laboratory was granted by KNAW Dierexperimenten Commissie.



## **Chapter 5**

### **REPRODUCTIVE SUCCESS AND GREAT TIT PERSONALITIES**

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& Joost M. Tinbergen

## SUMMARY

Intraspecific variation in reproductive decisions is generally considered as a reaction to environmental circumstances. We show that variation in reproductive parameters is also affected by intraspecific variation in personality. We studied reproductive parameters in a natural population of great tits during four years in association with a personality trait: exploratory behaviour as measured in a novel environment. Nest success, fledgling size and condition were all related to this personality trait. Slow-exploring females had a higher nest success and larger fledglings. Fledgling condition was affected by the interaction between male and female exploratory behaviour, with assortative pairs at both ends of the behavioural spectrum producing fledglings in the best condition. Fast-exploring males bred in nest boxes that produced heavy fledglings in other years. We hypothesize that fast-exploring individuals are better able in defending or obtaining a high quality territory, while slow-exploring individuals are either better parents or have better chicks which may in part explain the patterns in reproductive success. We discuss how these patterns in reproduction can explain earlier reported relationships between offspring recruitment and avian personality.

## INTRODUCTION

Individual organisms continuously react to their environment in order to maximize their fitness, but interestingly, even individuals of the same species differ in their behavioural reaction to the same environmental stimuli. This variation in behaviour is often not just noise around a certain optimal strategy, but is highly repeatable within individuals (Clark & Ehlinger 1987; Wilson et al. 1994; Gosling 2001). Reactions to different environmental stimuli are furthermore often structured in correlated responses (Boissy 1995; Koolhaas et al. 1997). These correlated responses are similar to variation in human personality (Wilson et al. 1994; Gosling & John 1999), and as in humans (Kagan et al. 1988; Bouchard & Loehlin 2001), this personality variation normally has a genetic background (Bakker 1986; Henderson 1986; Benus et al. 1991; Sluyter et al. 1995; Weiss et al. 2000; Drent et al. 2003). The existence of heritable variation in personality traits poses the question how natural selection acts on personality and how these alternative phenotypes can coexist (Wilson 1998), but so far fitness consequences have rarely been reported (Wilson et al. 1994; Réale & Festa-Bianchet 2003; *chapter 6*).

The variation we focus on is how individuals of a small songbird, the great tit *Parus major*, explore new environments (Verbeek et al. 1994). Earlier work on hand-raised great tits taken from a natural population showed that individuals differed consistently in their exploratory behaviour (Verbeek et al. 1994), and that exploration was correlated with aggressiveness (Verbeek et al. 1996; Drent & Marchetti 1999), competitive ability (Verbeek et al. 1999), and social learning (Marchetti & Drent 2000). Two-way artificial selection and reciprocal crossing experiments showed that avian personality is highly heritable (Drent et al. 2003; van Oers et al. In Press) and that components of great tit personality are genetically correlated (van Oers et al. In Press a). Recently we developed a laboratory test to measure the exploratory behaviour of free-living individuals (Dingemanse et al. 2002, *chapter 2*), which allowed us to examine the fitness consequences of this heritable trait in a natural population. This behavioural test is repeatable and parent-offspring regression yielded a heritability of 0.34 (Dingemanse et al. 2002, *chapter 2*; *chapter 6*). Variation in exploratory behaviour was unrelated to sex or condition, and we regard this variation as different strategies in how individuals cope with challenges in their environment (Verbeek et al. 1994; Verbeek et al. 1996), comparable with variation in personalities (Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003).

Fast-exploring and aggressive phenotypes are normally considered to have an advantage over slow-exploring and more docile phenotypes (Krebs 1978), and the naïve prediction would be that these genotypes would increase in the population. Slow-exploring great tits however are found to be more sensitive to changes in their environment (Verbeek et al. 1994; Drent & Marchetti 1999) and are better able to cope with social stress (Verbeek et al. 1999; Carere et al. 2001). Therefore these individuals may have a higher fitness than fast-exploring individuals under certain ecological circumstances and social environments. Recently we showed that exploratory behaviour affected dispersal (Dingemanse et al. 2003, *chapter 4*) and the ability to monopolize clumped food in the wild (*chapter 3*), and that the survival consequences of avian personality varied between years in interaction with gender (*chapter 6*). The number of offspring produced by these great tits that survived and recruited in the breeding population also related to their exploratory behaviour and selection again varied between years: in a rich year with high recruitment rates there

was disruptive selection, with pairs of either two extremely slow or two extremely fast parents producing most recruits. In two poor years with low recruitment rates intermediate parents produced most recruits. These correlations between numbers of recruiting offspring and exploratory behaviour can have their origin in either different reproductive success and/or differences in survival of their offspring during the non-reproductive period.

In this paper we examine the correlations between exploratory behaviour and reproductive parameters in four different years in a natural population of great tits to understand better when and how selection operates on avian personality. Knowledge about how selection on avian personality acts at different life-stages is essential to understand and predict how personality traits evolve and coexist in species that live in temporally changing environments. If personality affects reproductive strategy this may also alter the conventional thinking about optimal reproductive strategies, because these may differ between genotypes and therefore cannot easily be examined by manipulation without knowledge of individual personality. Knowledge of individual personality may also shed new light on mate choice, because the fitness of a pair does not only depend on the characteristics of each individual separately, but rather depends on the interaction between the personalities of both pair members (*chapter 6*).

## METHODS

### *Study area and field methodology*

Data were collected in a nest box breeding population of great tits in the southern Veluwe Area (study areas ‘Westerheide’ and ‘Warnsborn-West’ near Arnhem, The Netherlands) from 1999 to 2002. The study area consisted of a mixed pine–deciduous wood of 250 ha with about 600 nest boxes (for further details see Dingemanse et al. 2002, *chapter 2*). Nest boxes were checked at least twice a week from the beginning of April until the end of June. During the study period second broods (laid after a successful first brood) were rare and unsuccessful, and in this paper we therefore restrict the analyses to first broods only. Laying date is the date the first egg was laid, and clutch size is the number of eggs incubated. At the time the eggs were expected to hatch, nests were checked daily to record the day at which the eggs started to hatch (day 0). At day 7 the parents were caught in the nest box using a spring trap, and the chicks were ringed with uniquely numbered aluminium rings. Parents not ringed as nestlings were aged as either one year old or older based on the colour of their greater coverts (Jenni & Winkler 1994). At day 14, when chicks have reached their fledging mass and size, we measured fledging mass to the nearest 0.1 g and fledging tarsus length to the nearest 0.1 mm. Tarsus length is considered to be a structural measure reflecting the skeletal size in the individuals, and is referred to as fledgling size. We used fledgling mass at day 14 as a measure of chick condition by including fledgling size as covariate in the analyses (Keller & van Noordwijk 1993). At day 14 chicks were sexed on the basis of the colour of the greater coverts or using molecular markers (Griffiths et al. 1998). In 1999 37 out of 59 broods were sexed molecularly, and we cross-checked our sexing in the field with the molecular sexing, which showed that field estimates had an accuracy of 82%.

To measure exploratory behaviour we captured individuals in the field outside the breeding season using mist nets or roosting inspections, and transported them to the laboratory (Dingemanse et al. 2002, *chapter 2*). The birds always stayed for one night in the laboratory in individual cages (0.9×0.4×0.5 m) prior to testing. Individuals were tested alone during the morning following capture in a sealed room (4.0×2.4×2.3 m) with five artificial trees, and entered the room through a sliding door without handling. The exploration score used here is the number of movements (hops between branches within trees and flights among trees or other perches) during the first 2 min after the individual entered the room, corrected for date of capture based on within-individual changes in behaviour with capture date (Dingemanse et al. 2002, *chapter 2*), with fast explorers having higher exploration scores than slow explorers.

### *Statistical analyses*

All analyses were performed on mean values per nest and we included only those nests of which both parents were behaviourally tested. Sample sizes differ between analyses because in some years experiments were carried out in part of the area, and laying dates and clutch sizes were available for these nests but not the nest success or growth of the nestlings. In all analyses we tested the effects of year (factor with 4 levels), female age (factor with 2 levels distinguishing 1-year old from older individuals), male age (factor with 2 levels), and both female and male exploration score (covariates). We tested the quadratic effects of exploratory behaviour because we do not have *a priori* reasons to expect linear relationships. None of the quadratic effects were significant and they are not mentioned in the results. In the analyses of clutch size, nest success, and fledging size and condition we also included laying date in the analysis to account for seasonal effects on these reproductive parameters (Verhulst et al. 1995). Fledgling size depends not only on the environmental conditions during growth but also has a high heritable component (van Noordwijk et al. 1988), mid-offspring – mid-parent  $h^2$  in this study is 0.44,  $p < 0.001$ ,  $n = 150$  nests. To account for this heritable component we included the average tarsus length of the two parents as a covariate in the models on fledgling size.

All analyses were performed using general linear models (GLM). In case of binomial data we used logistic models, in all other cases we assumed a normal distribution. We tested all two-way interactions between explanatory variables. Because we carried out tests on at most 20 interactions per analysis (depending on the dependent variable), we include only the interaction terms for which the values of  $p$  were equal to or smaller than 0.01. In the results we only show those interaction terms that were significant on the basis of this criteria.

If individuals survived to the next year and bred again, they occurred more than once in the analysis. Although there is some pseudoreplication in case of multiple nests of the same individuals, the interaction between male and female exploration is significant in some analyses, which implies that the pair can be regarded as the independent unit of analysis. In 25 of the 225 cases male and female were the same in more than one year, but excluding these did not change the results. Excluding all multiple records of the same individual would have solved the problem of pseudoreplication, but with the cost of not being able to analyse age effects. In our opinion the reduction of the data set to single records per individual is also arbitrary in the choice of records and therefore we have chosen to use all nests for which the

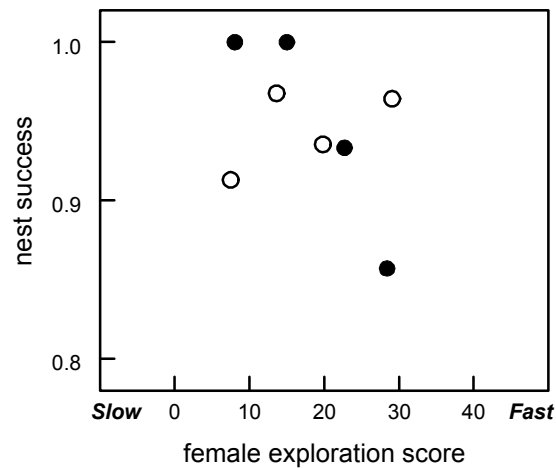
**Table 1** The effect of exploratory behaviour of males and females on fledgling size and condition in a natural population of great tits. The results of GLM analyses are given for the mean tarsus length per nest (fledgling size) and the mean fledgling body mass (fledgling condition). Data were collected in four years, and ages of the parents were divided in first year and older. In the analysis of fledgling size we include the mean tarsus length of both parents as an approximation of the genetic effect. In the analysis of fledgling condition we include the mean tarsus length of the brood to control for the variation in size. If we do not include fledgling tarsus the analysis of fledgling mass is qualitatively similar.

Variable	Fledgling size			Fledgling condition		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Year	11.42	3,142	0.000	<i>na</i>		
Female age	<i>na</i>			0.13	1,134	0.72
Male age	1.14	1,139	0.29	<i>na</i>		
Female exploration	<i>na</i>			<i>na</i>		
Male exploration	3.11	1,140	0.080	<i>na</i>		
Laying date	3.94	1,142	0.049	<i>na</i>		
Parental tarsus	34.85	1,142	0.000			
Female age × Female exploration	6.74	1,142	0.010			
Juvenile tarsus				<i>na</i>		
Year × Male age				4.98	3,135	0.003
Laying date × Fledgling tarsus				10.64	1,135	0.001
Female × Male exploration				7.82	1,135	0.006

exploratory behaviour of both pair members was known. This resulted in data sets in which between 72% and 82% of the records belonged to different individuals.

Correlations between exploratory behaviour and reproductive parameters can be either explained by variation in habitat quality, parental traits of males and females separately, and by interactions between these parameters. We estimated habitat quality on the basis of occupation and mean reproductive traits of the nest box in the years 1995-2002. With this aim we calculated for each brood in the period 1995-2002 the deviation of laying date, clutch size, fledgling number, fledgling tarsus length, and fledgling mass to the annual mean. Next we averaged these relative reproductive parameters for the same nest box over all years, excluding all nests in which one of the pair members of interest was involved. To avoid pseudoreplication in this measure of nest box quality we only included the first nest of a female if she bred multiple times in the same nest box. To estimate mean fledgling condition of the nest box we only used the nest box-specific relative fledgling mass because sample sizes for tarsus length were low. Because of sample size limits, in this analysis only we did not control for parental tarsus length when testing the effect of fledgling size, and here fledgling size was defined as the fledgling tarsus length of each nest box. These measures indicate whether a nest box is relatively early or late, and productive or not. We only used these relative nest box values if these were based on at least two broods (sample sizes differ depending on the number of measurements of different reproductive parameters). We performed ANCOVAs with these nest box-specific estimates of territory quality as dependent variables and male and female exploratory behaviour and their interaction as explanatory variables.





**Figure 1** The effect of female exploratory behaviour and laying date on the probability to fledge at least one chick in wild great tits. For graphical purposes we give the average probability per 25% category for female exploratory behaviour and for each female category we give the lower ('early birds'; solid dots) and upper ('late birds'; open dots) 50% of the laying date distribution (year  $\chi^2=15.4$ ,  $p=0.002$ , interaction female exploration  $\times$  laying date  $\chi^2=8.16$ ,  $df=1$ ,  $p=0.004$ ).

## RESULTS

### *Reproduction and exploratory behaviour*

Laying date was unrelated to female ( $F_{1,210}=0.02$ ,  $p=0.89$ ) or male ( $F_{1,211}=0.10$ ,  $p=0.75$ ) exploratory behaviour, but differed between years, and first-year females laid on average 2.5 days later than older females. Clutch size was also unrelated to both the exploratory behaviour of females ( $F_{1,209}=0.08$ ,  $p=0.78$ ) and males ( $F_{1,207}=1.85$ ,  $p=0.18$ ), and again varied between categories of year and female age.

The probability of fledging at least one chick correlated with female exploratory behaviour in interaction with laying date. Early in the season slow-exploring females had the highest probability of fledging at least one offspring, whereas later in the season this effect disappeared (figure 1). For the nests that fledged at least one chick, the number of fledglings did not correlate with either female ( $F_{1,152}=0.01$ ,  $p=0.98$ ) or male ( $F_{1,156}=1.23$ ,  $p=0.27$ ) exploratory behaviour.

