Relationships between behavioural traits in wild great tits *Parus major*

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Abstract

Animal personality can be defined as individual behavioural differences that are repeatable and consistent across time and/or contexts. In the model species great tit *Parus major*, studies on personality have shown consistent individual behaviour across behavioural axes, which have led to the use of only a single behavioural axis, ranging from shy to bold, to describe personality. However, personality studies have often focused on associations between only a few behavioural traits, and some of them have been restricted to behaviour in captivity. In addition, not all studies have found the same association between traits, questioning the use of only one personality axis.

This study conducted four behavioural tests on a wild great tit population. The tests included the measurement of behavioural response towards a human when being handled, towards an intruding human and a (caged) conspecific in the incubation period, and the response towards a predator model (an owl) during the nestling period. In total, 15 behavioural traits were measured, to study whether personality could best be explained by: (H0) independent behavioural traits, (H1) groups of behavioural traits, or (H2) one personality axis ranging from shy to bold. Additional purposes of the study was to investigate which of the measured traits that may explain personality, and if the behavioural responses were associated with body size and/or differed between sex and age categories.

The study found some evidence for repeatable behaviour within the study season. However, in general few significant associations were found between the traits, and the principal component analyses failed to reduce dimensionality of traits, supporting hypothesis H1. This is in agreement with personality studies on other taxa. Based on associations with boldness, some of the traits measured may be of help when characterising personality in wild great tits. The study found that males may be bolder than females, but no one-directional differences was found in behaviour between age classes, nor associations with body size. In addition, other factors, such as trial time/date may influence behaviour. Further studies testing repeatability for all traits and following individuals over several seasons and years are necessary to conclude whether the behavioural traits measured and associations found are consistent over time and/or contexts. Comparative studies with exploratory behaviour are also recommended for a better understanding of which of the traits measured could characterise personality.

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1 Introduction

Individuals have been found to differ consistently in behaviour within and across various contexts. For example, high within-individual repeatability has been reported for behavioural traits such as boldness, aggression, activity, exploration and sociability (Sih *et al.* 2015). Individuals also vary consistently in suites of these traits. This consistent individual behavioural variation is referred to by many terms, including behavioural syndromes, strategies, coping styles, temperaments and animal personalities (amongst others, reviewed in Réale *et al.* 2007). Even though the definitions of these terms vary slightly, the overall understanding of the terms seems to be that it represents individual-level variation in behavioural traits that is consistent over time and/or across contexts (Gosling 2001, Sih *et al.* 2004, Carere *et al.* 2005, Groothuis and Carere 2005, Réale *et al.* 2007). Consistent does not mean that trait values cannot change with for instance environmental changes or age, but that inter individual differences are largely maintained (Réale *et al.* 2007). For simplicity, only the term personality will be used henceforward.

Inter-level behavioural variation has been found to often be distributed in a non-random manner along particular behavioural axes (see below), suggesting that personality is likely to have ecological and evolutionary consequences (Dall *et al.* 2004). Therefore, personality studies have gotten increased attention the last decades. As a result, studies have shown that personality traits can be moderately heritable (e.g. Dingemanse *et al.* 2002, Drent *et al.* 2003), genetically correlated (e.g. van Oers *et al.* 2004a), affect reproductive success, disease susceptibility and survival (Koolhaas *et al.* 1999, Dingemanse *et al.* 2004) and have limited plasticity (van Oers *et al.* 2005). The discoveries of both phenotypical and genetic correlation between personality traits indicate that personality traits have probably not evolved in isolation, but as a package. These correlations are not necessarily adaptive and can generate trade-offs across situations that may be important in evolution (Carere *et al*. 2005). As personality may limit individual behavioural plasticity, individuals may not always be able to show an “optimal” behaviour in every situation. Therefore, a personality perspective could be of better help when trying to explain observed trade-offs, or apparently non-optimal behaviour, than by using single behavioural traits (Sih *et al.* 2004).

Personality studies may also be of importance at the population and species level. Individuals with different personalities may respond differently to changes in the environment (e.g.

climate or anthropogenic changes) and to experimental treatment or artificial housing (Dall *et al.* 2004, Wemelsfelder and Mullan 2014), and bias the sampling and estimation parameters of populations (Biro and Dingemanse 2009, Stuber *et al.* 2013). Personality may also affect ecological processes such as niche expansion, social organisation and dispersal (Réale *et al.* 2007). Personality studies could therefore be beneficial for the design and/or interpretation of studies, and for instance when developing measures for conservation of populations or species and animal welfare.

1.1 Personality in great tits *Parus major*

Individual behavioural variation has been characterised in a variety of animal taxa, ranging from small invertebrates to large mammals (Réale *et al.* 2007, Bell *et al.* 2009). One of the most important species for the advancement of personality studies has been the great tit *Parus major*. This small passerine is a generalist species and its distribution range all over Europe and large parts of central and south Asia, except the most alpine and harsh areas (Julliard *et al.* 2006, Bird Life International 2015). Because the great tit is widely common, resident and shows a great willingness to use bird feeders and nest boxes, the species is fairly easy to study and has become a model species for small birds in the field of ecology, including personality studies.

The main behavioural axes used in studies on personality in great tits are exploratory behaviour, aggressiveness and risk-taking behaviour (see summary of literature in Table 1 below). Studies on exploration have used never-before-seen objects and/or open-field environments to measure exploratory behaviour, e.g. by measuring latency to approach and nearest distance to an object (van Oers *et al.* 2004a), or flights and hops, or area covered within a time span in a novel environment (Dingemanse *et al.* 2002, Dingemanse *et al.* 2004). Agonistic or dominant behaviour, measured as for instance latency to attack, time spent in agonistic display or fraction of fights started have been used as measurement of aggressiveness (Veerbek *et al.* 1996, Carere *et al.* 2005). Risk-taking behaviour is measured as response to threatening situations, for instance when being startled or to the presence of a human or a predator, by recording the latency to return to foraging or nest box and alarm calling behaviour (Hollander *et al.* 2008, Cole and Quinn 2014).

Table 1. An unexhausted summary table of previous studies on personality traits and associations between different behavioural traits measured on great tits. "-", "+" and "0" indicates negative, positive or no association between traits, respectively. F and M represent female and male great tits. Exploratory behaviour is measured in captivity also when compared with other traits measured in their natural environment.

Personality trait	Association with other personality traits	Relation	Sex	Study environment	References	Comments
Exploration			M	Captivity	Veerbek *et al.* (1994)	Hand reared juveniles from a wild population.
Exploration			M, F	Captivity	Dingemanse *et al.* (2002)	Wild population.
Exploration			M, F	Captivity	Drent *et al.* (2003)	Wild population.
Exploration			M, F	Captivity		Two lines (hand reared) selected for EB.
Exploration			M, F	Captivity	(Dingemanse *et al.* 2004)	Wild population.
Exploration			M, F	Captivity	Both *et al.* (2005)	Wild population.
Exploration	Risk-taking	+	M, F	Captivity	van Oers *et al.* (2004a)	Hand reared from a wild population
Exploration	Aggression Dominance	+/0	M	Captivity	Veerbek *et al.* (1996)	Hand reared adults from a wild population
Exploration	Dispersal	+/0	M, F	Captivity (EB) Natural	Dingemanse *et al.* (2003)	Wild population
Exploration	Dominance	+/-	M, F	Natural	Dingemanse and de Goede (2004)	Wild population.
Risk-taking	Early EB	+	M, F	Captivity	van Oers *et al.* (2004b)	Two lines selected for high and low risk taking
	Boldness	+	M, F	Captivity		
	Adult EB	+	M, F	Captivity		
Exploration	Stress response	-	M, F	Captivity	Carere and van Oers (2004)	Two lines (hand reared) selected for EB.
Exploration	Aggression	+	M	Captivity	Carere *et al.* (2005)	Two lines (hand reared) selected for EB.
Exploration	Nest defence	+/-	M, F	Natural	Hollander *et al.* (2008)	Wild population
Exploration	Handling stress	+/0	M, F	Natural	Fucikova *et al.* (2009)	Nestlings from a wild population
	Handling stress	+/0	M, F	Captivity		Two selection lines (hand reared) for EB
Exploration	Dispersal	+/0	M, F	Natural	Quinn *et al.* (2011)	Wild population
Exploration	Collective behaviour	-	M, F	Natural	Aplin *et al.* (2013)	Wild population

Exploration	Collective behaviour	-	M, F	Natural	Aplin *et al.* (2014)	Wild population
	Risk-taking	0	M, F			
	Dominance	0	M, F			
Exploration	Risk-taking	+	M, F	Natural	Stuber *et al.* 2013	Wild population

Studies of the main behavioural axes have shown that the behavioural traits are repeatable within individuals and that there is consistent individual behavioural variation within the axes. More interestingly, studies on traits from different behavioural axes have shown that the individual variation in behaviour is also consistent across the behavioural axes, with exploration being positively correlated with aggressiveness and risk taking in great tits (van Oers *et al.* 2004b, Carere *et al.* 2005). These associations has led to the use of one personality axis ranging from shy to bold, known as the shyness-boldness continuum or reactive-proactive personality axis, which is one of the best-studied personality axis in non-human animals (Wilson *et al.* 1994, Cole and Quinn 2014). At one end of the axis, one finds extremely bold, or proactive, individuals. These are characterised by being fast explorers, more aggressive towards conspecifics and more risk-taking in threating situations when compared to the extreme shy, or reactive, individuals. Reactive individuals have been found to be more thorough when exploring, seeming more responsive, or plastic, in their behaviour than proactive individuals, which seems to have a more routine and less plastic way of exploring (Fucikova *et al*. 2009, Cole and Quinn 2014)

Differences in individual personalities also extend to social flocking behaviour through grouping tendencies and collective behaviour. More reactive individuals are found to behave more collectively, moving within-flock areas of higher density. More proactive individuals hold shorter-term associations and tend to move to, and feed, at the spatial periphery of flocks (Aplin *et al.* 2013, Aplin *et al.* 2014). Computational models based on empirical data have also indicated that groups consisting of variable personality types show the most effective coordinated action when exploiting a habitat patch (Aplin *et al.* 2014).