Fledging size correlated negatively with female exploratory behaviour, but not with male exploratory behaviour, and the effect was stronger in young than in older females (table 1, figure 2). The effect may have been caused by unequal brood sex ratios with respect to female exploratory behaviour, because male offspring have larger tarsi than female offspring. Inclusion of the observed sex ratio in the model showed that broods with more males indeed had longer tarsi, but the significance of female exploratory behaviour increased when sex ratio was added to the model, showing that slow-exploring females indeed had fledglings that were larger in size. Fledgling condition was affected by the interaction between male and female exploratory behaviour, with slow-slow and fast-fast pairs having chicks in best

**Table 2** ANCOVA of nest box-specific reproductive parameters ('nest box quality') and the exploratory behaviour of its occupants. The reproductive parameters of nest boxes were based on nests in which neither of the pair members was involved, and are only included if we had at least two records available for the nest box from different years from different parents. All measures are standardized with respect to the annual mean. Productivity is the number of fledglings.

Variable	Female behaviour			Male behaviour			Female × Male behaviour		
	<i>F</i>	<i>df</i>	<i>p</i>	<i>F</i>	<i>df</i>	<i>p</i>	<i>F</i>	<i>df</i>	<i>p</i>
Laying date	2.01	1,168	0.16	0.32	1,167	0.57	1.55	1,166	0.21
Clutch size	0.33	1,133	0.57	0.02	1,134	0.90	0.87	1,135	0.42
Productivity	2.85	1,114	0.09	0.63	1,113	0.43	0.71	1,112	0.40
Fledgling size	1.11	1,40	0.30	0.01	1,39	0.94	0.89	1,38	0.35
Fledgling condition	0.31	1,59	0.58	5.59	1,60	0.02	0.00	1,58	1.00

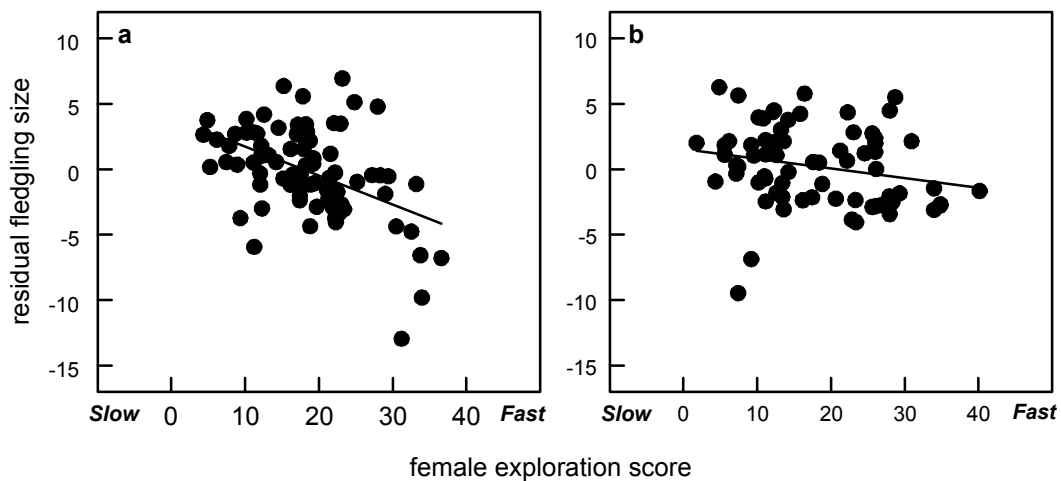
condition (table 1, figure 3). Fledgling condition was also affected by date, with chicks having lower condition when born later in the season. In the first and third year, young males had fledglings in lower condition than older males, while the pattern was reversed in the other two years.

#### *Territory quality and exploratory behaviour*

The nest box occupancy rate was not correlated with either female (logistic regression:  $\chi^2=0.08$ ,  $df=1$ ,  $p=0.78$ ) or male exploratory behaviour ( $\chi^2=0.74$ ,  $df=1$ ,  $p=0.39$ ), or their interaction ( $\chi^2=0.95$ ,  $df=1$ ,  $p=0.33$ ). We found no correlation between nest box-specific laying dates, clutch sizes or productivity and exploratory behaviour of either parent occupying the box (table 2). No correlation was found between exploratory behaviour of either pair member and the average size of the fledglings of the occupied nest box, but fast-exploring males occupied nest boxes in which young fledged at a higher than average condition (table 2). Nest boxes did not differ in exploratory behaviour of either the male (repeatability= $-0.09$ ,  $F_{35,46}=0.81$ ,  $p=0.74$ ) or female inhabitant (repeatability =  $-0.08$ ,  $F_{39,47}=0.83$ ,  $p=0.73$ , only nest boxes included with at least two values for either male or female exploratory behaviour), and hence the correlations between nest box quality and exploratory behaviour did not originate from certain personalities nesting more frequently in certain nest boxes. These analyses suggest that fast-exploring males occupy nest boxes of better quality.

## DISCUSSION

The coexistence of different heritable behavioural strategies can only be understood if we have good fitness measures and understand the selection pressures causing these patterns in fitness. In an earlier study we showed that exploratory behaviour in this small songbird strongly correlated with fitness components for both adult survival and

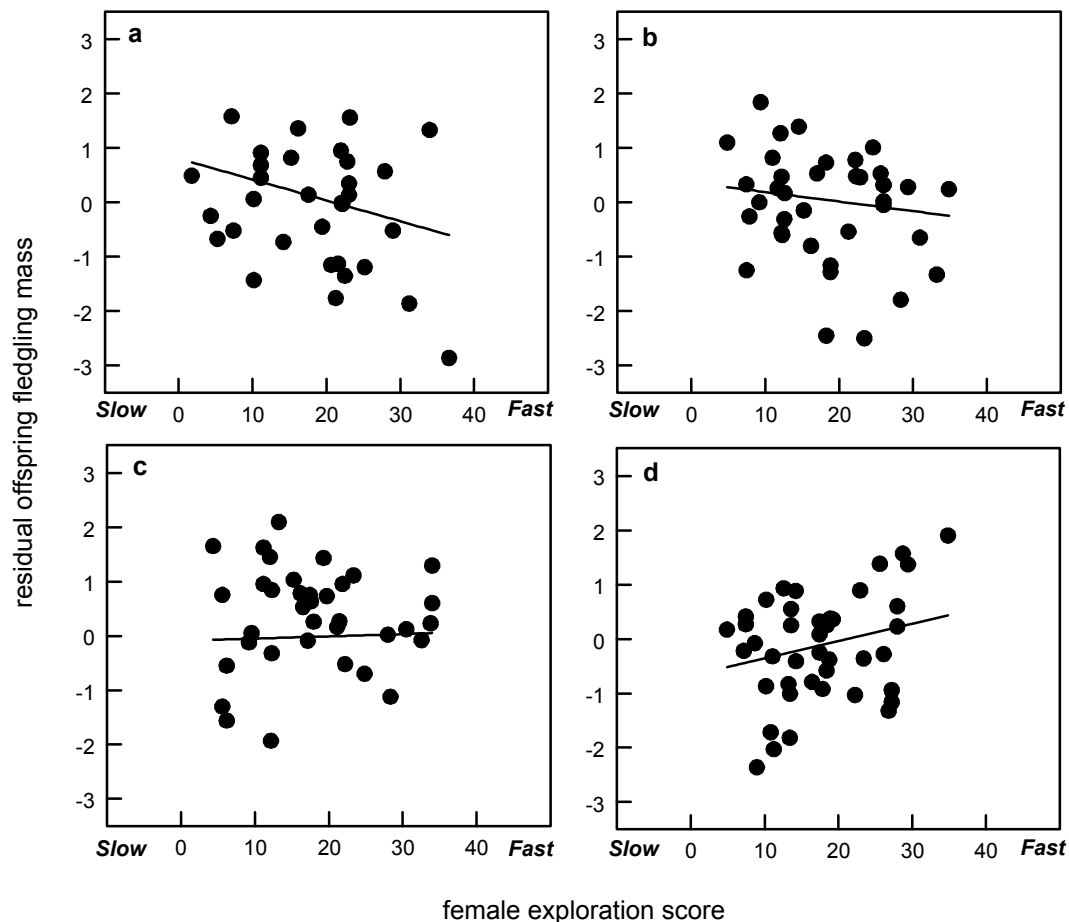


**Figure 2** The effect of female exploratory behaviour and age on mean fledgling size of their broods for (a) first-year old females and (b) older females. For presentational purposes fledgling size is expressed as the residual of tarsus length on year, laying date, female age and parental tarsus length (see table 1).

the annual number of recruiting offspring (*chapter 6*). In one year both pairs of either two slow-exploring or two fast-exploring individuals produced most recruiting offspring (*chapter 6*). Here we show that one of the underlying causes of these fitness patterns is that these pair combinations produce fledglings in best condition. Furthermore slow-exploring females had a higher probability to fledge at least one chick, fledglings of slow-exploring females were larger in size, and fast-exploring males bred in nest boxes that produced heavy fledglings when occupied by other birds.

One of the important findings is that offspring condition does not depend solely on the personality of each parent separately, but also on the interaction between male and female personality, with slow-slow and fast-fast pairs producing offspring in best condition. Because fledgling condition is an important determinant of fitness (Tinbergen & Boerlijst 1990; Both et al. 1999) one would expect selection to favour assortative mating with respect to exploratory behaviour, because this will enhance fitness for at least the birds at the opposite ends of the behavioural spectrum. Interestingly there is disassortative mating for older, but not for one-year old individuals (*chapter 6*). Although we do not expect disassortative mating based on the data presented in this paper, we suggested that medium-exploring birds had the highest survival and offspring recruitment on the long term (*chapter 6*). Thus, although assortative mating appeared to be adaptive in the breeding season, selection may nevertheless favour disassortative mating because this allows birds at the extremes of the behavioural distribution to increase their fitness by producing medium-exploring offspring.

The correlation between reproduction and these personality traits can be caused by variation in parental traits, territory quality, or both (Both & Visser 2000). Covariation between offspring condition and parental personality is likely to be in part mediated via territory quality, because fast-exploring males occupied better quality territories and fast-fast pairs produced offspring in best condition. This is consistent with the observation that fast-exploring territorial males outcompete slow-exploring



**Figure 3** Mean fledging condition per nest of juvenile great tits in relation to the exploratory behaviour of both parents. In graphs *a-d* the quartiles of the distribution of male exploratory behaviour are given, and the different graphs show (*a*) the lower 25% ('slowest') (*b*) the 25-50% ('slow-medium') (*c*) the 50-75% ('medium-fast') (*d*) the highest 25% ('fastest') of the distribution of male scores. For presentation purposes the fledging condition is expressed as the residual of fledging mass on year, male age, laying date, offspring tarsus length and the interactions between year  $\times$  male age and laying date  $\times$  tarsus (see table 1). Lines are the regression lines for the model with the mean male exploratory behaviour of each quartile included.

territorial males at clumped food sources in winter (*chapter 3*), and these fast-exploring males are thus expected to acquire territories with the best foraging habitats. Fast explorers may produce offspring of high fledging condition because their high quality territories provides them with food sources that are more easily exploited, matching their routine-like foraging habits (Verbeek et al. 1994; Drent & Marchetti 1999): territories of high quality are more likely to contain patches where food is abundant and easily found, like single large oak trees, highly suited for exploitation by animals that are routine-like in their behaviour. Although this could explain why some fast-exploring males had offspring of high condition, it does not account for the effect that slow-exploring pairs also had offspring fledging in high condition. The trait that may make slow-exploring parents better parents is that slow birds are well-adapted to forage under changing feeding conditions because they respond more quickly to

changes in food distribution and continuously explore alternative feeding options (Verbeek et al. 1994; Drent & Marchetti 1999). Such foraging behaviour may be particularly beneficial during chick feeding, because great tits feed their offspring with mobile and hidden invertebrate prey, and their foraging strategy may compensate for the lower quality of territories occupied by slow-exploring males. If slow-exploring mothers are indeed better adapted to provide nestling care, this may explain also why they had fewer nest failures and produced larger fledglings. Thus, both variation in habitat and parental behaviour – resulting from differences in aggressiveness and foraging strategies – may explain why offspring condition covaried with parental personality.

The effect of pair composition on offspring condition indicates that certain personality types do not form good teams: fast-exploring males have high quality territories but nevertheless produce offspring of low fledging condition when they have a slow-exploring mate. Similarly, slow-exploring males had low quality territories but can nevertheless produce offspring of high fledging condition if they have a slow-exploring mate. This effect of pair composition may reflect a frequency-dependent benefit of some behavioural component of avian personality. For instance, fast-exploring birds copy successful foraging strategies of others (Marchetti & Drent 2000), hence high quality territories may be particularly suitable for pairs that both display such social learning (i.e. fast-fast pairs). Similarly, low quality territories with less predictable food supplies may be particularly suitable for pairs that do not copy each others foraging habits.

In one out of three years we found that assortatively mated pairs at both ends of the behavioural spectrum produced most offspring surviving to breeding (recruits) in the local study area, while in two other years birds of intermediate exploratory behaviour produced most recruits (*chapter 6*). Because the probability of becoming a local recruit depends to a large extent on condition at fledging (Tinbergen & Boerlijst 1990; Both et al. 1999), the effect reported here that slow-slow and fast-fast exploring pairs have fledglings in the best condition can explain this pattern in recruitment rate in this one year, but not in the other two years. The single year where the fledgling condition and recruitment patterns match, was the year with high juvenile survival rates, and selection in that year may have operated on physical characteristics instead of behavioural characteristics of the juveniles. In years with low juvenile survival rates, selection on physical differences may be less important than behavioural traits and therefore in those years we found a tendency to stabilizing selection on exploratory behaviour despite the fact that chicks from pairs at both extremes of the behavioural spectrum have chicks that fledge in the best condition.

We have shown that intraspecific variation in reproductive success is not just the result of (noise around) a general reaction to the environment that is equal for every individual bird. Instead, individuals with different personalities have different reproductive output that in turn affects components of fitness. Variation in reproductive success can partly explain why pairs differ in the number of offspring that survive to become breeders, but selection acting on behavioural traits of offspring outside the breeding season appeared to be most important in years when few offspring survive.

### ACKNOWLEDGEMENTS

This project has benefited greatly from the help of Piet de Goede, Leontien Witjes, Kathelijne de Maijer, Henry Bouwmeester (fieldwork and testing of individuals), Mary-Lou Aaldering, Janneke Venhorst (aviary work) and Jan Visser (database management). Arie van Noordwijk, Kees van Oers, Ton Groothuis, Claudio Carere, Gerdien de Jong and Jaap Koolhaas have contributed in discussion and/or comments on earlier drafts. We are grateful to 'Het Gelders Landschap' for permission to work on their properties. C.B. and N.D. are supported by the Life Sciences Foundation (ALW grants 805-33-321, 805-33-324), which is funded by the Netherlands Organization for Scientific Research (NWO). Permission for short-term transport of great tits to the laboratory was granted by KNAW Dierexperimenten Commissie.

## Chapter 6

# **FITNESS CONSEQUENCES OF AVIAN PERSONALITIES IN A FLUCTUATING ENVIRONMENT**

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## SUMMARY

Individual animals differ in the way they cope with challenges in their environment, comparable with variation in human personalities (Wilson et al. 1994; Boissy 1995; Koolhaas et al. 1999; Gosling 2001). The proximate basis of variation in personality traits has received considerable attention, and one general finding is that personality traits have a substantial genetic basis (Boissy 1995; Koolhaas et al. 1999; Bouchard & Loehlin 2001; Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003). This poses the question how variation in personality is maintained in natural populations (Wilson et al. 1994; Wilson 1998). We show that selection on a personality trait with high heritability fluctuates across years within a natural bird population. Annual adult survival was related to this personality trait (behaviour in novel environments (Dingemanse et al. 2002, *chapter 2*) but the effects were always opposite for males and females, and reversed between years. The number of offspring surviving to breeding also related to their parents' personality, and again selection changed between years. The observed annual variation in selection pressures coincided with changes in environmental conditions (masting of beeches) that affects competitive regimes of the birds (Perdeck et al. 2000). We expect that the observed fluctuations in selection pressures play an important role in maintaining genetic variation in personalities through fluctuating competition over space and food in association with population density and personalities.



## INTRODUCTION

In a wide range of vertebrates, individuals differ in their propensity to take risks, particularly in novel or challenging situations (Wilson et al. 1994; Boissy 1995; Koolhaas et al. 1999; Gosling 2001). These individual differences in behaviour often arise early in life (Kagan et al. 1988; Verbeek et al. 1994), have a substantial genetic component (Boissy 1995; Koolhaas et al. 1999; Bouchard & Loehlin 2001; Dingemanse et al. 2002, *chapter 2*; Drent et al. 2003), and are regarded as personality differences (Wilson et al. 1994; Gosling 2001; Gosling & Vazire 2002) because they are expressed across many different situations (Kagan et al. 1988; Wilson et al. 1994; Boissy 1995; Koolhaas et al. 1999; Gosling 2001). The processes responsible for the maintenance of variation in personality in natural populations are largely unknown, but likely involve fluctuating selection pressures (Burger & Gimelfarb 2002) caused by environmental variability (e.g. ecological cycles) or frequency dependent selection (Wilson et al. 1994; Wilson 1998). Spatiotemporal variation in selection on personality has not yet been studied in natural populations, and only a few studies have measured selection on personality traits altogether (Armitage 1986; Eaves et al. 1990; Réale et al. 2000). By measuring the fitness consequences of an avian personality trait in the wild during three successive years we show that strong alternating selection acted on this personality trait. The direction of selection differed between sexes and years.

We have examined how natural selection acts on personalities in a natural population of a passerine bird, the great tit *Parus major*. Great tits are non-migratory territorial songbirds that live in forests in Europe and Asia. Individual great tits differ in the way they explore novel environments ('fast' versus 'slow') (Verbeek et al. 1994; Dingemanse et al. 2002, *chapter 2*). Individuals at the extremes of the trait distribution use alternative strategies to cope with novel or challenging situations (Verbeek et al. 1994; Koolhaas et al. 1999). Fast explorers have an active coping strategy: they are aggressive, bold in exploration, insensitive to external stimuli, and rely on routines, whereas slow explorers use a passive coping strategy: they are relatively non-aggressive, shy in exploration, sensitive to external stimuli, and readily adjust their behaviour to changes in their environment (Verbeek et al. 1996; Verbeek et al. 1999; Marchetti & Drent 2000). Exploratory behaviour is highly repeatable and has a substantial heritable component ( $h^2=0.3-0.6$ ) in both wild-caught (Dingemanse et al. 2002, *chapter 2*) and captive-bred (Drent et al. 2003) great tits. We measured phenotypic variation of exploratory behaviour in a natural population by taking individual great tits for a single day to the lab where an exploration test was performed in a novel environment, and released them afterwards (Dingemanse et al. 2002, *chapter 2*). We assessed survival between breeding seasons of these individuals and recruitment of their offspring in their natural habitat and examine correlations between these fitness components and their behavioural phenotype.

## METHODS

### *Data collection*

Data were collected from a nest-box population of great tits in the Westerheide area, central Netherlands, between 1998 and 2002. Outside the breeding season, we captured birds for behavioural scoring using standard methods (Dingemanse et al. 2002, *chapter 2*). Birds of unknown behavioural score were transported to the laboratory (1-32 birds per day) and housed individually. The following morning, we measured exploratory behaviour (Verbeek et al. 1994; Dingemanse et al. 2002, *chapter 2*) of each bird alone in a sealed room (4.0×2.4×2.3 m) containing five artificial trees, before we released them near their individual place of capture within 14-24 hours of capture. We used the total number of flights and hops within the first 2 min as an index of exploratory behaviour (Dingemanse et al. 2002, *chapter 2*). We corrected the scores for date of capture, based on within-individual changes in behaviour with capture date (Dingemanse et al. 2002, *chapter 2*). In the breeding season, we captured adults when their offspring were 8-10 days old and gave them individually numbered rings to allow identification when their chicks were ringed in the nest. We use two fitness components that are together a good approximation of the number of genes that a bird contributes to the population in the next breeding season. The first is the annual number of offspring that survive to the next breeding season that a pair produces (i.e. offspring recruitment). The second is the survival of adults from one breeding season to the next. Breeding adults were only included in the analysis if they were tested before the breeding season, to prevent effects of differential mortality between breeding and testing. Juveniles could not be tested before they became independent of their parents, consequently viability selection between hatching and testing could not be measured.

### *Survival analyses*

We estimated annual survival of adults between breeding seasons for the years 1999-2002. Because some individuals escape detection while they are alive, capture probabilities have to be accounted for when estimating true survival. We used MARK v.2.1 to simultaneously estimate both annual survival ( $\phi$ ) and capture probabilities ( $P$ ) (White & Burnham 1999). Our main goal was to test whether survival probabilities depended on individual behaviour (linear term:  $b$ ; quadratic term:  $b^2$ ), sex ( $s$ ), year ( $t$ ), and their interactions. The initial model  $\phi(b, b^2, s, t, b \times s, b^2 \times s, b \times t, b^2 \times t, s \times t, b \times s \times t, b^2 \times s \times t)P(s)$  estimated the relation between survival ( $\phi$ ) and the three-way interaction between behaviour (both linear and quadratic terms), sex, and year, including all lower-term interactions and main effects. Because capture probabilities ( $P$ ) have been shown to differ between male and female great tits, we also included sex-dependent capture probabilities in this initial model. We then fitted simpler models and used the Akaike's Information Criterion (AIC) to select the most parsimonious model (White & Burnham 1999), the model that fits the data best with the fewest parameters, resulting in the lowest QAICc value (see table 1). Parameter estimates of the best models were examined to evaluate whether the model could be further simplified, for instance by grouping factor levels with similar parameter estimates (Crawley 1993). We tested the significance of explanatory variables by comparing nested models using likelihood ratio tests (LRL). We corrected for overdispersion by adjusting the quasi-

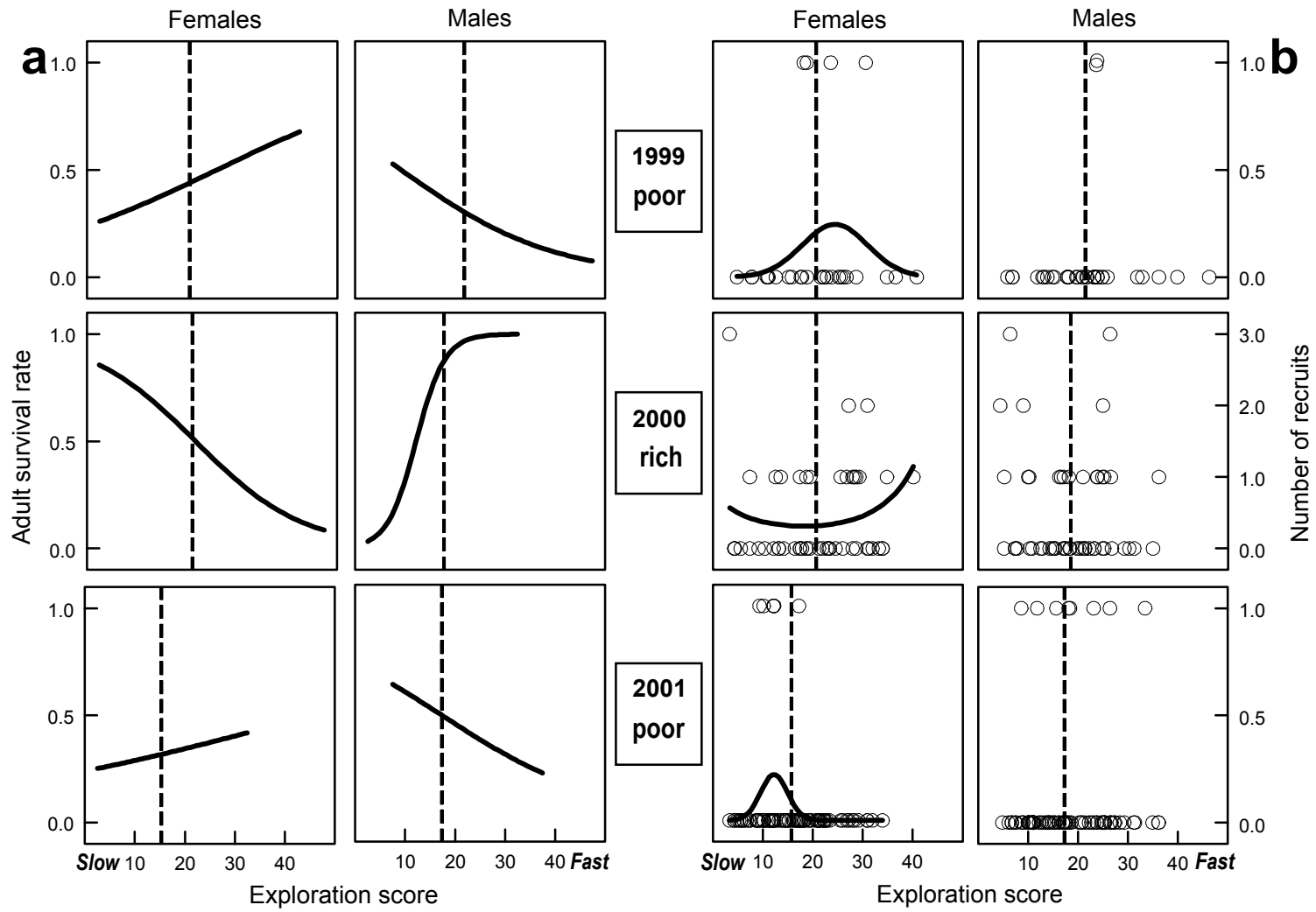
**Table 1** Adult survival analysis: Model selection of adult survival rate ( $\phi$ ) and recapture rate ( $P$ ) between breeding seasons (years) of great tits as a function of individual exploratory behaviour  $b$ , sex  $s$ , and year  $t$  ( $t_1=1999-2000$ ,  $t_2=2000-2001$ ,  $t_3=2001-2002$ ) or  $t_{1\&3}$  vs  $t_2$  (combined estimate for  $t_1$  and  $t_3$  versus  $t_2$ ). Models are sorted in ascending order by their QAICc values after correcting for overdispersion ( $c\text{-hat}=1.7559$ ). Note that not all models are shown.

Model	QAICc	No. of parameters	Qdeviance
1 $\phi(b, t_{1\&3} \text{ vs } t_2, b \times s, b \times t_{1\&3} \text{ vs } t_2, b \times s \times t_{1\&3} \text{ vs } t_2)P(\cdot)$	260.98	7	246.616
2 $\phi(b, s, t_{1\&3} \text{ vs } t_2, b \times s, b \times t_{1\&3} \text{ vs } t_2, s \times t_{1\&3} \text{ vs } t_2, b \times s \times t_{1\&3} \text{ vs } t_2)P(\cdot)$	263.58	9	245.000
3 $\phi(b, s, t, b \times s, b \times t_{1\&3} \text{ vs } t_2, s \times t, b \times s \times t_{1\&3} \text{ vs } t_2)P(\cdot)$	267.03	11	244.173
4 $\phi(b, s, t, b \times s, b \times t, s \times t, b \times s \times t)P(\cdot)$	271.32	13	244.126
5 $\phi(b, s, t, b \times s, b \times t, s \times t)P(\cdot)$	276.37	11	253.512
6 $\phi(b, b^2, s, t, b \times s, b^2 \times s, b \times t, b^2 \times t, s \times t, b \times s \times t, b^2 \times s \times t)P(\cdot)$	280.88	19	240.334
7 $\phi(b, b^2, s, t, b \times s, b^2 \times s, b \times t, b^2 \times t, s \times t, b \times s \times t, b^2 \times s \times t)P(s)$	282.85	20	240.034

likelihood parameter ( $c\text{-hat}$ ). Although these estimates of adult survival do no account for dispersal they are unlikely to be biased because in this species dispersal is restricted to juveniles (Greenwood & Harvey 1982).

#### *Analysis of offspring number*

The number of offspring a pair produced that survived to breeding was determined by catching most breeding adults in the each breeding season (capture probability =  $0.727 \pm 0.098$ , estimate based on the survival analyses in MARK) and counting the number of recaptured young per pair in the next breeding season that bred in our study area. We analysed the number of surviving offspring using general linear models (GLM) with Poisson errors (Crawley 1993). Exploration scores as linear and quadratic terms were included in the models, because we did not have a priory expectations of the shape of the effects. We have not always tested both male and female parents before the breeding season, and therefore we give separate analyses for the effect of male and female parent exploratory behaviour as well as the simultaneous effect of both sexes. Sample sizes depend on the number of parents tested. In the analysis of male exploration score on the number of surviving offspring there were too few offspring in 1999 to include this year in the model, and this model is based on 2000 and 2001 only, and for the same reason the analysis of the simultaneous effect of both parents was restricted to 2000. The estimates are based on local recruits and do not include dispersal. We have no means of controlling for dispersal patterns quantitatively.