Personality studies of the great tit have also helped forward the understanding of genetic basis for animal personalities, as studies have found that some personality traits can be heritable and genetically correlated (e.g. Dingemanse *et al.* 2002, Drent *et al.* 2003, Quinn *et al.* 2009). Studies on both captive and wild great tits have also found an association between genetic polymorphisms and variation in personality, and that the strength or presence of this association varies between wild populations (Fidler *et al.* 2007, Korsten *et al.* 2010). In addition, studies have found that individual differences in personalities in great tits may have significant fitness effects, both with regard to survival and reproductive success (Dingemanse *et al.* 2004, Both *et al.* 2005). Therefore, studies of the great tit based on the use of the reactive-proactive axis to quantify personality represent one of the most comprehensive examinations of the importance of personality to date (Aplin *et al.* 2014).

1.2 Limitations of personality studies

Experiments on exploratory behaviour have contributed significantly to the characterisation of personality in great tits. Personality is often easier to study in a controlled laboratory setting than in the field, as one can observe differences in behaviour relatively unaffected by environmental variation. Even though this may be an optimal way to demonstrate consistent individual behavioural variation, it has the disadvantage of taking the animals out of their natural habitat where their personalities have evolved. Studies on the association between personality traits measured in their natural environment are more limited (Table 1).

Some personality traits are becoming well documented along the shy-bold axis for the great tit. However, most of the studies have only looked at the association between one, or a few, personality traits from different behavioural axes. Furthermore, the association patterns are not always the same compared between studies (Table 1). As personality seems to be composed of correlated traits across behavioural axes, one may expect to find relationships between not only a couple, but several behavioural traits. As the studies have only looked at a few traits, often in captivity, they restrict the measured behaviour to only one or two contexts. In addition, as there is not a clear association pattern between all types of behaviours, a single personality axis ranging from shy to bold may not be an optimal way of characterising personality in great tits.

1.3 Present study

This study will investigate the association between several behavioural traits measured on wild population of great tits in their natural environment in various contexts. The study thus provides a potential to reveal whether personality can be characterised by a small number of independent traits, by a limited number of groups of behavioural axes, or by a single personality axes only going from shy to bold (reactive to proactive) individuals. The following hypothesis will be investigated:

H0: Personality can only be explained by a great number of traits that are more or less independent of each other. Under this hypothesis no, or very low correlation is expected between the traits. For instance, an individual could express bold behaviour in several contexts, without these traits necessarily correlating with each other.

H1: Personality can be explained by a limited number of behavioural axes, which can be expressed differently according to circumstance. For instance, an individual could be bold in all relations to a threat of a predator (e.g. exposure to a human, or an owl). However, boldness in this regard may be different between a predator situation, and for instance, behaviour towards a competing conspecific. Under this hypothesis, behavioural traits can be grouped with high correlations between traits within, but not between, groups.

H2. Personality can be explained by one single behavioural axis, going from shy to bold. For instance, an individual will score bold on behavioural traits in all contexts, and these behavioural traits will be correlated in a shy-to-bold manner.

A second purpose of the study is to try to find out which behavioural traits that best reflects a certain personality, like boldness, based on the results in the present study and previous literature on personality. This study may be beneficial for future studies, as it may help characterise personality in wild populations of great tits. Additionally, if strong associations are found between traits, reduction of number of measurements could be possible in future studies.

In great tits, one may expect males to be bolder than females, because exploration has been associated with dominance in great tits (Dingemanse and de Goede 2004), and male great tits are dominant to females (at least outside the breeding season) (Hansen and Slagsvold 2004). Dominance may also be affected by body size, weight and age (Veerbek *et al.* 1996). A third aim is therefore to investigate if birds of different sex and age categories differ in their behavioural response, and if behaviour is associated with morphological measurements.

In this study, several behavioural traits were measured on a population of wild great tits in different contexts, namely by exposing them to different threatening situations through four behavioural tests. Three tests represented different situations of risk of predation and were aimed to measure risk-taking behaviour and boldness when: handled by a human after being captured, threatened by an approaching human during incubation, and exposed to an avian predator (an owl) during the nestling period. The last test aimed to measure the individuals' aggressive response to a (caged) conspecific intruder. Correlation between individual traits and generalised principal component analyses were used to study whether the behavioural traits were independent (predicted from H0), could be grouped into a few components of behaviour (predicted from H1), or can be classified by using only one axis, going from shy to bold (predicted from H2). A necessary first step was to test the basic assumptions of personality, that a specific trait is repeatable within a context. This was tested by measuring response of the same individual twice as it is a prerequisite in the definition of personality, but also to control for that not all variation observed is due to measurement errors. The latter could potentially lead to a false acceptance of the first hypothesis (H0). Variation within traits were also analysed in relation to age, sex and body measurements, and possible confounding factors, such as trial date and time of day.

2 Material and methods

2.1 Study area and population

The study was carried out in an area called Dæli, in Bærum, Norway (60°00´N, 10°38´E). The main data sampling for this study was conducted from March throughout June 2014. Dæli is a 1.6 km^2, mixed deciduous-coniferous woodland area, provided with approximately 550 nest boxes and 25 feeding stations evenly distributed. The Dæli area seems to be a high quality area for great tits, supporting approximately 70-100 breeding pairs each year. The great tit population is monitored from early spring to summer each year, and all individuals that are raised and nest in Dæli are ringed with colour rings and an aluminium ring with an ID-number. During the breeding season, some great tits are cross-fostered to blue tits *Cyanistes caeruleus* and *vica verca* (see for instance Wiebe and Slagsvold 2015). The study population of great tits used in the present study did not include individuals from cross-fostering experiments.

2.2 Fieldwork

The fieldwork took place in the breeding season (March – July) of 2014. The nest boxes were inspected regularly to note content and to identify owners, to monitor birds' breeding attempts and perform behavioural tests. For other study purposes, several fitness measurements and survival/mortality were also recorded during the fieldwork (see Thorsteinsen 2015).

2.2.1 Capturing and identifying individuals

To help identifying nest box owners, adult and juvenile birds were captured in mist nets at feeding stations in autumn or with traps in their nest boxes during spring. Local recruits (individuals raised at Dæli) and settled immigrants were identified based on their colour-ring combination and ID-number given as nestlings (14-16 days old) or when previously captured, respectively. New immigrants, i.e., birds not previously captured at Dæli, were given a special colour-ring combination according to age (one-year old and older) and year when caught, and an individual aluminium ring with an ID-number using standard ringing equipment. Both local recruits and immigrants were used as focal birds for the present study.

2.2.2 Age, sex and body measurements

Age and sex was noted using previous data taken for already ringed individuals, or by using plumage traits for new immigrants (method described by Svensson (1975)). Age was noted as one-year old or older. Body measurements were taken for all adult birds captured at the study site, to see if the various behaviours were associated with the condition of the individuals. The body measurements were mainly taken when the birds were captured in mist nets for identifying and in-hand test trials (see below). Body mass (g) was obtained by weighting the birds in a bag attached to a spring balance, and wing length (mm) and tarsus length (mm) was measured with a sliding calliper.

2.2.3 Behavioural tests

During the breeding season, four behavioural response tests were conducted on great tits in the wild, measuring all together 15 behavioural traits. Two of the tests, in-hand test (1) and conspecific intruder test (3), were slightly modified already existing methods (Karlsen and Slagsvold 1997, Andersen 2012). The other two, attentiveness test (2) and predator model test (4) were new.

To reduce differences between observers (cf. Andersen (2012)), the same person (T. Slagsvold) conducted all trials of the in-hand test, conspecific intruder test and predator model test, and some of the attentiveness test trials together with two master students (C. Thorsteinsen and T. Ø. Stræte).

The conspecific intruder test and predator model test were only performed once on each breeding pair, whilst the attentiveness test was conducted two times for a subsample of females to test for repeatability. Only the first trial was used when comparing with behavioural traits from other tests. Data on the in-hand test were available for all birds present in spring 2014. Data were collected from spring 2014 (N = 69), spring or autumn 2013 (N = 48 and N = 61), or in spring or autumn 2012 (N = 3 and N = 1).

A total of 259 great tits were captured during the field season. Data for at least one or more behavioural tests was collected for in total 197 birds. After exclusion of birds due to e.g. treatment (cross-fostered) or missing data, 181 individuals were used for statistical analysis. Out of these individuals 95 were females and 86 were males.