**Figure 1** The relation between two fitness components and individual personality for three successive years (1999-2001) in male and female great tits. (a) Annual adult survival as a function of individual exploratory behaviour. Lines represent the slopes of the linear relationship between adult survival and individual behaviour, calculated from the model  $\phi(b,s,t,b \times s, b \times t, s \times t, b \times s \times t)P(\cdot)$ . Number of live encounters per year = 37, 58, 78 (females 1999-2001) and 36, 46, 64 (males 1999-2001; effective sample size = 319). (b) Number of offspring surviving to breeding (recruits) as a function of the exploratory behaviour of their parents. The solid line gives the significant regression line from a Poisson regression (mothers: year  $\times$  exploratory behaviour (both linear and quadratic term included)  $\chi^2_4 = 11.7$ ,  $p=0.03$ ; males (only 2000 and 2001):  $\chi^2_2 = 1.32$ ,  $p=0.52$ ). The dotted line gives the arithmetic mean exploration score for the sex and year combination.

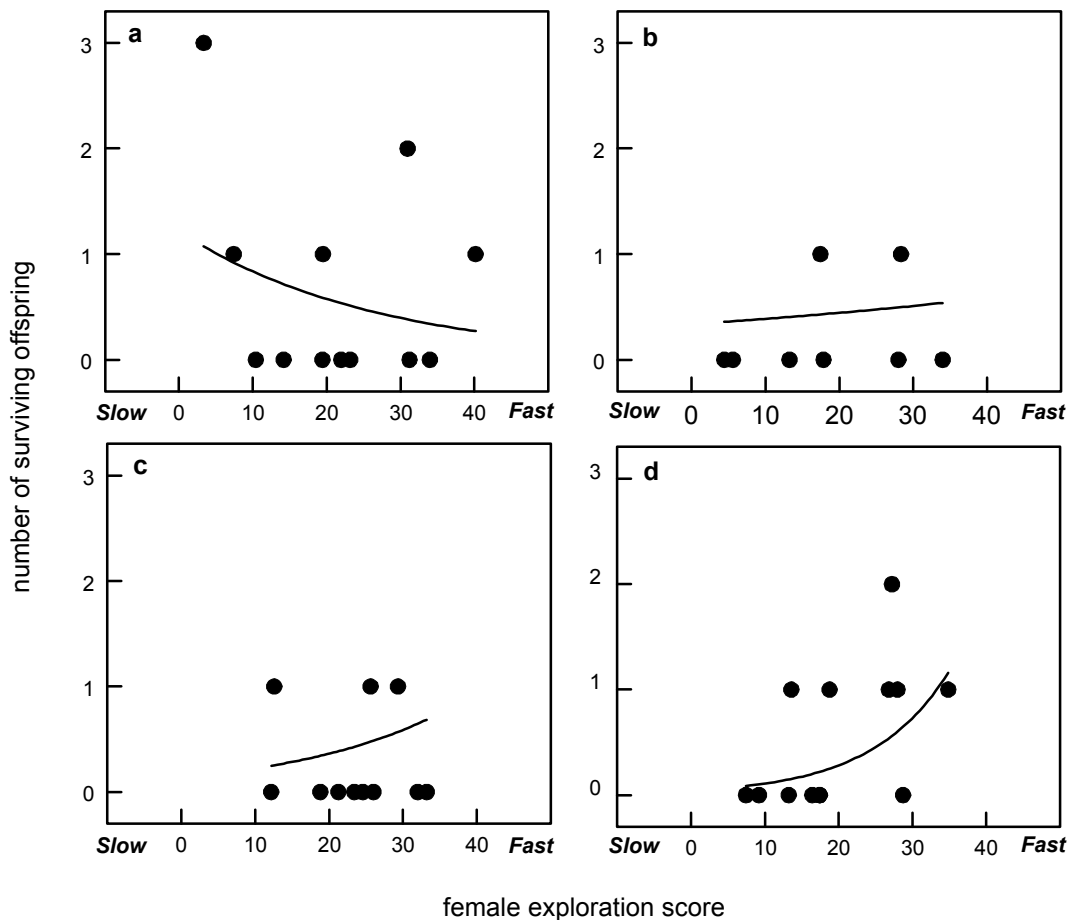
## RESULTS AND DISCUSSION

Selection on avian personality measured by adult survival between breeding seasons fluctuated strongly between the years and was in each year opposite for males and females (figure 1a, see table 1, LRT Model 4 vs 5,  $\chi^2=9.386$ ,  $df=2$ ,  $p=0.0092$ ). In 1999 and 2001 slow-exploring males and fast-exploring females tended to survive better, while in 2000 the reverse was observed (the effects of individual behaviour were linear within each combination of sex and year; LRT Model 4 vs 6,  $\chi^2=3.792$ ,  $df=6$ ,  $p=0.7048$ ). In both sexes, the slopes and intercepts were similar for the first and third year (LRT, Model 2 vs 4,  $\chi^2=0.837$ ,  $df=4$ ,  $p=0.9284$ ), and the most parsimonious model included a common intercept for the first and the third year as well as a three-way interaction between individual behaviour, sex, and year (table 1, model 1), indicating that within sexes the selective regimes were similar in 1999 and 2001 but different in 2000.

The number of offspring surviving to breeding in the local study area was related to the personality of the mother, and again fluctuated between years (figure 1b). In two years with low winter food (1999 and 2001), few young recruited as breeders in the local population, and selection tended to be stabilising. In contrast, in one year with high recruitment (2000) selection tended to be disruptive, with individuals at both ends of the distribution producing more recruits. For fathers there was not a significant effect of their personality on the number of recruits produced, although the trends in fathers were similar as in mothers and did not differ significantly in an analyses including both fathers and mothers (year  $\times$  sex  $\times$  exploration score:  $\chi^2=3.753$ ,  $df=2$ ,  $p=0.153$ ; sex  $\times$  exploration score:  $\chi^2=0.002$ ,  $df=1$ ,  $p=0.964$ ). For the middle year (2000) we had enough data to analyse the combined effect of fathers' and mothers' personality on the number of recruits produced. In this year the number of recruits depended on the phenotypes of the partners: pairs of two fast-exploring partners or two slow-exploring partners had the highest fitness, while other combinations had lower fitness (figure 2; interaction: male  $\times$  female exploratory behaviour:  $\chi^2=4.162$ ,  $df=1$ ,  $n=44$ ,  $p=0.046$ ). The disruptive selection in 2000 (figure 1b) is thus not only determined by the personality of mothers, but also by the personality of their mates (figure 2).

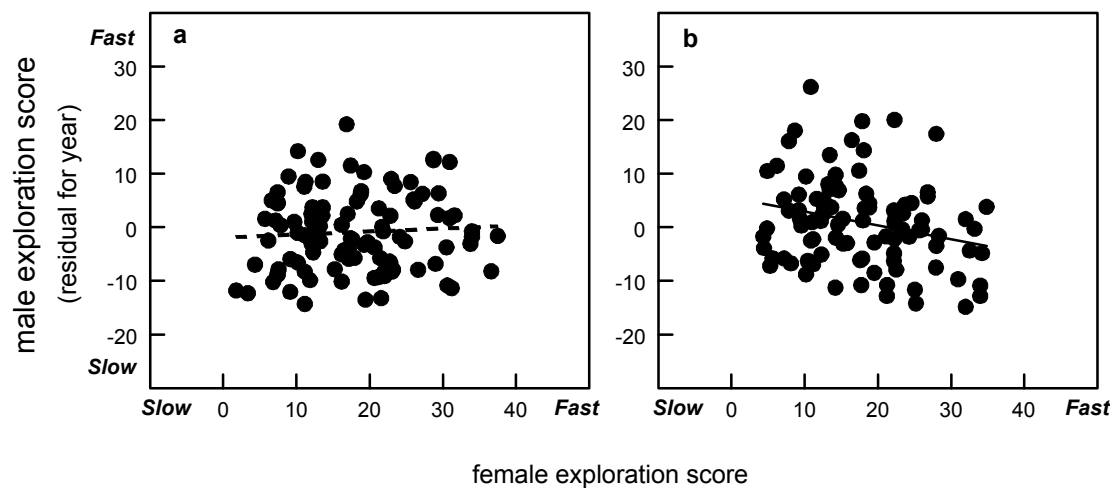
Fast-exploring parents have offspring that disperse furthest (Dingemanse et al. 2003, *chapter 4*). As a consequence we underestimate the real number of surviving offspring of those parents, and pairs of two fast-exploring parents are thus expected to perform even better than suggested in figure 2. We are aware that this bias in the estimated offspring survival can affect our estimates of selection but it cannot explain the annual variation in selective pressures for this fitness component, because patterns of dispersal did not differ between years (Dingemanse et al. 2003, *chapter 4*). Recently we have collected additional support for the finding that the interaction between parents' exploratory behaviour indeed affects the number of recruits. We found that assortative pairs of extreme phenotype also produce offspring of highest fledgling condition (*chapter 5*).

Because assortative pairs produce most viable offspring per breeding season, we expected the birds to pair assortatively with respect to exploratory behaviour. Contrary to this expectation, the birds were mated disassortatively, although this pattern occurred only when the male partner was an older bird (figure 3; ANOVA with male phenotype as dependent: female phenotype  $\times$  male age:  $F_{1,191}=5.67$ ,



**Figure 2** The effect of the exploratory behaviour of both parents on the number of offspring surviving to breeding in the year 2000. On the x-axis we give the exploratory behaviour of the females. Male exploration scores are divided in 4 groups of equal number, and the different graphs show (a) the lower 25% ('slowest') (b) the 25-50% ('slow-medium') (c) the 50-75% ('medium-fast') (d) the highest 25% ('fastest') of the distribution of male scores. The regression lines are from a general linear model with Poisson errors, and the average score of the male of each quartile is entered in the equation of each graph.

$p=0.018$ ). Two hypotheses can explain these intriguing findings. First, mates adjust their own behaviour after pair formation to contrast their partners' exploratory behaviour, but since most individuals were tested as juveniles before they mated we reject this possibility. Alternatively, if intermediate phenotypes have highest fitness, disassortative mating may be an adaptive mate choice because parents at the extremes of the trait distribution can only produce intermediate offspring by pairing disassortatively. Support for this is found in the lower variance in adult survival for intermediate phenotypes (figure 1a), resulting in a higher overall life expectancy. Because exploratory behaviour is heritable (Dingemanse et al. 2002, *chapter 2*) ( $h^2$  estimates based on mid-parent mid-offspring regressions for the years 1999-2001 are on average  $0.340 \pm 0.138$  (GLM controlling for year:  $F_{1,60}=6.049$ ,  $p=0.017$ )), disassortative mating may thus allow adults to produce offspring with the highest life expectancy and hence increase their lifetime fitness.



**Figure 3** The observed correlation between male and female exploratory behaviour of pairs of great tits: (a) one-year old males (b) older males. Data are analysed with ANCOVA with male exploratory behaviour as dependent variable (year:  $F_{3,191}=3.80$ ,  $p=0.01$ , male age  $\times$  female exploratory behaviour:  $F_{1,191}=5.67$ ,  $p=0.02$ ). Female age was not significantly correlated with male exploratory behaviour, nor any of the other interaction terms (all  $p>0.14$ ).

Selection on a personality trait in this wild bird population changes from year to year, but what is the ecological background of these differences? The observed annual variation in selection pressures coincided with annual changes in environmental conditions – the presence of mast seeding of beeches *Fagus sylvaticus*. The winters of 1999/2000 and 2001/02 were without beech mast ('poor' winters), while in 2000/01 there was a good beech crop ('rich' winter) and we found similar selection patterns in the two poor winters but an opposite pattern in the rich winter for both fitness components (figure 1). We therefore suggest that the observed annual changes in selection pressures may have their origin in this environmental cycle. Beech masting results both in more relaxed competition for food during winter but also results in increased competition for territory space in the following spring because both juvenile and adult survival is higher in years with beech masting (Perdeck et al. 2000). The consequences of beech masting are likely to differ between classes of individuals and this may explain why selection on personality in adults differed between the sexes. Because females are subordinate to males, we expect them to be most affected by competition for winter food while we expect males to be most affected by competition for territorial space. Fast-exploring females may benefit from their aggressiveness when competing for clumped resources in poor years, while slow-exploring females may survive better in rich years because in those years overt aggressiveness may be maladaptive and results in increased mortality (Sih et al. 2003). Similarly, we suggest that fast-exploring territorial males may benefit from their aggressiveness in rich years when competition for territorial space is increased because their aggressiveness may make them more successful in excluding the large numbers of competitors (i.e. non-territorial juveniles) from their territories. Hence, they may survive better because they are less likely to lose their territory. Again, when competition is relaxed, overt aggressiveness may result in net costs rather than net benefits and in those years selection may favour slow-exploring territorial males.



Earlier work on this species showed that selection on juveniles acts on their physical characteristics (i.e. body condition at fledging; Tinbergen & Boerlijst 1990) especially during years with high densities (Both et al. 1999). The large number of recruits for the assortative fast and slow pairs in the rich year may indeed be explained by higher fledgling condition of their offspring (*chapter 5*). Interestingly, while these pair combinations also produced relatively heavy offspring in the poor years (*chapter 5*), they nevertheless did not produce most recruits. Hence, the extent to which selection favoured certain physical and behavioural characteristics may have differed between poor and rich years.

Although we do not fully understand the processes maintaining genetic variation in personality traits, QUOTE the fluctuating selection reported in this paper helps to maintain high levels of genetic variation in avian personality (Burger & Gimelfarb 2002). However, spatiotemporal variation in selection also lead to the question why animals that occupy temporally changing environments are relatively inflexible in their behaviour. Theoretical models predict that temporal variation in selection can maintain a mix of phenotypically flexible and inflexible genotypes (Wilson & Yoshimura 1994)QUOTE. QUOTEHence, fluctuating selection on avian personality may in part have resulted from selection favouring individuals that are more flexible in their behaviour. Studies on shyness-boldness in humans show that intermediate phenotypes are more flexible in their behaviour (Kagan et al. 1988). The indication that adults of intermediate phenotype had the highest life expectancy (figure 1a) may thus result from their behavioural flexibility. Interestingly, this phenotype did not have the highest survival within any of the six classes of sex and year (figure 1a) suggesting that this phenotype is a jack of all trades and master of none.

## ACKNOWLEDGEMENTS

Piet de Goede, Mary Lou Aalderink and Janneke Venhorst helped collecting the data. David Thomson was of great help in the analysis of the survival data. Claudio Carere, Ton Groothuis, Gerdien de Jong, Jaap Koolhaas, Kate Lessells, Arie van Noordwijk, Kees van Oers, Marcel Visser and Jon Wright contributed by discussing ideas and/or commenting on an earlier draft. We are grateful to ‘Het Gelders Landschap’ for permission to work on their property. N.D and C.B. are supported by Life Sciences Foundation (ALW grants 805-33-321, -324). Permission for short-term transport of great tits to the laboratory was granted by KNAW Dierexperimenten Commissie.



## **Chapter 7**

### **SUMMARY AND DISCUSSION**

## INDIVIDUAL VARIATION IN BEHAVIOUR

Individuals encounter many different social and physical environments during their life. Evolutionary theory predicts that individuals should behave optimally in each environment to maximize their inclusive fitness, and therefore should show *flexibility* in their behaviour when the optimal behaviour differs between the various environments they encounter (Via & Lande 1985; Stearns 1989; Gomulkiewicz 1998; Schlichting & Pigliucci 1999). Rapidly accumulating empirical evidence for a wide range of vertebrate and invertebrate species indicates, however, that while individuals show some degree of flexibility (e.g. Carere 2003), they *differ consistently* in their behaviour in standard test situations even when controlling for between-individual differences in individual history, state, sex, or size (Wilson et al. 1994; Boissy 1995; Koolhaas et al. 1997; Gosling 2001). Not only do individuals differ along one axis but different behavioural axes are often correlated (see Huntingford 1976; Verbeek et al. 1994; Koolhaas et al. 1997). Thus, one type of behaviour (e.g. shyness/boldness) predicts another type of behaviour (e.g. aggressiveness), comparable to personality axes of human behaviour (Wilson et al. 1994; Budaev 1997; Gosling & John 1999; Gosling & Vazire 2002). This thesis studied how and when natural selection acts on avian personality to help understand how individual variation in personality is maintained in natural populations.

Heritable differences in individuals raised under controlled conditions could be masked by the larger variation in conditions during growth and early experiences in nature. In *chapter 2* we show that wild-caught great tits differ in their exploratory behaviour in a standard test situation (see also Coleman & Wilson 1998; Réale et al. 2000), confirming the many studies that used laboratory-bred animals. Measures of exploratory behaviour were consistent for recaptured individuals, indicating not only that individuals from the wild differed consistently in their behaviour but also that behavioural characteristics of the individual are measurable in individuals that grew up in the wild (Boake 1989; Falconer & Mackay 1996). Moreover, birds explored the novel environment quicker when confronted with the same challenge a second time but only when the time period between the subsequent tests was short, indicating that our exploration score reflected behaviour towards *novel or challenging situations* and not ongoing activity (Verbeek et al. 1994). Resemblance between parents and offspring (*chapter 2* and *6*) showed that genetic differences were underlying the individual variation in exploratory behaviour of wild individuals, supporting the findings of two earlier studies on hand-reared great tits that showed resemblance between siblings (Verbeek et al. 1994) and a significant response towards both upward and downward selection for a composite measure of exploratory behaviour (Drent et al. 2003). Although we did not measure whether different behavioural traits (exploration, boldness, aggressiveness, risk-taking behaviour) were correlated in wild-caught great tits as they are in laboratory-reared individuals (Verbeek et al. 1994, 1996; Drent & Marchetti 1999; van Oers In Press), resemblance between wild-caught birds and their laboratory-reared offspring strongly suggested a link between behaviour of wild great tits and the covarying behaviours reported for laboratory-bred great tits (Drent et al. 2003; van Oers In Press a). Hence, our measure of behaviour in a novel laboratory room can be used as a predictor of individual personality (*chapter 2*). The finding of individual and heritable variation in exploratory behaviour of wild great tits indicates that phenotypic selection on this personality trait can result in evolutionary consequences (Fisher 1930; Endler 1986). This poses the question how

this genetic variation in behaviour is maintained in natural populations (Clark & Ehlinger 1987; Wilson et al. 1994; Huntingford et al. 1994; Mousseau et al. 2000).

The existence of individual and heritable variation in exploratory behaviour of wild great tits allows one to study selection throughout life once the individual phenotype has been determined. This approach of measuring selection after assessing the individual phenotype under controlled conditions is now increasingly being applied in other species, including yellow-bellied marmots (Svendsen 1974; Armitage 1986), bighorn sheep (Réale et al. 2000; Réale & Festa-Bianchet 2003), pumpkinseed sunfish (Wilson et al. 1993), Trinidad killifish (Fraser et al. 2001), and brown trout (Höjesjö et al. 2002), and provides a useful methodology to study the ecological consequences of individual behaviour (Wilson 1998). Relationships between fitness and personality can however be misleading when part of the phenotypic variation in behaviour is caused by other factors with non-permanent effects on the behavioural phenotype (e.g. condition). Between-individual variation in behaviour can, for instance, also be expected when individuals differ in state due to trade-offs between conflicting demands (Houston & McNamara 1999; Mangel & Stamps 2001). Observed selection on behaviour may therefore reflect selection on other traits and not on personality *per se*. The behavioural phenotype of wild great tits was, however, unrelated to body condition during early life or during the measurement, and cut across axes of age and sex (*chapter 2*), indicating that exploratory behaviour does not reflect condition or state (Wilson et al. 1994; Verbeek et al. 1994).

### CAUSES OF VARIATION IN FITNESS

The few available field studies indicate that personality traits are subject to selection, with individual behaviour affecting components of fitness in several vertebrate species (Armitage 1986; Eaves et al. 1990; Réale et al. 2000; Fraser et al. 2001; Réale & Festa-Bianchet 2003). The ability to predict how and when selection acts on personality traits requires both the measurement of selection on these personality traits as well as identification of the underlying causes of this variation in fitness as function of the interaction between behaviour and the environment.

In our study species, the great tit, exploratory behaviour covaries with aspects of foraging behaviour: slow explorers take longer to develop a foraging habit when trained to associate food with certain features of their environment (Drent & Marchetti 1999) but respond more quickly to changes in food distribution because they continuously explore alternative feeding options, appearing to make more 'errors' (Verbeek et al. 1994; Drent & Marchetti 1999; Marchetti & Drent 2000). Because searching for food is fundamental for survival and reproduction (e.g. chick-feeding), relationships between survival and personality or between offspring quality and personality may relate to differences in foraging behaviour. Slow-exploring individuals are also relatively non-aggressive but well-adapted to cope with social stress (Verbeek 1998; Verbeek et al. 1999; Carere et al. 2001). The relation between fitness and exploratory behaviour may thus depend on the competitive regime (e.g. the amount of competition for space or food) or the social environment (van Oortmerssen & Busser 1989; Verbeek et al. 1996). Earlier studies on aviary groups of juvenile male great tits showed that slow explorers gain on average higher dominance ranks than fast explorers (Verbeek et al. 1999). This is because fast explorers have difficulty to cope with defeat and slow explorers are able to gain dominance by

preferentially attacking birds that are recovering from defeat (Verbeek 1998). Because high-ranking juveniles are more likely to become territorial early in life, suffer lower risk of predation, and are less likely to disperse to other areas in case of severe competition (Drent 1983, 1984; de Laet 1985; Ekman 1989), relationships between fitness and personality may be caused by differential ability to outcompete others (Verbeek 1998).

The relation between both winter dominance rank and personality (*chapter 3*) and natal dispersal and personality (*chapter 4*) in wild juvenile great tits indicates that personality affects competitive ability in the juvenile phase: fast explorers had lower dominance ranks than slow explorers in non-territorial juvenile males on feeding tables in winter (*chapter 3*). The finding that immigrants were faster explorers than locally born birds and that fast-exploring parents had offspring that dispersed furthest (*chapter 4*) is in agreement with the observation that fast explorers are ill-adapted to cope with social stress (Verbeek 1998; Carere et al. 2001) and consequently lose competition over resources that can be monopolized. Juvenile fast explorers may thus make the-best-of-bad-situation and disperse to avoid areas where they are outcompeted by others (Clobert et al. 2001). Laboratory experiments indicate that fast explorers gain low ranks because they are physically forced to stay in social groups and therefore unable to flee and recover when facing social defeat (Verbeek 1998). In the wild, juvenile fast explorers may escape their inability to cope with social stress if they can resort to sites where they can dominate others, for instance if they succeeded in occupying a territory. In agreement with this expectation, we found that the relation between dominance and exploratory behaviour was state-dependent: fast explorers had lowest ranks in non-territorial birds but highest ranks in territorial birds (*chapter 3*). This state-dependent relation between dominance and personality implies that fast explorers would benefit from early settlement. If, therefore, non-territorial fast explorers actively search a larger area for potential vacancies than slow explorers in order to settle as early as possible, this could result in larger dispersal distances (*chapter 4*), early settlement, and higher dominance ranks in winter when successful (*chapter 3*). Hence, investment in early settlement could allow fast explorers to avoid social environments where they perform poorly (Wilson & Yoshimura 1994; Zhivotovsky et al. 1996). Nevertheless, the pay-off of such behavioural strategy is likely to depend both on the number of conspecifics, the number of vacant territories during autumn (Drent 1983; Tinbergen et al. 1987), and the frequency with which other individuals employ different settlement strategies (Maynard Smith 1982; Kokko & Lundberg 2001).

## FITNESS AND AVIAN PERSONALITY

We measured the fitness consequences of avian personality by analysing the relation between exploratory behaviour and production and quality of offspring (*chapter 5*), numbers of offspring that survived and recruited into the breeding population (*chapter 6*), and annual adult survival (*chapter 6*).

### *Production and quality of offspring*

In *chapter 5* we show that parental exploratory behaviour does not explain variation in laying date, clutch size, or fledgling number but does explain part of the variation in nest success and offspring condition. Slow-exploring females were more likely to produce at least one fledgling and also produced larger fledglings. Thus, female exploratory behaviour appeared to affect breeding performance during the early chick-feeding phase because size at fledging (i.e. tarsus length) is largely determined by feeding conditions in the first week after hatching (see Keller & van Noordwijk 1994). For pairs that produced at least one fledgling, the number of fledged offspring was not related to male or female personality but fledgling condition was: both male and female exploratory behaviour affected fledgling condition, with slow-slow and fast-fast pairs producing offspring in best condition (i.e. offspring with high body mass).

Fast-exploring males bred in territories of higher than average quality (*chapter 5*). Hence, both variation in quality of the foraging habitat within the territory and parental quality may explain why reproductive performance correlated with parental personality (see Both & Visser 2000). Slow-exploring birds are well-adapted to forage under changing feeding conditions because they respond more quickly to changes in food distribution and continuously explore alternative feeding options (Verbeek et al. 1994) – essential during the chick-feeding phase when great tits forage on mobile and hidden prey. Slow explorers may therefore be better parents, explaining both why slow-exploring mothers were more likely to produce (larger) fledglings and why slow pairs produced offspring in good condition despite the fact that slow males bred in territories of lower than average quality. Because fast-exploring birds are more routine-like in their foraging behaviour, they may only produce high quality offspring in territories where food is abundant and easily found. Thus, fast-fast pairs may in part have produced high quality offspring because fast-exploring males have high quality territories. Interestingly, despite their high quality territories fast-exploring males nevertheless produced offspring in poor condition unless they had a fast-exploring mate. This effect of pair composition may reflect a frequency-dependent benefit of some behavioural component of avian personality. For instance, fast-exploring birds copy successful foraging strategies of others (Marchetti & Drent 2000), hence high quality territories may be particularly suitable for pairs that both display such social learning (i.e. fast-fast pairs). Similarly, low quality territories with less predictable food supplies may be particularly suitable for pairs that do not copy each others foraging habits (i.e. slow-slow pairs).

### *Offspring survival and recruitment*

We were unable to quantify selection on individual exploratory behaviour during the first year of life, because we could not measure exploratory behaviour between hatching and independence (*chapter 2*). The results presented in *chapters 5* and *6* nevertheless suggest that in some years there was stabilising viability selection on this personality trait in the juvenile phase. The substantial heritability of exploratory behaviour (*chapter 2*), allows us to approach selection on juvenile phenotypes by comparing offspring production (*chapter 5*) and offspring recruitment (*chapter 6*) in relation to parental exploratory behaviour. The number of fledglings produced did not relate to parental behaviour but the number of recruiting offspring did, indicating that

natural selection during the juvenile phase acted between fledging and first breeding. Because slow-slow and fast-fast pairs produced fledglings of higher body condition than other pair combinations (*chapter 5*) and in one year with abundant winter food (2000) they also produced more recruits (*chapter 6*), selection on exploratory behaviour during the juvenile phase probably acted indirectly via fledgling condition rather directly on exploratory behaviour of the juveniles in years with rich winters. In beech masting years, both juvenile and adult survival is high (van Balen 1980; Perdeck et al. 2000), resulting in increased competition among juveniles for territory space (Drent 1983). Because selection on fledgling mass increases with increasing density (Both et al. 1999), heavy offspring are likely to survive better not because mass affects survival in adverse conditions (Perrins 1965) but rather because mass is an indicator of competitive ability (Both et al. 1999). Thus, selection favours offspring that can outcompete others (i.e. those in good condition) in winters with abundant winter food, explaining why assortative pairs of extreme phenotype had highest offspring recruitment in 2000 (*chapter 6*). In the two years that lacked abundant winter food, however, medium-exploring parents produced more recruits, despite the fact that slow-slow and fast-fast pairs produced fledglings in better condition, suggesting that in these years selection mainly acted on offspring personality rather than on offspring condition. It is however unlikely that the stabilizing selection on personality during the juvenile phase in the two years with poor winters (*chapter 6*) also resulted from individual variation in competitive ability mediated via fledgling condition, because medium-exploring parents do not produce offspring in good condition (*chapter 5*) but also because medium-exploring juveniles do not have highest dominance ranks in winter (*chapter 4*). Selection may favour offspring of medium-exploring parents after fledging because factors other than competitive ability largely determine juvenile survival. Studies on humans show that children at the extremes of the behavioural distribution of the shyness-boldness axis are less variable than those in the middle (Kagan et al. 1988). Therefore, an interesting possibility is that unlike the extreme phenotypes medium-exploring birds are more flexible in their behaviour (e.g. during foraging they may choose to either stick to routines like fast explorers or continuously search for alternative feeding options like slow explorers), and that natural selection favours more flexible instead of stable phenotypes under certain environmental conditions (Wilson et al. 1994). If so, juvenile medium-exploring birds may better survive in years when food supplies are low and variable in space and time, causing increased juvenile mortality. In that case medium-exploring parents may have highest offspring survival unless conditions in winter causes severe competition among juveniles (e.g. for space or partners). Studies on phenotype-limited variability in behaviour are however largely lacking, in part because laboratory studies usually focus on the extremes of the behavioural distribution (e.g. slow versus fast; Verbeek et al. 1994; active versus passive copers; Koolhaas et al. 1999).