Test 1: In-hand test

The aim of this test was to measure an anti-predator response of focal birds towards a human when held in hand. Birds were caught in mist nets and transported away from the capture site in bird bags. Only one bird was taken out of its bag at the time and released before testing a new individual. Date, time of capture, time when taken out of the bag, ID, and body measurements were noted before each behavioural test trial began. The test included measurements of six different behavioural traits and the following was noted for each trait during the test:

1. **Breathing rate**: Number of chest movements. The bird was held on its back in the hand and the number of chest movements during a period of 30 seconds was noted.

2. **Screaming**: No/Yes. Whether or not the bird screamed during the trial.

3. **Biting**: Score from 0-6. An index finger was lead towards the bird's bill six times and the number of times the bird bit out of the six tries was noted.

4. **Tonic immobility**: 0-180 degrees. The bird was laid on its back in the palm of one hand. The hand holding the bird was then slowly tilted towards the palm of the other hand and the approximate angle degree of the hand when the bird left the hand was noted.

5. **Alarm call**: No/Yes. Whether or not the bird made any alarm calls when leaving the hand.

6. **Distance hand**: The approximate horizontal distance (m) between the hand (release site) and the bird's first perching site after leaving the hand.

Breathing rate was measured twice during the trial, in the beginning (after identification, before all other measurements) and at the end of the trial (before tonic immobility/release). This was done to see if the handling influenced the birds' breathing rate, as it has been found that breathing rate (as a measure of stress response) can increase with handling (Fucikova *et al.* 2009), and to check for repeatability in breathing rate. Mean breathing rate value was used in the subsequent analyses.

Test 2: Attentiveness test

The second test was performed on incubating females to test their anti-predator response to a human, and how persistent they were to stay on the nest (attentiveness) when disturbed. Nest box number, date and time of day were recorded before approaching the nest box and the following seven behavioural traits were measured for each female during the trial:

1. **Hissing**: No/Yes. Whether or not the female made hissing sounds and flapped her wings/tail when an index finger was inserted in the nest box opening and wriggled inside for five seconds.

2. **Attentiveness**: Score from 1 to 4 depending on when the female left the nest box during the trial: 1) when the lid was lifted off and the observed looked inside and then moved away, 2) when a hand was put slowly down to the nest material along the back wall of the nest box and held there for five seconds, 3) when a hand touched the females tail for five seconds, 4) if the female still remained on the nest after being disturbed as described above. Birds that did not voluntarily leave the nest box were carefully lifted of the nest to continue the test.

3. **Call inside**: No/Yes. Whether or not the female screamed inside the nest box during the time when measuring attentiveness.

4. **Call leaving**: No/Yes. Whether or not the female made alarm calls when she flew away from the nest box.

5. **Distance box**: The approximate horizontal distance (m) between the nest box and the first place the female perched after leaving the nest box.

6. **Call after 2 min**: No/Yes. Whether or not the female made alarm calls 2 minutes after she flew out of the nest box.

7. **Distance after 2 min**: The approximate horizontal distance (m) between the nest box and where the female was situated 2 minutes after leaving the nest box.

Test 3: Conspecific intruder test

The third test aimed to record the response of females and males to a caged, live conspecific intruder during the incubation period. A cage with a great tit female was placed on the ground 3-4 m in front of the nest box and the response was observed from a far (~20 m). The trial duration was 5 x 1 minute, where time spent ≤ 2 m of the cage was recorded the female (0-300 sec), and whether or not the male visited the cage per minute (score 0-5). Even though different measurements were performed, the response variable for this test was called conspecific response for both sexes. For practical reasons, only two female stimuli birds were used in the test. There was no significant difference in conspecific response between individuals that were tested with different stimuli birds (Appendix table 1.1).

Test 4: Predator model test

The last test aimed to record the response of females and males to a predator model late in the nestling period (10-14 days after hatching). The predator model was a stuffed specimen of a Tengmalm's owl *Aegolius funereus*, a known natural predator of small passerine birds, including great tits (Cockrem and Silverin 2002). The model was placed on the nest box lid. The trial duration consisted of five consecutive minutes, where the nearest distance (m) between the predator model and the focal tit (predator response) was noted for each minute by the observer, who kept a ~15 m distance. The average distance was used for the subsequent analyses.

2.3 Ethical considerations

Research on birds in the Dæli area has been ongoing since 1995 and is approved by the Norwegian Animal Research Authority. There is no reason to believe the birds used in the present study suffered, except for risks associated with handling, which is involved in any trapping and ringing of birds.

2.4 Statistical analyses

All analyses were performed with the statistical computer software R.3.2.2 (R Core Team 2014). All tests were two-tailed and the alpha level of significance was 0.05.

2.4.1 Normality and transformation of variables

Normality of data was checked with Shapiro-Wilks normality test, quantile-quantile plots and histograms (results not shown). Variables that did not meet the normality criteria for parametric tests were tried transformed using log-, square root- and arcsine functions. Where transformation did not help, the original values were kept and non-parametric analyses were applied. Only three variables were transformed (log-transformed: breathing rate and distance from nest box, square root transformed: distance after 2min). Transformed variables were back-transformed for easier interpretation in figures and tables.

2.4.2 Repeatability

Repeatability was tested for variables measured more than once. Pearson- and Spearman's rank correlation were used for quantitative variables, and Fisher's exact test of independence for binary variables. Due to some females leaving the area surrounding the nest box during the attentiveness test, two variables (call after 2 min and distance after 2 min) from this test did not have a large enough sample size to give a meaningful test, and were therefore excluded. Student's paired t-test and Wilcoxon signed rank test were used to compare first and second measurement of quantitative variables.

A previous study by Andersen (2012) on the same study population found consistency between first and second measurements within observers and that different observers did not systematically differ in their measurements. Based on this and the fact that most test trials in the present study were performed by the same observer, repeatability between observers was not tested for.

2.4.3 Variation within behavioural traits

All behavioural traits were tested for associations with body measurements as well as differences between sex and age categories. Associations with trial date and time of day were also tested for all traits. Traits measured during the in-hand test were also tested for association with time spent in bird bag and differences between seasons when captured. Standard correlation and comparison tests were used (same as stated below).

2.4.4 Relationship between behavioural traits

Associations and linear correlations between pairs of behavioural variables were tested by the use of comparison tests (Student's two-sample t-test, Mann-Whitney U test), correlation tests (Pearson, Spearman's rank) and tests of independence (Chi-square test, Fisher's exact test). P-values were corrected for multiple testing using false discovery rate correction (Benjamini and Hochberg 1995). Both global and separate analyses were used when analysing behavioural traits measured for both sexes (traits from in-hand- and predator model test). Conspecific response was analysed separately as the trait was measured differently for females and males. Significant relationships between pairs of traits were also analysed in appropriate models (analyses of variances (ANOVA), -covariance (ANCOVA) and logistic regression) with sex and interaction with sex included as independent variables. All tests are stated where used.

An exploratory multivariate analysis was used to study similarities between individuals and relationships between behavioural variables, with the aim to reduce the dimension of the data set. This was performed with the FAMD (Factor Analysis for Mixed Data) function in the FactoMineR package in R (Husson *et al.* 2015). FAMD is a generalised principal component method that includes both categorical and continuous variables, making it possible to study the relationship between all the behavioural variables measured in this study. According to Husson *et al*. (2015), FAMD can roughly be seen as a mix between a principal component method (PCA) for continuous variables and multiple correspondence analysis (MCA) for categorical data. PCA aims to reduce the dimensionality of the data while retaining most of the variation in the data set, by identifying directions, or principal components (PCs), along which the variation in the data set is maximal (Ringnér 2008). I.e., it replaces the initial variables by new hypothetical PC variables and places them in order based on the amounts that the individual PCs contribute to the sum of the variances of the original variables. This way the data can be represented by a relatively small number of components instead of values for several variables (Maindonald and Braun 2003). MCA can be seen as a generalisation of PCA, analysing the pattern of relationships of several categorical variables by making an indicator matrix (individual x variables matrix) where each level of a category is coded into dummy (0/1) variables (Abdi and Valentin 2007). In FAMD, PCA scaling of continuous variables to unit variance and MCA scaling of categorical variables ensure a balanced influence of both types of variables in determining the dimensions (equivalent to principal components) of variability (Husson *et al*. 2015). As for standard PCA, the FAMD results can be plotted, offering "views" of the data that may be insightful, e.g. by visualising similarities and differences between groups and correlation between variables and the dimensions produced. Continuous variables were scaled to mean zero and variance one.

3 Results

In total, variation within and relationships between 15 behavioural traits were analysed. Due to the amount of analyses, mainly significant results ($p < 0.05$) or tendencies of so ($p < 0.10$) will be emphasised in the result-part. All results can be viewed in the Appendix.

3.1 Repeatability

Significant repeatability was found for breathing rate and distance from box for both sexes and females respectively (Table 2a, see Appendix table 2.1 for separate analyses on breathing rate for females and males). There was also a tendency for repeatability in the females will to stay on the nest when disturbed by a human during incubation (attentiveness; Figure 1E, Appendix table 2.1). A Fisher's exact test found consistency in the call leaving variable (Table 2b), indicating that females that called when flying away from the nest box during the first trial also called when flying away during the second trial. No consistency was found between the repeated measurements of hissing or call inside the nest box (Table 2.b).

Table 2. Table 2a shows correlation between first and second measurement of three quantitative behavioural traits measured on great tits during the in-hand test (1) and attentiveness test (2). Table 2b shows Fisher's exact tests of independence between first and second measurement of three dichotomous behavioural traits measured on wild great tit females during the attentiveness test. OR = odds ratio. Significant p-values ($p < 0.05$) are marked in bold.

a)

Analysis	Trait	r^1/r_s^2	N	p
Both sexes	Breathing rate (1)	0.90^1	181	< **0.001**
Females	Attentiveness (2)	0.34^2	30	0.068
	Distance box (2)	0.53^1	25	**0.007**

^{1}: Pearson correlation test (r), ^{2}: Spearman's rank correlation test (r_s)

b)

Trait	Trial 1	Trial 2 No	Trial 2 Yes	N	OR	p
Hissing (2)	No	17	5	29	4.26	0.16
	Yes	3	4			
Call inside (2)	No	17	5	29	2.46	0.36
	Yes	4	3			
Call leaving (2)	No	2	1	25	Inf	**0.010**
	Yes	0	22			

3.1.1 Comparison of first and second measurement

Breathing rate was found to be significantly higher in the second measurement for both females and males, but the difference in number of chest movements was very small (Paired-sample t-test, Figure 1A, Appendix table 2.2). Even though there was only a tendency for repeatability in the attentiveness trait ($p < 0.10$), attentiveness score was found to be significantly higher in the second measurement for females (Wilcoxon signed rank test, Figure 1B, Appendix table 2.2). No difference between the measurements was found for the distance box variable measured on females (Paired-sample t-test, Figure 1C, Appendix table 2.2).

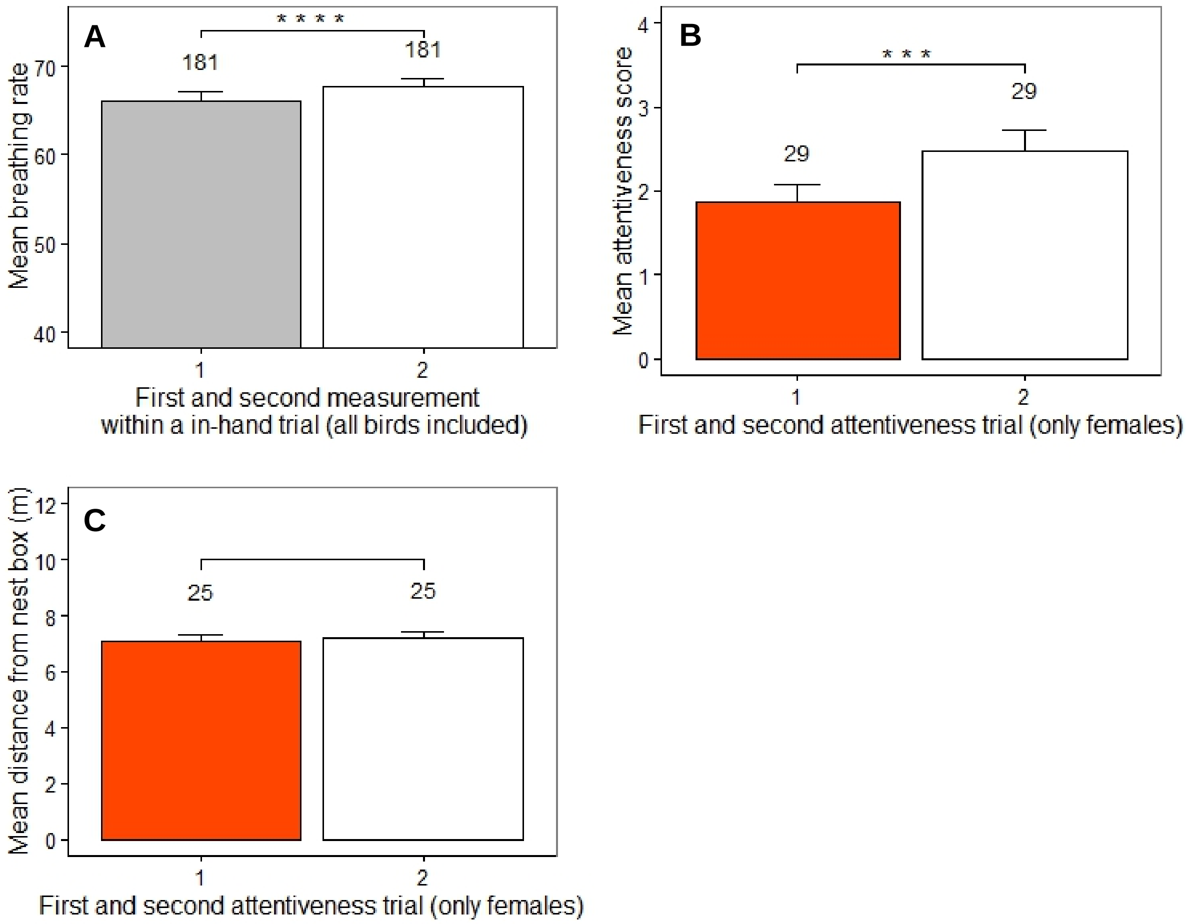

Figure 1. Barplots showing comparison of mean value (+SEM) between first and second measurement of three behavioural traits measured on great tits during the in-hand test and attentiveness test (females only). A: mean (of mean) breathing rate, B: mean attentiveness score, C: mean distance from nest box (m). Numbers over error bars indicate sample size for each group. Annotations (*) indicate level of significance: **** = $p < 0.001$, *** = $p < 0.05$. No asterisk = p-value not significant.

3.2 Variation within behavioural traits

3.2.1 Relationship between behavioural- and morphological traits

There were no clear relationships between behavioural and morphological traits (Appendix 3.1 and 3.2). For males, heavier individuals had a higher breathing rate than individuals with a lower body mass (r = 0.25, N = 86, p = 0.019). Also, alarm calling males had a longer tarsus than not-alarming males. However, the difference was biological speaking insignificant (Student's two-sample t-test, mean tarsus length of alarm calling males: 228.7 mm, and not-alarming males: 224.9 mm, t = - 2.40, p = 0.019). Females that had a shorter distance to the predator model (i.e. stronger response) had a longer tarsus than females with long distance to the predator model (r = - 0.33, N = 65, p = 0.008).

3.2.2 Comparison of behaviour between age and sex categories

All behavioural traits were analysed for differences between one-year old and older individuals (Appendix table 4.1). Global analyses showed that one-year olds screamed more and had a weaker response to the predator model compared with older birds. The same association between age and screaming was found in the separate analyses for each sex, but was only significant for females. Separate analyses did not reveal significant age-differences in predator response. When analysing traits only measured on females, a difference between age categories was found for the attentiveness trait, with one-year old females laying significantly longer on the nest than older females when disturbed by a human.

Differences between sexes were analysed for all behavioural traits measured the same way for female and male great tits. Mann-Whitney U-tests revealed that males bit significantly more times than females (Figure 2A, Appendix table 4.2), and had a significantly shorter distance (i.e. stronger response) to the predator model than females (Figure 2B, Appendix table 4.2). There were no differences in mean values for the other variables tested for both sexes (Appendix table 4.2).

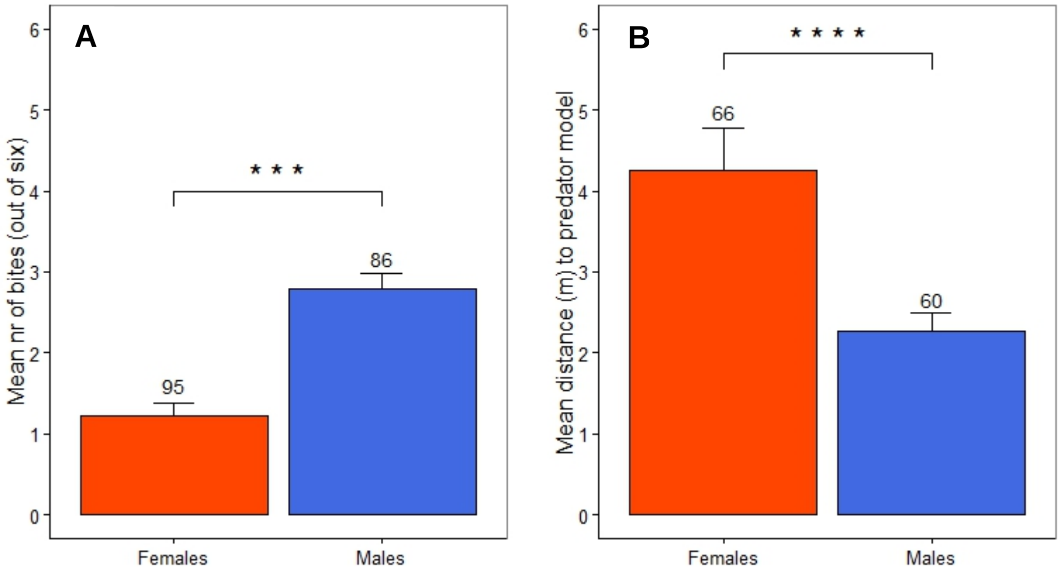

Figure 2. Barplots showing comparison of mean (+SEM) biting score (A) and mean predator response (B) between female and male great tits. Traits are measured during the in-hand test and predator model test, respectively. Numbers over error bars indicate sample size for each group. Annotations (*) indicate level of significance: **** = p < 0.001, *** = p < 0.05.