Although dominance (*chapter 3*) and dispersal patterns (*chapter 4*) indicated that exploratory behaviour negatively affected competitive ability in juveniles, we have no evidence for a negative relation between juvenile survival and exploratory behaviour. These apparently contradicting results may reflect that fast explorers are (a) successful in avoiding social environments where they perform poorly or (b) well-adapted to new circumstances (i.e. successful dispersers; Fraser et al. 2001).



### *Adult survival*

In *chapter 6* we show that selection on personality in adults fluctuated between years. For adult males, survival between breeding seasons was positively related to exploratory behaviour in a beech masting year ('rich winter') when both juveniles and adults survive well, competition for food is low, and competition for territories is high (van Balen 1980; Perdeck et al. 2000), but this effect reversed in years without abundant beech crop ('poor winters'). For adult females survival was negatively related to exploratory behaviour in rich years, but positively in poor years. The consequences of beech masting are likely to differ between the sexes, which could explain why in each year viability selection differed between the sexes (*chapter 6*): because females are subordinate to males (*chapter 3*) we expect them to be most affected by competition for food while males are most affected by competition for territory space. Thus, in both sexes, fast-exploring adults may benefit from their aggressiveness (Verbeek et al. 1996; Drent & Marchetti 1999) and dominance (*chapter 3*) and survive well in highly competitive situations while slow explorers do not have to pay the costs associated with aggressiveness and therefore survive well when competition is relaxed.

### *Age specificity*

The competitive regime outside the breeding season appeared to differentially affect selection on adults and juveniles. While in adults fast-exploring birds may survive better in highly competitive situations and slow-exploring birds survive better when competition is relaxed (*chapter 6*), juveniles birds in good condition may survive better in highly competitive situations and medium-exploring birds survive better when competition is relaxed (see above). These different survival patterns for juveniles and adults are likely to result from age-specific differences in foraging success, risk of predation, competitive ability, dominance in winter flocks, and territorial status.

We observed disassortative pairing for personality when looking at the partners of adult males but not when considering the partners of juvenile males (*chapter 6*). This disassortative pairing seems inappropriate in beech crop years, because in those years assortative pairs of extreme phenotype produced most recruits (*chapter 6*). Two hypotheses can explain this finding. First, disassortative pairing is not adaptive but a by-product of the strong directional selection on adult survival that was opposite for males and females. While in juveniles there may be random mating for personality, the observed opposing viability selection on adults can result in disassortative pairs in older birds, because pairs of great tits usually stay together. Second, disassortative mating may result from adaptive mate choice, if intermediate phenotypes have highest fitness. Support for this is found in the finding that selection favoured the extreme types with respect to adult survival in any year-sex combination. Hence, the multiplicative effect of this survival selection, together with the regularly occurring stabilising selection on offspring recruitment, may result in highest overall fitness of medium-exploring individuals in this population. Disassortative mating may thus allow adults to increase their lifetime fitness. Because at the time of mate choice birds cannot predict the occurrence of beech masting (Perdeck et al. 2000), and medium-exploring birds have highest fitness in the long term, the best strategy is to pair with a mate of as opposite phenotype as possible. Because females compete

among themselves for males with territories of high quality, juvenile males may not acquire the mate best suited to their personality. Direct mate choice experiments are needed to test whether these mating patterns reflected adaptive mate choice for personality.

## EVOLUTIONARY ISSUES

Because exploratory behaviour of wild great tits is heritable (*chapter 2 and 6*) and affects components of fitness (*chapter 5 and 6*), selection on exploratory behaviour can lead to evolutionary change (Fisher 1930; Endler 1980). In our study population, selection on exploratory behaviour varied between adult males and females, age-classes, and years with different selective regimes. On the basis of the observed fitness patterns we expected that medium-exploring birds had highest overall fitness in this population (*chapter 6*; see above). These results have two important implications. First, it poses the question of how genetic variation in personality, as shown in the laboratory (Drent et al. 2003) and the wild (*this thesis*), is maintained. Second, and more importantly, our results imply that the population composition (i.e. population mean and variation) of alternative heritable phenotypes is likely to vary in space (e.g. between populations) and time (e.g. within populations; *this thesis*), and both within and between species, because selection on personality depends both on the environment, life history, and the ecology of the species (Greenberg & Mettke-Hofmann 2001).

### *Genetic variability within and across populations*

Both genetic and ecological theories explain why genetic variation in quantitative traits persists in natural populations and both are needed to understand the amount of genetic variation. First, genetic theories explain genetic variation by a balance between mutation and selection or between mutation and drift (e.g. Lande 1975; Roff 1997). In large and continuous populations, mutation can result in high additive genetic variance for traits that are affected by several loci of small effect (Lynch & Walsh 1998), like personality traits (see Bouchard & Loehlin 2001; van Oers 2003). Second, ecological theories explain genetic variation by spatiotemporal variation in selection pressures (Foster & Endler 1999; Mousseau et al. 2000). In species with overlapping generations that vary in numbers (e.g. birds and mammals), temporal variation in selection pressures can allow high levels of genetic variation (Sasaki & Ellner 1997) over and above variation caused by ongoing mutation (Burger & Gimelfarb 2002). Hence, the regularly occurring variation in competitive regimes that resulted in temporal variation in selection pressures (*chapter 6*) is likely to maintain genetic variation at higher levels – or deplete genetic variation at a lower rate – than expected from a situation where the environment is constant. Migration between habitats or populations that differ in selective regime (i.e. spatial variation in selection) also allow high levels of genetic variability (Via & Lande 1985, 1987). We have some evidence for variation in the frequency distribution of exploratory behaviour between years in the same population and between populations in the same year, based on behavioural differences of both wild-caught adult great tits and their nestlings that were raised in a common environment (Dingemanse & van Oers, In Preparation). Because those populations differed both in habitat and breeding density

(i.e. birds were faster in the population with high densities), both spatial and temporal variation in selective pressures may allow high levels of genetic variation in great tit personality. Thus, genetic variation in personality within and between populations may be adaptive (Foster & Endler 1999; Mousseau et al. 2000), resulting from spatiotemporal variation in selection. Hence, populations or species that differ in ecological conditions may not only differ in average personality, as shown for fish (Huntingford et al. 1994), songbirds (Greenberg 1999) and parrots (Mettke-Hofmann et al. 2002), but also in the amount of variation at population level (i.e. the trait frequency distribution).

### *Personality in an ecological context*

In parrots, interspecific comparison showed that differences in exploratory behaviour, measured as latency to explore novel objects, were related to differences in ecological factors at the species level (Mettke-Hofmann et al. 2002). Fast-exploring parrot species inhabited rich environments with high interspecific competition, i.e. environments that pose selection on short latencies to explore food sources. Furthermore, island species were more explorative and curious than mainland species, consistent with the idea that inherent costs of exploration (e.g. risk of injury or predation) were lower on islands because they lacked predators. These behavioural observations, that were based on birds that were kept in zoos for several generations, suggest that the relation between ecological factors and interspecific variation in exploratory behaviour were caused by differential selection on a heritable trait (Mettke-Hofmann et al. 2002). Such comparisons of different species or different populations within a species (e.g. Huntingford et al. 1994) can reveal the key elements of the environments that pose selection on personality traits.

Based on our knowledge about the consequences of avian personality for foraging strategies (Verbeek et al. 1994; Drent & Marchetti 1999; Marchetti & Drent 2000) competitive ability (Verbeek et al. 1996, 1999; Drent & Marchetti 1999), and its fitness consequences under different environmental conditions (*this thesis*), one can formulate hypotheses regarding the evolution of behavioural strategies towards novel or challenging situations under different environmental or ecological conditions, that can later be tested by experimental manipulation or comparative approaches.

Selection on exploratory behaviour is likely to relate both to the physical and social environment because exploratory behaviour covaries with foraging strategy and social learning. Fast explorers are routine-like in their foraging behaviour and readily copy successful foraging strategies of others, while slow explorers respond more quickly to changes in food distribution, continuously exploring alternative feeding options, and avoid foraging strategies used by others (Verbeek et al. 1994; Drent & Marchetti 1999; Marchetti & Drent 2000). Therefore, selection on exploratory behaviour is likely to depend on the distribution (i.e. clumped versus scattered) and predictability of food, further depending on whether animals forage alone or in social groups, and whether animals cooperate or compete during foraging.

When food is rich in supply, clumped and/or predictable (a) selection on solitary foragers may favour fast explorers because they are routine-like in their foraging behaviour, (b) selection on animals that compete for food in social groups may favour fast explorers because they are aggressive, dominant, and obtain food by scrounging, and (c) selection on birds that cooperate during foraging (e.g. in systems

with bi-parental care) may favour fast explorers because their social learning allows them to quickly find food that is suited for routine-like exploitation. When food availability is low, scattered, and less predictable (a) selection on solitary foragers may favour slow explorers because they quickly respond to changes in food distribution, (b) selection on animals that search and compete for food in social groups may favour a mix of behavioural strategies because the pay-off of scrounging (i.e. fast explorers) and producing (i.e. slow explorers) is frequency dependent (Barnard & Sibly 1981), and (c) selection on animals that cooperate during foraging may favour slow explorers because social learning (i.e. copying) does not increase but rather decrease foraging success in such environments. Thus, the combination of certain social and physical environments likely results in either directional, positive frequency dependent selection, or negative frequency dependent selection, either depleting or maintaining genetic variation (Maynard Smith 1982).

In species that defend territories, selection on exploratory behaviour is likely to vary with territorial status and the density of conspecific competitors. When competition for space is severe, (a) selection may favour fast explorers in territorial species, because they can maintain their territories through their aggressiveness (see Chitty 1967; see Krebs 1978) with new settlements occurring at the expense of territorial slow explorers, however (b) selection may favour non-territorial slow explorers because their ability to cope with social stress – resulting in high dominance ranks prior to settlement – may allow them to become locally dominant despite constant harassment of and defeat by territorial animals. When competition for space is relaxed, selection may favour slow explorers, because the benefits of aggressiveness in such environments may not outweigh the costs, although the aggressiveness of non-territorial fast explorers may allow them to settle among territorial slow explorers.

In summary, the interplay of frequency and density dependent processes is likely to either the maintenance or depletion of genetic variation in personality (Wilson et al. 1994). In addition, selection on exploratory behaviour may favour medium-exploring animals in variable environments if they are indeed more flexible in their behaviour, but favour individuals at the extremes of the behavioural distribution in stable environments (Wilson et al. 1994; DeWitt et al. 1998).

### *Selection on correlated behaviour*

Great tits personalities consist of suites of genetically correlated behavioural traits: exploratory behaviour, boldness, foraging behaviour, risk-taking and aggressiveness are all covarying (Verbeek et al. 1994, 1996; Drent & Marchetti 1999; van Oers In Press) and genetically correlated (van Oers 2003). Although we only measured behaviour in novel environments for our wild great tits, the relation between fitness and exploratory behaviour may have reflected selection on other traits that are part of the behavioural syndrome (Lande & Arnold 1983), such as aggressiveness or foraging behaviour. Certain aspects of their foraging behaviour may allow slow-exploring birds to produce offspring in good condition (*chapter 5*), while the aggressiveness of fast-exploring adults may allow them to survive well in highly competitive environments (*chapter 6*). Hence, our ability to predict how selection will act on personality in other study systems will largely depend on knowledge about the species' life history and knowledge about how various behavioural traits are correlated. For instance, the absence of a relationship between boldness and

dominance in wild bighorn ewes *Ovis canadensis* (Réale et al. 2000) may reflect that boldness in this species is not genetically correlated with aggressiveness or ability to cope with social stress. Unlike in great tits (*chapter 6*), in bighorn sheep selection on boldness may therefore not vary with competitive regime. Field studies on pumpkinseed sunfish moreover showed that although behavioural components underlying animal personality (i.e. boldness, exploration, foraging) differ between individuals, the behavioural components were not correlated (Coleman & Wilson 1998). From an evolutionary perspective, selection may or may not favour certain combinations of personality traits (Wilson 1998) that are usually assumed to be inherently correlated (Kagan et al. 1988). Thus, because in some species animal personality may be context-specific (Wilson et al. 1994) rather than domain-general (Kagan et al. 1988), caution is needed to extrapolate our results to other species. Nevertheless, behavioural responses towards novel or challenging situations covary in the same way in many species of mammal, bird, and fish (e.g. Huntingford 1976; Koolhaas et al. 2001; Greenberg & Mettke-Hofmann 2001), implying that the same environmental conditions may result in qualitatively similar selective pressures in different species. More fitness and comparative studies are clearly needed to understand the adaptive aspects of variation in animal personality in the wild. Nevertheless, one can already predict that fast explorers do well when food is clumped and risk of losing fights is low, and more variation in behaviour is expected in more variable environments. It seems that the intra-individual variation in behaviour is limited and therefore variable environments allow the coexistence of alternative phenotypes.



## **Chapter 8**

### **SAMENVATTING**

### Individueel gedrag in een evolutionaire context

In een groot aantal gewervelden (apen, knaagdieren, vissen, vogels) en ongewervelden (insecten, octopi) verschillen individuen consistent in hun gedrag wanneer ze geconfronteerd worden met nieuwe of stressvolle situaties. Vergelijkbaar met persoonlijkheidsverschillen bij mensen zijn sommige dieren agressief en assertief, terwijl andere dieren juist minder agressief en verlegen of terughoudend zijn. Deze individuele verschillen in gedrag zijn voor een belangrijk deel genetisch bepaald: bij mensen, apen, knaagdieren en vogels kan zo'n veertig tot zeventig procent van de variatie in gedrag tussen individuen verklaard worden door genetische verschillen.