3.2.3 Seasonal differences and associations with capture time

Seasonal differences within in-hand traits

Seasonal differences within behavioural traits were analysed for the in-hand measured behavioural traits both globally and within sexes. There was a significant difference in mean breathing rate between individuals captured during autumn and spring in all analyses (Appendix table 5.1). Individuals captured in autumn had a higher breathing rate than individuals captured during spring (Figure 3). The global analysis also found that individuals captured during autumn bit more, screamed more and perched further away from the hand (Appendix table 5.1). There were more screamers amongst females captured during autumn than spring, and males captured during autumn perched further away from the hand than males captured in the spring.

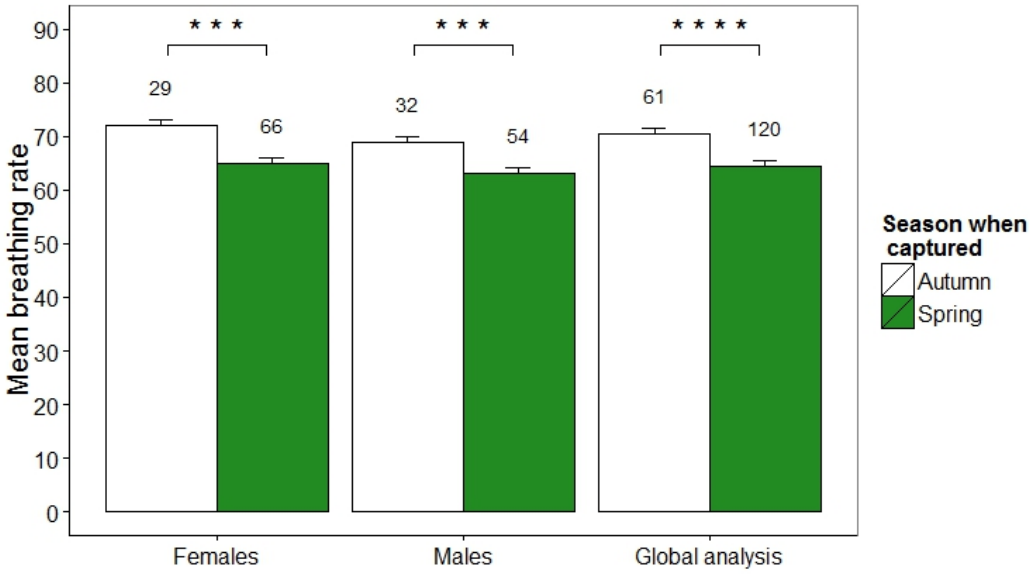

Figure 3. Comparison of mean (+SEM) (of mean) breathing rate, measured during the in-hand test, between individuals of great tits captured during different seasons. Comparisons were made within sexes and for both sexes combined (global analysis). Numbers over error bars indicate sample size for each group. Annotations (*) indicate level of significance: **** = $p < 0.001$, *** = $p < 0.05$.

Effects of capture time

Effect of capture time (trial date and time of day) was analysed within seasons for behavioural traits measured during the in-hand test, which were also tested for an effect of time held in bird bag. Breathing rate was associated with trial date within seasons. During autumn, great tits captured earlier in the season had a lower breathing rate than those captured later in the season (Figure 4, Appendix table 6.1). During spring, birds that were captured earlier in the season had a higher breathing rate than those captured later in the spring (Figure 4, Appendix table 6.1).

Birds that were captured earlier in the spring also bit more than individuals captured later in the spring, but the correlation was not significant in the separate analysis for males (Appendix 6.1). A significant difference in mean trial date was found between screaming and non-screaming males, with screaming males being captured later in the spring than non-screamers (by approximately 20 days, Appendix 6.2). A non-significant trend was found for females, but with screamers being captured earlier than non-screamers (by approximately 21 days, Appendix 6.2). Thus, no difference in spring trial date was found in the global analysis (Appendix table 6.2). An opposite relationship for females and males were also found between spring trial date and alarm calling, with female alarm callers being caught (approximately 24 days) later in the spring than non-callers, while male alarm callers were caught earlier than non-callers (Appendix table 6.2). The difference in mean trial date for the alarm call trait was only significant in the female analysis.

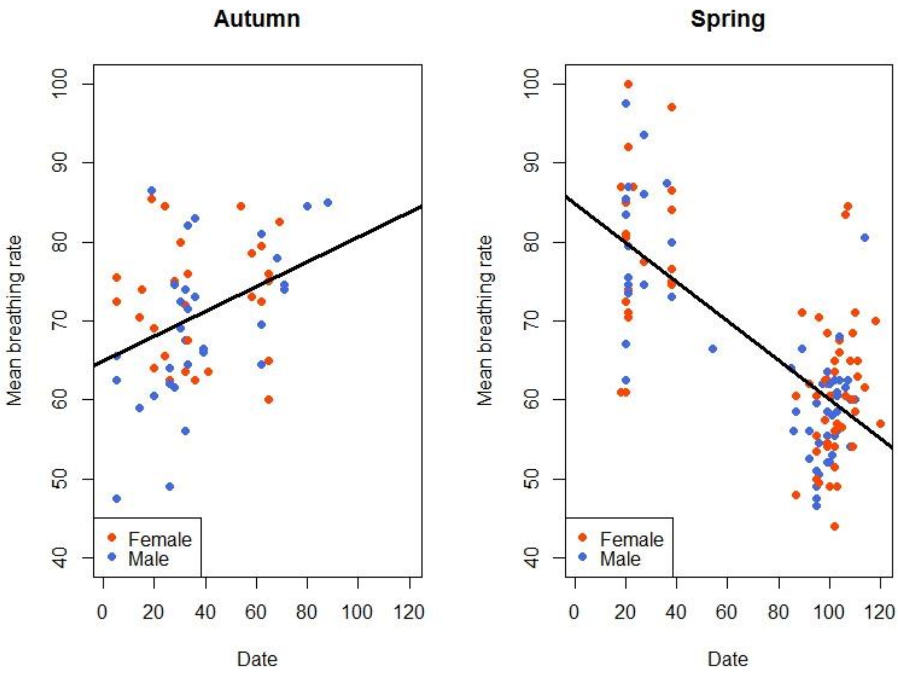

Figure 4. Scatterplot showing correlation between mean breathing rate measured in great tits and date when captured within seasons: Autumn: 1 = 1st of September (r_s = 0.33, N = 66 p = 0.009), Spring: 1 = 1st of March (r_s = -0.43, N = 120, p < 0.001).

Biting was negatively correlated with time of day in the global and male analysis, with individuals captured earlier in the day biting more times than individuals captured later in day (Appendix table 6.1). Screamers were caught earlier in the day than non-screamers and the difference was significant in the global analysis and for males (Appendix table 6.2).

Birds that were kept in the bird bag for a longer time before being tested during the in-hand test bit more than birds that were kept for a shorter time (Appendix table 6.1). Longer time in the bird bag was also associated with a higher breathing rate and a longer (perch) distance from the hand, but was not significant in the separate analysis for females (Appendix table 6.1).

Some associations between trial date and time of day and behavioural traits were also found when analysing traits from the attentiveness test. Females that were tested earlier in the spring perched closer to their nest box after leaving it when disturbed by a human (Appendix table 6.3). Females that called after 2 min. after leaving the nest box were on average tested later in day than females that did not make calls (Appendix table 6.4). Birds that were tested earlier in the day had stronger predator response than birds tested later in the day (Appendix table 6.5). No effect of capture time was found for the conspecific response trait for neither females nor males (Appendix table 6.5).

3.3 Relationships between pairs of behavioural traits

Relationships between pairs of behavioural traits were analysed both with global and separate analyses for behavioural traits measured the same way for female and male great tits, i.e. behavioural traits from the in-hand test and predator model test. For an overview over the results, simplified summary tables (Table 3 and 4) are given to show the relationships between the variables. Detailed statistics for the summary tables can be viewed in Appendix 7. Some relationships are illustrated in figures to show the range of variation in the traits and sample sizes.

3.2.1 Global analyses

The results from global analyses on the association between behavioural variables measured for both female and male during the in-hand- and predator model test are summarised in Table 3. Very few relationships between the traits accounted for were significant in the analysis. Breathing rate was significantly positively correlated with distance moved away from hand, indicating that individuals with a low breathing rate perched closer to the human after escaping during the in-hand trial (Appendix table 7.1a). Individuals that screamed bit significantly more than individuals that did not scream (Appendix table 7.1b). These associations were also significant after correcting for multiple testing. Non-callers perched further away from the release site than callers, but the difference was not significant (Appendix table 7.1b).

Table 3. Summary table showing the association between the behavioural traits measured for female and male great tits during the in-hand- and predator model test. "+"[1], "-"[2] and "0" indicated positive, negative and no association, respectively. +++/- - -: $p < 0.05$, ++/- -: $p < 0.10$, +/-: $0.10 \leq p \geq 0.50$, 0: $p > 0.50$. Association marked in red are significant association robust to correction for multiple testing.

	Breathing rate	**Biting**	**Screaming**	**Immobility**	**Alarm call**	**Distance hand**	**Predator response**
Breathing rate							
Biting	+						
Screaming	-	+ + +					
Immobility	0	-	+				
Alarm call	-	0	-	-			
Distance hand	+ + +	0	0	+	- -		
Predator response	+	-	0	+	-	+	

[1] +: positive correlation / yes category has a higher mean value
[2] -: negative correlation / no category has a higher mean value
Note: Please see Material and methods for definition of traits

3.3.1 Separate analyses for females and males

Associations between all the traits measured, analysed separately for female and male great tits, are summarised in Table 4 and detailed statistics are given in Appendix 7.

Comparisons with global analysis

As for the global analysis, there were few significant relationships between the behavioural traits from the in-hand and predator test. For females, screamers bit significantly more than non-screamers (Figure 5A, Appendix table 7.1a). This difference was also evident in the global analysis, repeated above (Figure 5A, Table 3). The same trend was found for males, but it was not statistically significant (Figure 5A, Table 4, Appendix table 7.1a). However, the association between biting and screaming for females was not significant after correcting for multiple testing. Non-screaming males had a higher breathing rate than screamers (Figure 5B, Table 4, Appendix table 7.1b). The same non-significant association was obtained from the global analysis (Table 3), while in females, screamers tended to have a higher breathing rate than non-screamers (Table 4, Appendix table 7.1b). However, this association was also non-significant for males when correcting for multiple testing.

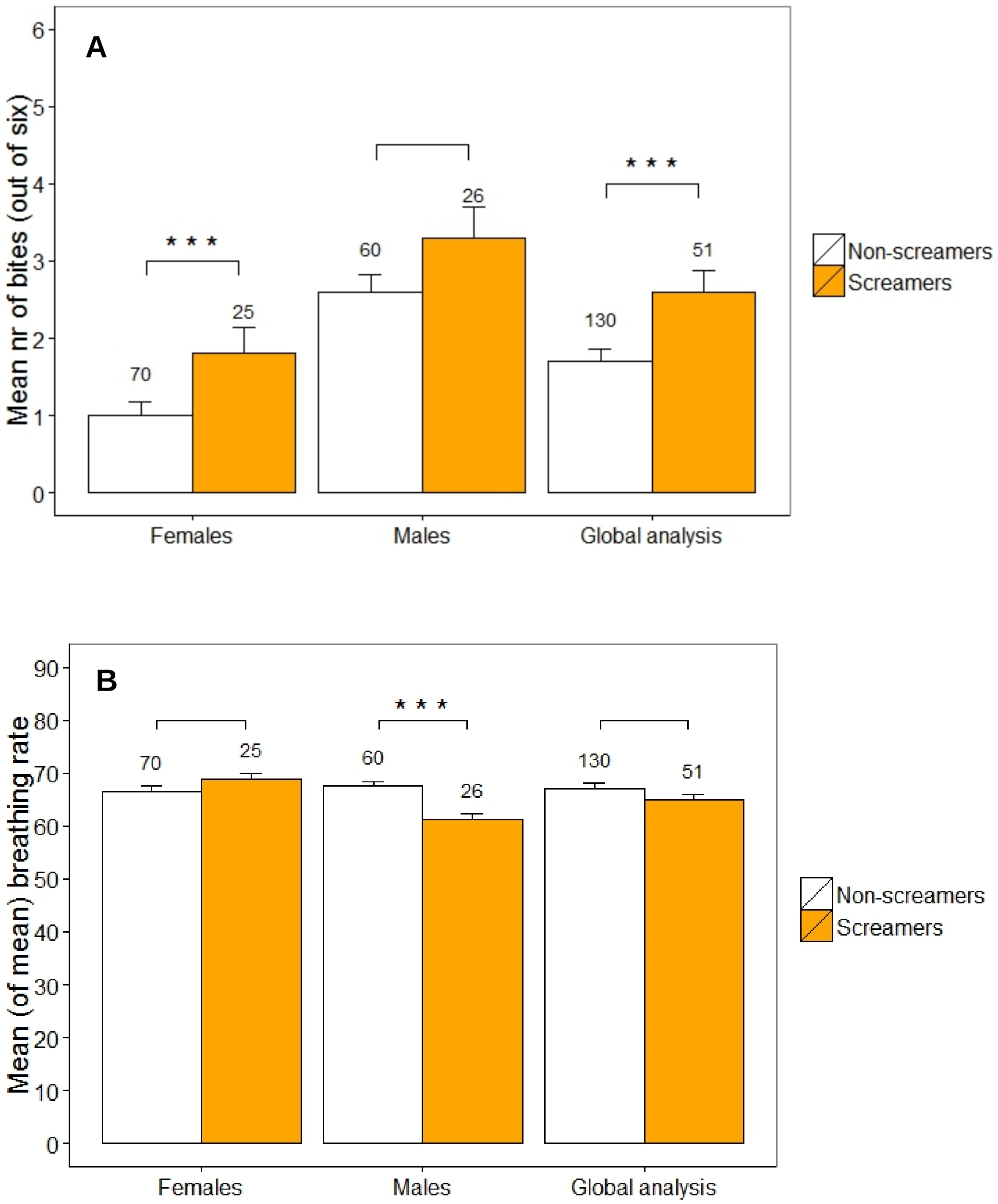

Figure 5. Barplots showing comparison of mean (+SEM) biting score (A) and breathing rate (B) between screaming and non-screaming great tits. Comparisons were made within sexes and for both sexes combined (global analysis). Numbers above error bars indicate sample size for each group. Annotations (*) indicate level of significance based on uncorrected p-values: *** = $p < 0.05$. No asterisk = p-value not significant.

Table 4. Association between all the behaviour traits measured on female and male great tits during all four behaviour tests conducted in the present study. Results are from separate analyses for females (below the diagonal) and males (above the diagonal). "+"[1], "-"[2] and "0" indicated positive, negative and no association, respectively. No sign indicates no data (variables not measured on males). - - - -/++++: p < 0.001, +++/- - -: p < 0.05, ++/- -: p < 0.10, +/-: p > 0.10, 0: p > 0.50.

	Breathing rate	Biting	Screaming	Immobility	Alarm call	Distance hand	Hissing	Call inside	Attentive-ness	Call leaving	Distance box	Call 2 min	Distance 2min	Predator response	Conspecific response
Breathing rate	●	+	- - -	0	+	+ +								+ +	-
Biting	+ + +	●	+	0	-	+ + +								+	0
Screaming	+	+ + +	●	+	0	-								0	+
Immobility	-	-	+	●	+	+								+	+
Alarm call	-	+	-	- - -	●	-								-	-
Distance hand	+ + +	-	0	+	- -	●								+	-
Hissing	+	+ +	+	+ +	0	-	●								
Call inside	0	0	+ +	0	0	0	+ + +	●							
Attentiveness	0	+	+	0	0	+	0	+ + +	●						
Call leaving	0	+	+	0	+ +	+ +	0	0	+	●					
Distance box	+ + +	+	+	0	+	+	0	0	-	0	●				
Call 2 min	0	0	0	0	-	0	-	0	0	-	0	●			
Distance 2 min	0	0	-	0	0	+	0	0	-	+	+ + + +	-	●		
Predator response	0	-	0	+	-	+	0	0	0	0	+ +	0	+	●	-
Conspecific response	- -	+	+	0	+	- - -	-	+	0	- -	0	0	+	-	●

[1] +: positive correlation / yes category has a higher mean value

[2] -: negative correlation / no category has a higher mean value

Note: Please see Material and methods for definition of traits

As found in the global analysis, breathing rate was positively correlated with distance moving away from hand for both females and males analysed separately. The association was significant for females (also after correction of multiple testing), but not significant for males (Figure 6A, Appendix table 7.1a). A significant positive association was found between biting and distance from hand for males (Figure 6B, Table 3, Appendix table 7.1a). For females, an opposite, but non-significant relationship was found for the same traits (Figure 6B, Appendix 7.1a), and no relationship between the trait was found in the global analysis (Table 3).

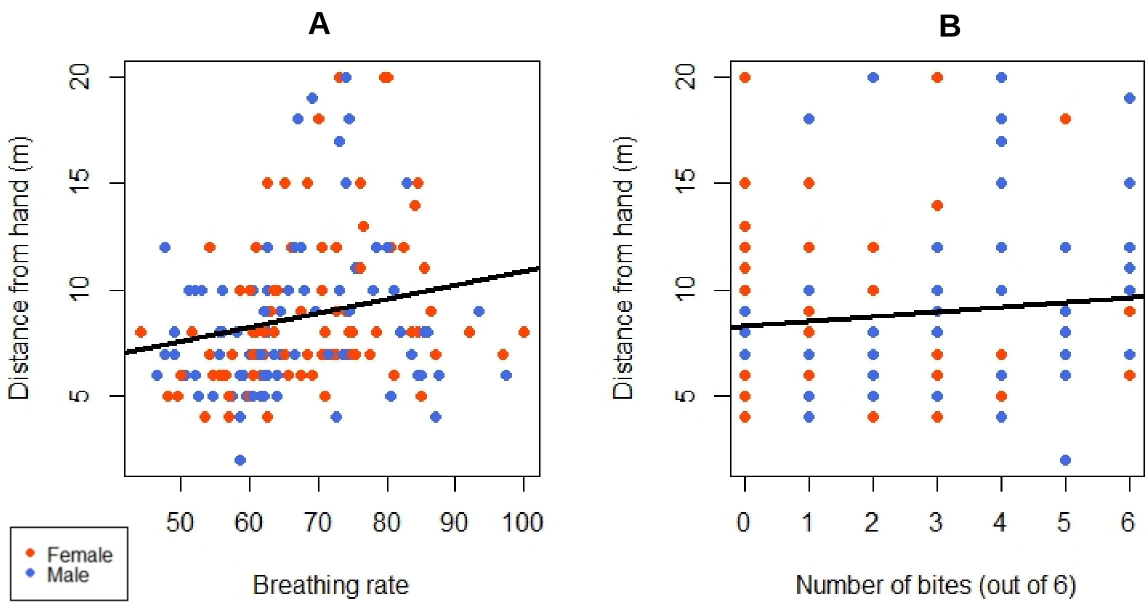

Figure 6. Scatterplots showing correlation between behavioural traits measured on female and male great tits during the in-hand test. A: Distance from hand (m) vs mean breathing rate (global analysis: r = 0.25, N = 181, p < 0.001). B: Distance from hand (m) vs. biting (global analysis: r = 0.04, N = 181, p = 0.58).