Vanuit een evolutionair perspectief is goed te begrijpen waarom er gedragsverschillen bestaan tussen verschillende soorten of tussen verschillende populaties van dezelfde soort: evolutie door natuurlijke selectie leidt tot organismen die aangepast zijn aan hun specifieke leefomgeving. Maar ook individuen uit dezelfde populatie blijken consistent te verschillen in hun gedrag. Deze gedragsverschillen zijn op het eerste gezicht minder makkelijk te begrijpen: als een bepaald gedragstype net iets langer leeft en/of meer nakomelingen nalaat dan een ander gedragstype (een hogere 'fitness' heeft), dan zullen de genen van dit type in volgende generaties in frequentie toenemen. Hierdoor neemt de genetische variatie in dit kenmerk af in volgende generaties. In een weinig veranderlijke leefomgeving zal daarom gemiddeld genomen alleen het gedragstype wat tot de hoogste fitness leidt behouden blijven.

Onderzoek aan persoonlijkheidskenmerken bij dieren heeft zich tot op heden vooral gericht op de genetische achtergrond en de invloed van de omgeving op de ontwikkeling van de individuele persoonlijkheid, waarbij doorgaans onderzoek gedaan is aan gedomesticeerde diersoorten (paarden, ratten, muizen, varkens). Hoewel persoonlijkheidsverschillen dus in een groot aantal diersoorten zijn beschreven, is nog maar heel weinig bekend over *waarom* dieren verschillen in karakter en *hoe* deze individuele variatie in gedrag in het wild behouden blijft. Hiervoor is het niet alleen van belang om te weten hoe persoonlijkheidskenmerken zich ontwikkelen onder invloed van genen en omgeving, maar ook om de consequenties van het resulterende gedrag voor de fitness van het individu onder verschillende leefomstandigheden te onderzoeken. Alleen dan is het mogelijk om te begrijpen onder welke condities individuele variatie kan worden behouden.

Een mogelijke verklaring voor het voortbestaan van variatie in gedragskenmerken binnen populaties ligt in de variabiliteit van de leefomgeving (in tijd of ruimte). Wanneer bepaalde gedragstypen onder bepaalde (sociale of fysieke) omstandigheden een hogere fitness hebben en andere typen juist in andere omstandigheden, dan zouden verschillende gedragstypes naast elkaar kunnen voortbestaan. De fitnessconsequenties van persoonlijkheidskenmerken zijn echter vrijwel onbekend, gedeeltelijk omdat maar weinig studiesoorten geschikt zijn voor het meten van zowel individueel gedrag als fitness onder natuurlijke omstandigheden. De processen die verantwoordelijk zijn voor de instandhouding van variatie in gedrag binnen natuurlijke populaties zijn derhalve grotendeels onbekend. Dit proefschrift beschrijft de resultaten van een veldstudie aan een persoonlijkheidskenmerk in een wilde bosvogel, de koolmees *Parus major*, waarbij onderzocht is of (a) wilde mezen ook verschillen in hun persoonlijkheid en in welke mate de persoonlijkheid bepaald wordt door genetische en omgevingsfactoren, (b) wat de consequenties zijn van persoonlijkheid voor de fitness van het individu, en (c) of de fitnessconsequenties afhankelijk zijn van de leefomgeving waarin natuurlijke selectie optreedt.



### Persoonlijkheidsverschillen in koolmezen

In een laboratoriumstudie aan in gevangenschap opgegroeide koolmezen werd gevonden dat koolmezen consistent verschillen in hun gedrag wanneer ze geconfronteerd worden met een onbekende omgeving, object, of soortgenoot (Verbeek 1998). Wanneer de mezen geïntroduceerd werden in een 'vreemde ruimte' (een kamer met 5 bomen) reageerden ze heel verschillend: sommige dieren vlogen snel van boom tot boom, terwijl andere dieren zich veel langzamer door de ruimte verplaatsten. Snelle verkenners waren ook snel in het benaderen van nieuwe objecten in het kooitje waarin ze gehouden werden, waren meer routinematig in hun voedselzoekgedrag en waren relatief agressief naar andere koolmezen. Deze verschillen in 'persoonlijkheid' of 'temperament' (correlaties tussen verschillende gedragingen) waren niet simpelweg het gevolg van verschillen in activiteit of lichaamsconditie. De verschillen tussen de mezen verdwenen namelijk wanneer ze herhaaldelijk werden blootgesteld aan dezelfde stimulus, wat aangeeft dat de mezen verschillen in hun reactie op nieuwe of uitdagende situaties, en niet op de situatie *per se*. Kruisingsexperimenten in het laboratorium, waarbij gebroed werd met de meest extreme dieren ('snel' met 'snel', en 'langzaam' met 'langzaam') en waarbij vervolgens het gedrag van ouders met dat van hun nakomelingen werd vergeleken, toonden aan dat persoonlijkheidsverschillen bij koolmezen voor een groot deel overerven van ouders op kinderen (Drent et al. 2003). Het NWO-programma waar dit onderzoek deel van uitmaakt en waarin zowel de genetische structuur, de ontogenie, en de fitnessconsequenties van persoonlijkheden bij koolmezen werden onderzocht was een logisch vervolg op deze bevindingen.

### Persoonlijkheidsverschillen in wilde koolmezen?

Een eerste stap in het meten van de fitnessconsequenties van persoonlijkheidskenmerken is het meten van individueel gedrag van wilde dieren. De gedragsstudies aan de koolmezen in gevangenschap (zie boven) lieten al zien dat verschillende gedragskenmerken sterk met elkaar correleren. Hierdoor kan men de 'persoonlijkheid' van koolmezen aan de hand van één enkel gedragskenmerk meten. Tijdens het veldonderzoek maten we daarom aan de hand van het exploratiegedrag de 'persoonlijkheid' van de wilde koolmezen (1342 individuen van 1998 tot 2003). Hierbij werd gequantificeerd hoe snel gevangen mezen een 'vreemde ruimte' in het laboratorium in Heteren verkenden (zie figuur 1 op bladzijde 22). Hierna werden de dieren individueel gemerkt (geringd met zowel een aluminium ring met een uniek nummer als met een unieke kleurringcombinatie) en weer losgelaten in het veld. Om te controleren of wilde koolmezen ook consistent van elkaar verschillen in hun gedrag werden teruggelaten koolmezen voor een tweede maal naar het laboratorium gebracht en nogmaals aan dezelfde gedragstest onderworpen (*hoofdstuk 2*). Wilde koolmezen bleken inderdaad consistent van elkaar te verschillen: het exploratiegedrag in de eerste test correleerde met dat in de tweede. Exploratiedrag verschilde niet tussen mannen en vrouwen, hing niet samen met leeftijd van het dier, en was niet gecorreleerd aan lichaamsconditie. Het gedrag van koolmezen kon wel voorspeld worden aan de hand van het gedrag van hun ouders, hetgeen zowel aangeeft dat exploratiegedrag van wilde mezen een genetische basis heeft en dat er bij wilde koolmezen genetische variatie bestaat in dit gedragskenmerk.

Het kunnen aantonen van consistente en overerfbare verschillen in gedrag van wilde koolmezen vormde de basis voor het resterende onderzoek beschreven in dit proefschrift. De volgende secties beschrijven de relatie tussen exploratiegedrag in de vreemde ruimte en kenmerken die de fitness van het individu beïnvloeden.

### **Dominantie en dispersie**

Verschillen in overleving (zie verderop) zouden wel eens samen kunnen hangen met dominantiestatus van het individu. Met dit idee in het achterhoofd onderzochten we de relatie tussen individuele persoonlijkheid en dominantie in het veld. Hiertoe observeerden we agressief gedrag op voedertafels in de winter. Juveniele snelle exploreerders bleken daar de laagste dominantiepositie te hebben (*hoofdstuk 3*). Dit gold echter alleen voor juveniele vogels zonder territorium: territoriale snelle koolmezen hadden juist de hoogste dominantie posities. Eerder werk aan koolmezen in gevangenschap gaf ook al aan dat hoewel snelle koolmezen agressiever zijn, ze waarschijnlijk lager in de hiërarchie eindigen omdat ze slecht kunnen omgaan met sociale stress. ‘Lefgozers’ zijn slechte verliezers, vooral wanneer ze niet kunnen ontsnappen aan het leven in sociale groepen (Verbeek 1998). In overeenstemming met deze observatie vonden we dat nakomelingen van snelle ouders verder van huis tot broeden kwamen, en dat immigranten de vreemde ruimte sneller verkenden dan lokaal uitgevlogen mezen (*hoofdstuk 4*). Snelle koolmezen worden dus waarschijnlijk gedwongen om het gebied te verlaten wanneer er veel competitie om voedsel of ruimte optreedt, omdat dominante (vaak adulte) dieren deze bronnen kunnen monopoliseren. Als snelle koolmezen alleen hoge dominantieposities kunnen krijgen wanneer ze een territorium bezitten, is het juist voor deze dieren belangrijk om zich zo vroeg mogelijk na het uitvliegen te vestigen. Verschillen in vestigingsstrategie zouden dus ook kunnen verklaren waarom snelle mezen verder van huis broeden dan langzame mezen. Op deze manier kunnen snelle koolmezen misschien sociale omgevingen waarin ze slecht functioneren vermijden .

### **Fitnessconsequenties van persoonlijkheden**

#### *Aantallen en conditie van nakomelingen*

In *hoofdstuk 5* onderzochten we de relatie tussen persoonlijkheid en broedsucces. Exploratiegedrag van koolmezen was niet van invloed op de legdatum, het aantal geproduceerde eieren, of het aantal uitgevlogen nakomelingen. Exploratiegedrag van broedende koolmezen hing wel samen met de kans om überhaupt uitgevlogen jongen te produceren en ook met het gewicht van de jongen op het moment dat ze het nest verlaten (‘uitvlieggewicht’). Langzame vrouwen produceerden vaker ten minste één uitgevlogen nakomeling, en produceerden tevens grotere nakomelingen. Het uitvlieggewicht van de nakomelingen – een goede voorspeller van de overlevingskans van koolmezen in hun eerste winter – hing samen met de persoonlijkheid van beide ouders. Paren waarin beide ouders van hetzelfde gedragstype waren produceerden zwaardere jongen dan andere oudercombinaties. Daarbij broedden snelle mannen in territoria van hogere kwaliteit dan andere type mannen (*hoofdstuk 5*; het relatieve

broedsucces en uitvlieggewicht van de bezette nestkast in andere jaren werd gebruikt als een maat voor de kwaliteit van het territorium).

De relatie tussen de persoonlijkheid van beide ouders en het uitvlieggewicht van hun nakomelingen kan samenhangen met het combinatie van oudertypes *per se*, de kwaliteit van het broedterritorium, of met beide factoren. De gedragsstudies aan koolmezen in gevangenschap gaven aan dat langzame mezen beter zijn aangepast aan het vinden van voedsel in een veranderlijke omgeving, omdat zij snel reageren op veranderingen in de verspreiding van voedselbronnen en continu alternatieve opties in de gaten houden. Dit is essentieel tijdens het voederen van nestjongen, omdat de overleving van nestjongen vooral afhangt van de hoeveelheid en kwaliteit van het voedsel aangeleverd door de ouders. Het is daarom goed mogelijk dat langzame koolmezen betere ouders zijn. Dit kan verklaren waarom langzame vrouwen een grotere kans hadden om tenminste één uitgevlogen nakomeling te produceren en waarom juist zij grotere nakomelingen hadden. Het gedrag van langzame dieren zou tevens kunnen verklaren waarom langzame vrouwen zwaardere jonge produceren met een langzame man ondanks het slechte territorium dat deze mannen bezetten. Langzame dieren zijn minder geneigd fourageergedrag van andere dieren te kopiëren. Mogelijk hierdoor zijn paren van langzame dieren goed in staat een territorium van lage kwaliteit optimaal te benutten. Snelle dieren ontwikkelen daarentegen eerder routines wanneer ze zoeken naar voedsel en kunnen daarom efficiënt voedselbronnen uitputten. Dit gedrag is waarschijnlijk een voordeel in territoria waar veel voedsel aanwezig is of waar het voedsel makkelijk te vinden is, wat kan verklaren waarom ook snelle paren zware jongen produceerden.

Ouderparen met een tegenovergesteld karakter waren minder succesvol in het produceren van zware nakomelingen: langzame vrouwen gepaard met snelle mannen produceerden lichtere jongen ook al bezetten juist deze mannen territoria van bovengemiddelde kwaliteit. Mogelijk zijn bepaalde type territoria vooral geschikt voor bepaalde combinaties van gedragstypes: een langzame vrouw die broedt met een snelle man in een bovengemiddeld territorium verliest wellicht kostbare tijd aan het verkennen van alternatieve voedselbronnen, terwijl een snelle vrouw in een slecht territorium van een langzame man juist niet voldoende voedselbronnen kan vinden om de groei van haar jongen te garanderen.

#### *Adulte overleving en recruterings van nakomelingen*

De consequenties van individueel gedrag op de overleving en voortplanting werden onderzocht door respectievelijk het vangen en terugvangen van 'geteste' koolmezen, en het tellen van het aantal nakomelingen wat zich vestigde in de broedpopulatie (zogenaamde 'recruten'; *hoofdstuk 6*). In de periode van 1999 tot 2002 werden sterke effecten van persoonlijkheid gevonden op de overleving van adulte koolmezen. Selectie op persoonlijkheid van adulte mezen veranderde van jaar tot jaar, en verschilde elk jaar tussen mannen en vrouwen. In de twee jaren dat er weinig wintervoedsel in het gebied aanwezig was (lage 'beukennoten index', 1999 en 2001) overleefden snelle vrouwen en langzame mannen beter. In het jaar met veel wintervoedsel (hoge beukennoten index, 2000) was het precies omgekeerd: langzame vrouwen en snelle mannen overleefden beter.

Ook het aantal nakomelingen wat in de populatie tot broeden kwam was gerelateerd aan de persoonlijkheid van de ouders. In de magere jaren recruteerden meer nakomelingen van 'intermediare' ouders in de broedpopulatie, terwijl in het

beukennotenjaar juist de nakomelingen van de meer extreme gedragstypes (= uiterst langzame of snelle ouders) in de populatie tot broeden kwamen.

In het beukennotenjaar werd ook een effect van de paarcombinatie gevonden. We vonden meer nakomelingen van paren waarvan beide partners extreem snel of extreem langzaam waren terug als broedvogel. Omdat juist deze paarcombinaties ook zware nakomelingen produceerden (*hoofdstuk 5*) en in jaren met veel competitie zware nakomelingen beter overleven (Both et al. 1999), denken we dat de snelle en langzame paren in het beukennotenjaar de meeste recruten produceerden omdat in dit jaar zware juvenielen de winter beter overleefden. Hoewel deze paarcombinaties ook in andere jaren relatief zware jongen produceren vonden we in jaren met weinig beukennoten juist minder nakomelingen van deze vogels terug in de broedpopulatie. Dit resultaat geeft aan dat in sommige jaren de winteroverleving van juveniele mezen samenhangt met hun uitvlieggewicht, en in andere jaren waarschijnlijk meer met hun exploratiegedrag.

### Natuurlijke selectie in een veranderlijke omgeving

De fitness studies (*hoofdstukken 5 en 6*) geven aan dat er in het wild sterke selectie optreedt op persoonlijkheid van koolmezen. Selectiedrukken verschillen zowel tussen mannen en vrouwen als tussen verschillende fitnesscomponenten (de overleving van adulten versus de productie van recruten). Deze resultaten roepen de vraag op wat de ecologische achtergrond van deze variërende selectie is. Omdat de veranderingen in selectiedruk samenvielen met de aanwezigheid van wintervoedsel, wordt vermoed dat deze ecologische cyclus ten grondslag ligt aan de jaarlijkse veranderingen in selectie op persoonlijkheden in koolmezen. In zogenaamde ‘mastjaren’, jaren met uitzonderlijk veel beukennoten, ervaren de koolmezen minder competitie om wintervoedsel. In dit soort jaren overleeft een groter deel van de mezen en komen vervolgens meer mezen tot broeden, hetgeen leidt tot meer competitie om territoriale ruimte in het voorjaar. Verwacht kan worden dat het effect van beukennotenooft in territoriale koolmezen verschilt tussen mannen en vrouwen. Omdat mannen dominant zijn over vrouwen zal er bij vrouwen vooral competitie optreden om voedsel, maar bij mannen juist om ruimte (territoria). Als dit het geval is, overleefden de snelle mannen wellicht beter in jaren met veel competitie om territoria (2000) omdat zij agressiever en dominantier zijn (*hoofdstuk 3*), terwijl hun agressie vooral kosten met zich meebrengt in jaren met weinig competitie om territoria. Overeenkomstig overleefden snelle vrouwen wellicht beter in jaren met veel competitie om wintervoedsel (1999, 2001), maar juist slechter in jaren waarin agressie voornamelijk nadelig is.

Bepaalde type persoonlijkheden werden vaker samen broedend aangetroffen dan andere (*hoofdstuk 6*). Snelle mannen waren vaker gepaard met langzame vrouwen en langzame mannen met snelle vrouwen dan verwacht op basis van toeval. Deze ‘disassortatief’ gepaarde dieren produceren waarschijnlijk nakomelingen van een intermediair gedragstype, omdat exploratiegedrag gedeeltelijk genetisch bepaald is (zie *hoofdstuk 2*). Op basis van de fitnessgegevens (*hoofdstuk 6*) is aannemelijk te maken dat deze paarkeuze best eens ‘adaptief’ zou kunnen zijn, dus leidt tot een hogere fitness, en wel om twee redenen: (a) hoewel bij zowel adulte mannen als vrouwen de extreme gedragstypes van jaar tot jaar beter overleven, wordt verwacht dat intermediaire adulten al met al langer leven omdat hun jaarlijkse overlevingskans minder varieert; en (b) in jaren zonder beukennoten, die frequenter voorkomen dan

beukennotenmastjaren, produceren intermediare vrouwen meer recruten. Door met een heel verschillend type partner te paren kunnen de mezen dus nakomelingen produceren die langer leven dan gemiddeld en tevens meer kleinkinderen produceren.

Variërende selectiedrukken kunnen in belangrijke mate bijdragen aan het behoud van genetische variatie in natuurlijke populaties. Hoewel dit veldonderzoek aantoont dat natuurlijke selectie op de persoonlijkheid van koolmezen inderdaad fluctueert, vermoeden we tegelijkertijd dat intermediare gedragstypes al met al de hoogste fitness hebben (zie boven). Als dit zo is zal de beschreven fluctuerende selectie de erosie van genetische variatie kunnen vertragen, maar mogelijk niet bijdragen aan het behoud van genetische variatie in dit persoonlijkheidskenmerk. Deze bevindingen geven daarentegen tegelijkertijd aan dat de samenstelling van populaties waarschijnlijk varieert in zowel tijd (tussen jaren binnen populaties) als ruimte (tussen (sub)populaties binnen jaren) in afhankelijkheid van de omgeving.



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# **DANKWOORD**

Veel mensen hebben op zeer uiteenlopende wijze bijgedragen aan de totstandkoming van dit proefschrift, hetzij door samenwerking bij het verzamelen of uitwerken van gegevens, het spuien van goede ideeën, of door morele ondersteuning in drukke tijden. Onderzoek doe je duidelijk niet alleen.

Allereerst wil ik Piet Drent bedanken, niet alleen voor zijn dagelijkse begeleiding, maar ook omdat hij aan de wieg van het ‘koolmezenproject’ stond: jaren van vasthoudendheid in het bestuderen, opfokken, en kruisen van koolmezen mondde uit in een grote project-subsidie van NWO waardoor drie OIO’s en een post-doc tussen 1998 en 2003 onderzoek konden doen in een vrijwel onontgonnen veld van de gedragsecologie. Ik ben Piet zeer dankbaar voor zijn vertrouwen in mijn alternatieve – maar risicovolle – aanpak van het veldproject (het meten van gedrag van *wilde* koolmezen in het laboratorium) na het falen van ons oorspronkelijke plan (koolmeesjongen van selectielijnen introduceren in het wild). Gelukkig bleek dat we me het alternatieve plan juist meer konden onderzoeken dat we voorheen voor mogelijk hadden gehouden. Piet’s kennis van koolmezen bleek zeer waardevol in alle fasen van het onderzoek.

Christiaan Both heeft tijdens de hele periode op het NIOO in belangrijke mate bijgedragen aan de inhoud van dit proefschrift. Ik ben hem erg dankbaar voor de constructieve samenwerking en hulp bij zowel de ideeënvorming als het veldwerk en het schrijven. Naast zijn stimulerende enthousiasme en hulp in wetenschappelijk opzicht, kon ik in tijden van sociale onrust altijd bij hem terecht, en hiervoor ben ik hem zeer erkentelijk.

Arie van Noordwijk heeft als promotor, maar ook als co-auteur van twee hoofdstukken zijn bijdrage geleverd aan de inhoud van dit proefschrift, vooral door te letten op de grote lijnen in de schrijffase. Daarnaast stimuleerde hij me tijd te investeren in schrijven van beursaanvragen toen mijn proefschrift nog niet klaar was, waardoor ik na de afronding direct weer een nieuw onderzoek kon opstarten

Een team van collega onderzoekers (Piet Drent, Ton Groothuis, Jaap Koolhaas, Joost Tinbergen, Gerdien de Jong en Arie van Noordwijk; Kees van Oers, Claudio Carere, en Christiaan Both) stonden me bij met wijze raad in het ‘coping style’ NWO-programma. Hoewel het niet altijd eenvoudig bleek te zijn alle neuzen dezelfde kant op te krijgen, heeft de samenwerking duidelijk geleid tot een project met meerwaarde. Ik ben Joost Tinbergen en Jaap Koolhaas in het bijzonder dankbaar voor de leuke en constructieve discussies op de schaarse momenten waarop we elkaar in Groningen troffen.

Een belangrijk deel van het praktische werk bestond uit het meten van exploratie-gedrag van wilde mezen in het lab. Mezen vangen in het bos, vervoeren naar het instituut, confronteren met een vreemde omgeving en weer loslaten in het bos. Het klinkt simpel, maar het was een boel werk, zeker omdat we de mezen na terugkomst in het bos intensief observeerden. Het vele werk wat daarbij kwam kijken had ik zonder hulp van anderen onmogelijk kunnen doen. Piet de Goede leerde me in het eerste veldseizoen de fijne kneepjes van het vak en heeft me tijdens het hele project op allerlei momenten bijgestaan met voeren, vangen en observeren van de mezen en het regelen van de avondcontroles. Daarnaast fungeerde hij in de eerste jaren ook vaak als luisterend oor in tijden van frustratie of wanhoop.

De ‘dames’ Mary-Lou Aaldering en Janneke Venhorst, voorafgegaan door Bart van IJmeren, hielden een oogje in het zeil wanneer de mezen in het lab logeerden en gaven ondersteuning bij het voeren van de mezen in het lab en schoonhouden van de kooitjes. Onze ‘vrijwilligers’, Maarten Hageman, Michel Geven en Dirk Zoetebier

hielpen ieder jaar trouw met het controleren van nestkasten in het broedseizoen en de winter, waardoor we van een groot terrein informatie kregen over het wel en wee van geringde koolmezen. Gedurende het hele project werd ik ondersteund door ‘Keultjes’, die vaak in een handomdraai en met zijn typische skeptische glimlach de meest wonderlijke voederautomaten construeerde, en mij redde wanneer ik de veldauto weer eens in de modder vastgereden had.

Een flink aantal studenten hielpen mee met het vangen en testen van de mezen, waardoor we uiteindelijk het gedrag konden meten van meer dan 1000 individuen. Leontien Witjes, Marloes van den Anker, Anna den Held, Kathelijne de Maijer, Job Stumpel, en Emma Versteegh: bedankt voor jullie inzet.

Kate Lessells ben ik erkentelijk voor het lezen van manuscripten die voorzien van heldere kritiek snel terugkwamen, voor de mogelijkheid onze mezen snel te kunnen sexen, maar ook voor een heerlijke rustpauze in de Camargue. Christa Mateman bepaalde de sexe van juveniele mezen op basis van bloedmonsters, waardoor ik zelf (gelukkig) niet het lab in hoefde. David Thomson heeft me vaak bijgestaan in statistisch opzicht, wat vooral duidelijk maakte hoe weinig ik daar eigenlijk van begreep. Marcel Visser hield de druk op de ketel tijdens het schrijven en overtuigde me van de noodzaak om nog voor het boekje af was te beginnen met schrijven van een beursaanvraag, hoewel ik daar op dat moment natuurlijk niet op zat te wachten. I am very grateful to Judy Stamps, Andy Sih, Alison Bell, and Denis Réale for stimulating conversations on conferences in Zürich, Montreal and Grünau and for valuable comments on our work.

Mevrouw Boetzelaer en het Gelders Landschap (in het bijzonder de heer Zwanenveld) worden bedankt voor hun toestemming om onderzoek te mogen doen in de terreinen Oosterhout en Westerheide.

Dank ook aan Kees van Oers en Christel Mols voor de leuke tijd op het instituut. We begonnen ongeveer tegelijkertijd aan ons promotiewerk en hebben veel lief en leed samen gedeeld (zoals de cursus proefdierkunde in Amsterdam). Kees heeft me vaak uit de brand geholpen met veld- of labwerk, en was een zeer geschikte kamergenoot, met wie ik te pas en te onpas kon bespreken wat me bezighield. Christel had alles altijd zo goed georganiseerd dat ik vaak geparasiteerd heb op haar gevoel van verantwoordelijkheid. Rinse Wassenaar en Leonard Holleman droegen zichtbaar bij aan een goede sfeer in de afdeling, hoewel ik het natuurlijk doorgaans te hard aan het rennen was om dat op te merken. De komst van nieuw bloed (Tobi, Philip, Eric en Margriet) maakten dat de afdeling wat meer opbloede, waardoor er naast de werk- en literatuurbesprekingen ook het interessante fenomeen ‘science-lunch’ ontstond, waardoor we veel meer met elkaars werk bezigwaren.

Ik ben Titus en Vera de Meester zeer dankbaar voor de aangename jaren in Bennekom: het was bijzonder prettig om bij jullie, Bella, en de bosuilen te wonen, en ik denk met veel genoegen terug aan de leuke jaren, de mooie omgeving, en de gezellige etentjes. Dank ook aan Jonne Rodenburg voor een goede vriendschap in drukke tijden. I am most grateful to Tobi Limbourg at whose place I stayed when visiting the NIOO after I had moved to Texel. I very much enjoyed the relaxed evenings that we spent together, especially those involving Haägen Dasz’s ‘Lemon cream pie’ and Voyager-shows featuring the amazing Seven-of-Nine. Dank ook aan Daphna Lavy voor het oppassen op de kleine Merlijn tijdens mijn laatste maar drukke veldseizoen.

Mijn familie wil ik bedanken voor hun onvoorwaardelijke steun en vertrouwen, mijn schoonouders voor de rustige weekendjes waarin we lekker konden bijtanken, Kees voor het gebruik van zijn laptop, en ‘de vriendjes’ voor de veel te schaarse maar altijd reuze gezellige weekenden.

Tenslotte mijn laatste woord van dank aan Anne. Zij was mijn steun en toeverlaat tijdens mijn gehele promotietijd en ontwierp op de valreep ook de omslag van dit boekje. Jouw vertrouwen in mijn kunnen maakten gaven mij de energie om stug door te bijten tijdens veldwerk, analyse, en het schrijven van manuscripten. Ik was er al met al veel te weinig voor je en besteedde meer tijd aan mijn werk dan eerlijk was, zeker na de geboorte van onze eerste zoon. Hopelijk kan ik dat de komende tijd wat compenseren en hebben we nu meer tijd om van andere dingen te genieten.

## Curriculum vitae

Niels Dingemanse was born on March 13, 1974 in Tholen, The Netherlands. During the years of his secondary school he spent his time identifying birds, insects, and plants, as a member of a Dutch young naturalist club (NJN). He attended the Comenius College at Hilversum as a secondary school, where he finished his VWO exam in 1992. In the same year he started his biology degree at the Vrije Universiteit in Amsterdam. He moved to Groningen University in 1993, where he specialised in animal ecology and graduated *cum laude* in 1997. In the course of his study he performed three undergraduate projects. The first project was on parental correlates of offspring sex ratio in Eurasian Oystercatchers with Dik Heg (Groningen University). The second project was on resource competition in fruit-feeding butterflies in Uganda under supervision of Paul Brakefield (Leiden University). The third project was an experimental study on provisioning rules of parents and helpers in the Arabian babbler in Israel with Jon Wright (University of Wales, Bangor).

Between February 1998 and April 2003 he worked on his PhD at the Netherlands Institute of Ecology. He is currently doing post-doctoral research on predator-induced natural selection on stickleback personality at the University of Wales, funded by a TALENT stipend from the Netherlands Organisation for Scientific Research.

Niels is married and is a father of two sons.

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