Due to sex differences in some variables, all relationships between variables were analysed in appropriate models with sex as a factor. Most of the relationships (or lack thereof) found in separate analysed held even though sex was included in the model. One exception was the association between alarm call and immobility found for females, where only sex and the interaction with sex were significant (Appendix 7.3a and b). Sex had a significant main effect on biting and predator response in all models (data not shown), as found in the simple comparison analyses between the sexes.

Behavioural traits measured for females

Between attentiveness traits measured during the incubation period and traits measured during other tests, some significant associations were found (Table 3). Females that had a higher breathing rate perched further away from the nest box during the attentiveness test (Appendix table 7.2a). A positive association was found between hissing and call inside, indicating that hissing females also made calls inside the nest box (Appendix table 7.2b). However, the association between breathing rate and distance from box, and hissing and call inside, were not significant after correcting for multiple testing. The only significant associations that were robust to multiple correction where between traits measured during the attentiveness test. Distance from nest box to perch site (distance box) and distance after 2 min after leaving the nest box were positively correlated (Appendix table 7.2a). Females that called inside the nest box had a higher attentiveness score than non-callers (Appendix 7.2b).

3.4 FAMD-analyses

FAMD analyses were divided into global and separate analyses for the in-hand behavioural traits, and separate analyses including all behavioural traits measured for males and females. Variation explained by the first dimensions is given for each analysis (Table 4-7).

3.4.1 Behavioural traits measured during the in-hand test

Global analysis

All six behavioural traits from the in-hand test were analysed together, and age and sex was added as supplementary variables, i.e. they had no influence on the dimensions of the analysis, but could help interpret the dimensions of variability. The first dimension did not explain more than 23 % of the variance in the data set. The first and second dimension resumed ~ 43 % of the total variance, which increased to 60 % when including dimension 3 (Table 5). The first five dimensions are shown (by default), although only six traits were included in the analysis.

Table 5. Shows the five first dimensions retrieved from the global FAMD analysis on all traits measured on great tits during the in-hand test. Variance is the eigenvalue for each dimension. Percentage of variance show how much percentage of the total variance in the dataset is explained by each eigenvalue/dimension. Cumulative percentage of variance shows how much of the total variance is explained by the current and all preceding dimensions.

	Dim. 1	**Dim. 2**	**Dim. 3**	**Dim. 4**	**Dim. 5**
Variance	1.36	1.20	1.07	0.93	0.77
Percentage of variance	22.73	19.99	17.76	15.48	12.76
Cumulative percentage of variance	22.73	42.72	60.47	75.96	88.72

Behavioural traits from the in-hand test are plotted on dimensions 1 and 2, and 1 and 3, in Figure 7. The variables factor map did not show any clear structure of behavioural traits. Breathing rate, screaming and distance from hand contributed the most to dimension 1 and 2, whereof the former two contributed most to dimension 2 and the latter to dimension 1. Immobility and biting contributed most to dimension 3. Immobility contributed weakly to dimension 1 and 2, but was strongly linked to dimension 3. (Appendix table 8.1a and b).

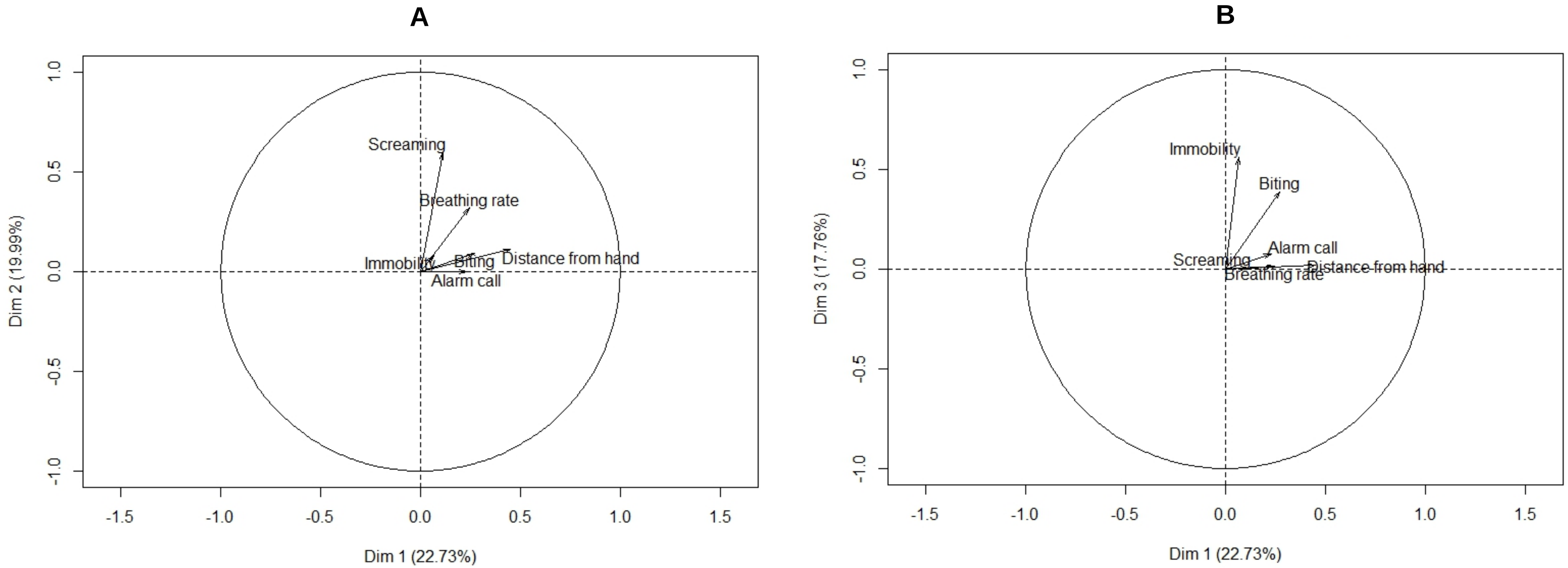

Figure 7. Variables factor maps from a global FAMD-analysis on behavioural traits measured on great tits during the in-hand test, showing how the traits score on A: dimension 1 (x-axis) and 2 (y-axis) and B: dimension 1 (x-axis) and dimension 3 (y-axis). Percentage indicate how much of the total observed variance the corresponding dimensions explain.

There were no difference between groups of supplementary variables as illustrated in Figure 8. Sex was linked to the three first axes, but the correlations were weak (Appendix table 8.1b). Females had in average higher coordinates on dimension 1, while males had lower coordinates. The opposite was true for dimension 2. Age was only weakly linked with dimension 2, with older birds having in average higher coordinates and younger birds lower coordinates.

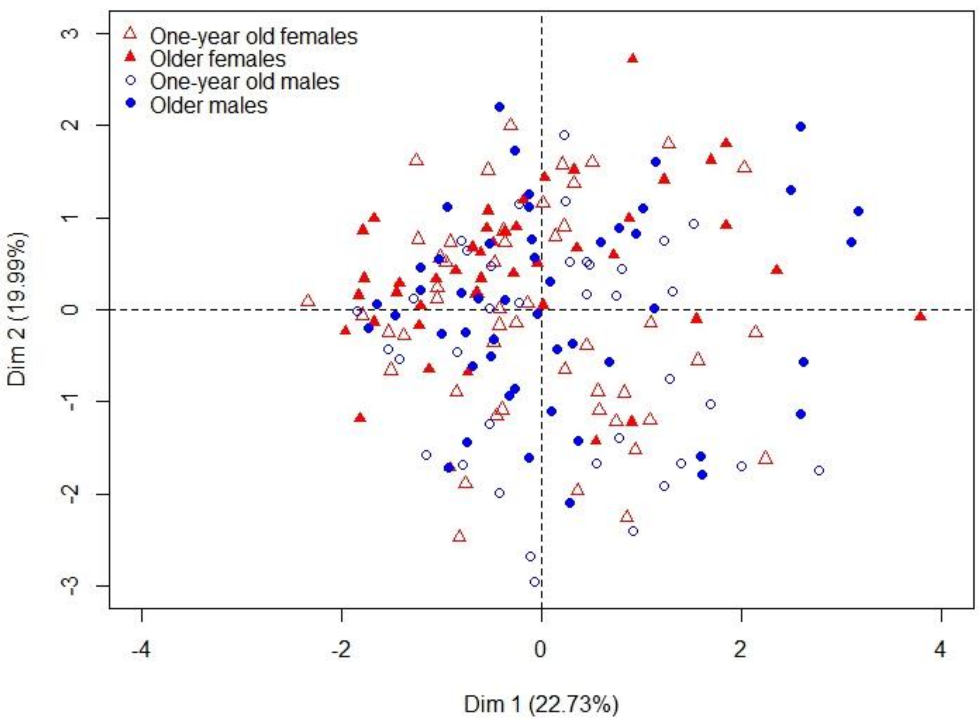

Figure 8. Individual factor map from global FAMD-analysis on great tit behavioural traits from the in-hand test. Individual visualisation is based on supplementary variables (age and sex) from the analysis. Percentage indicate how much of the total observed variance the corresponding dimensions explain.

Separate analyses

The five first dimensions retrieved from separate analysis on in-hand behavioural traits for females and males are shown in Table 6. The dimensions from each analysis explained similar (but slightly higher) percentage of total variance as the dimensions from the global analysis.

Table 6. Separate FAMD-analyses for female (a) and male (b) great tits including behavioural traits measured during the in-hand test. See Table 5 for further explanation.

a) Females

	Dim. 1	**Dim. 2**	**Dim. 3**	**Dim. 4**	**Dim. 5**
Variance	1.49	1.31	1.15	0.77	0.69
Percentage of variance	24.78	21.78	19.23	12.74	11.54
Cumulative percentage of variance	24.78	46.56	65.79	78.53	90.07

b) Males

	Dim. 1	**Dim. 2**	**Dim. 3**	**Dim. 4**	**Dim. 5**
Variance	1.39	1.32	1.20	0.83	0.66
Percentage of variance	23.21	21.92	19.95	13.88	11.09
Cumulative percentage of variance	23.21	45.12	65.08	78.95	90.04

When comparing the separate analyses, the dimensions explains approximately the same amount of total variance for females and males. However, the variables factor maps from each analysis with the two first dimensions showed a different construction of the behavioural traits for female and male great tits (Figure 9). In the female analysis, immobility, biting and alarm call contributes most to the two first dimension (Appendix table 8.2a). The male structuring was more similar to the global analysis: breathing rate, screaming and distance from hand contributed the most to the first two dimensions and immobility scored high on dimension 3 (Appendix table 8.2b).

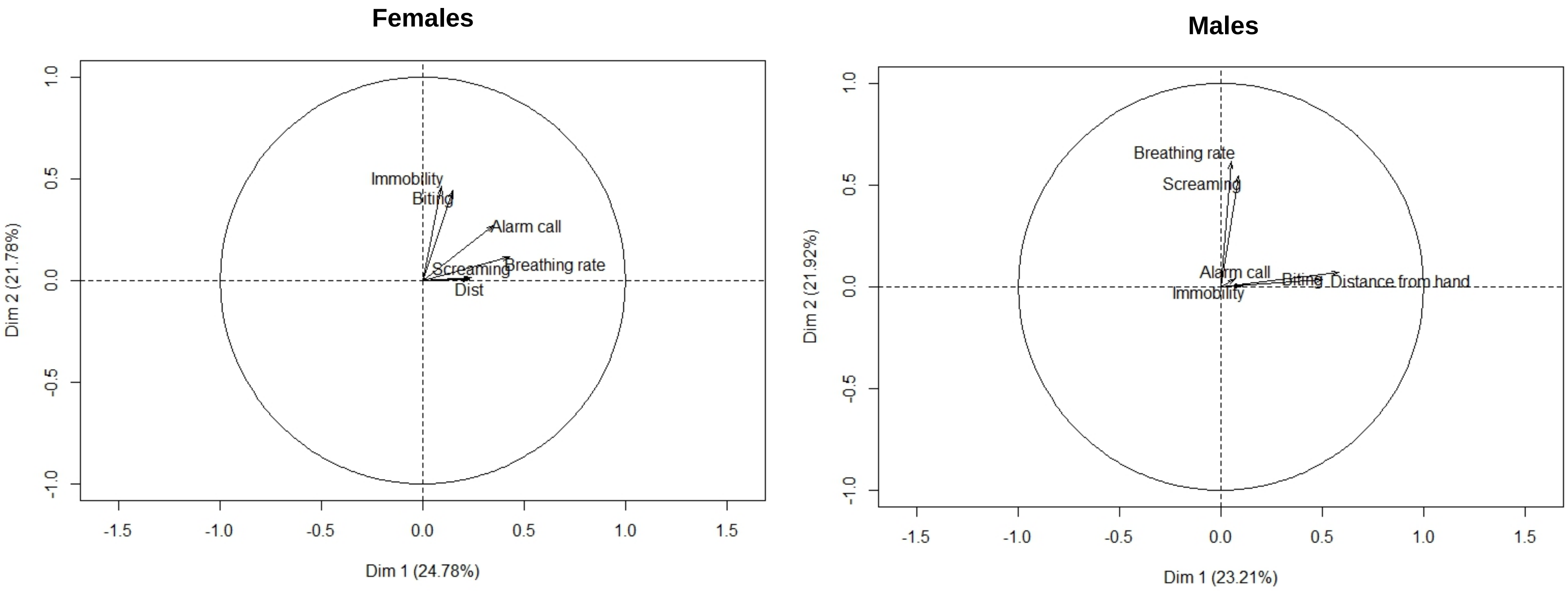

Figure 9. Variables factor maps from separate FAMD-analysis on behavioural traits measured on female and male great tits during the in-hand test, showing how the traits align with dimension 1 (x-axis) and 2 (y-axis). Percentage indicate how much of the total observed variance the corresponding dimensions explain.

3.4.2 All behavioural traits measured for females and males

The purpose was to study where the traits measured in other than the in-hand test were located in a space of dimension 1 and 2 along with the traits measured in the in-hand test.

Females

In a total analysis on behavioural traits for females, 13 behavioural traits were included (Appendix table 8.3a and b). The first five dimensions explained ~ 60 % of the total variance in the dataset, where of the first two only explained ~ 28 % (Table 7). To resume over 90 % of the total variance, 11 dimensions had to be included (data not shown).

Table 7. FAMD-analysis on all behavioural traits measured on female great tits. See Table 5 for further explanation.

	Dim. 1	**Dim. 2**	**Dim. 3**	**Dim. 4**	**Dim. 5**
Variance	1.98	1.68	1.54	1.34	1.26
Percentage of variance	14.22	12.97	11.88	10.37	9.69
Cumulative percentage of variance	15.22	28.20	40.08	50.42	60.12

None of the behavioural traits contributed much, nor were they linked strongly to the three first dimensions (Appendix table 8.3a and b). As most of the traits clustered around the origin, only the five behavioural traits that contributed the most to the first two dimensions are shown in Figure 10. Conspecific response contributed to both dimensions, but was stronger linked to the dimension 1. Call leaving was somewhat linked along the second dimension, with callers having in average higher coordinates than non-callers (Appendix table 8.3b). Of the variables not shown, predator response was not associated with any of the three first dimensions, and hissing and call inside were only weakly linked to the first dimension. The supplementary variable, age, was not linked with any of the first three dimensions (Appendix table 8.3b).

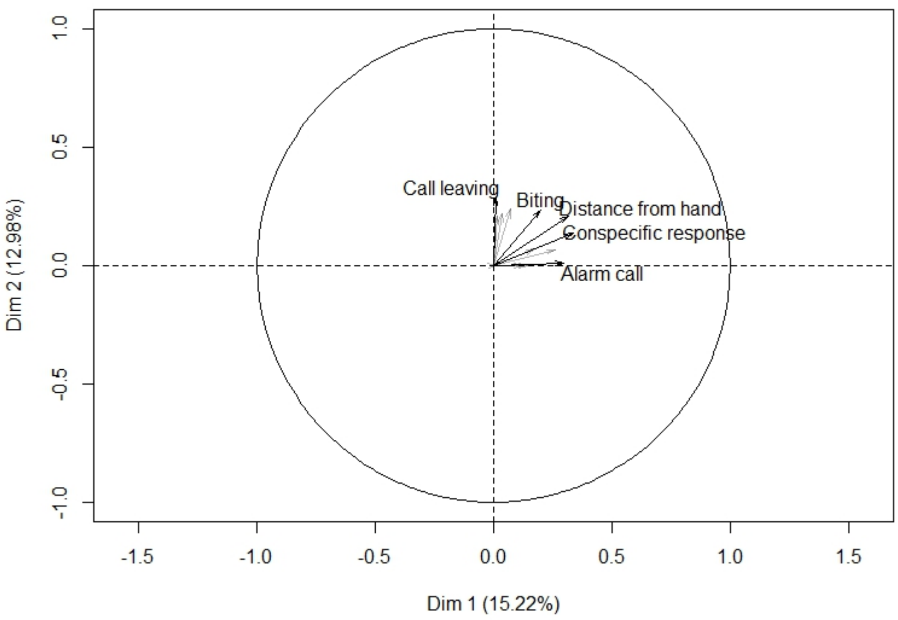

Figure 10. Variables factor map from separate FAMD-analysis on (all) behavioural traits measured on female great tits, showing how the traits align with dimension 1 (x-axis) and 2 (y-axis). Only the five traits that contributed the most to the first two dimensions is given. Percentage indicate how much of the total observed variance the corresponding dimensions explain.

Males

The FAMD-analysis on all behavioural traits measured on male great tits included six traits measured during the in-hand test, one from the conspecific intruder test, and one from the predator model tests (Figure 11, Appendix table 8.4a and b). The first five dimensions explained ~ 80 % of the total variance in the data set (Table 8).

Table 8. FAMD-analysis on all behavioural traits measured on male great tits. See Table 5 for further explanation.

	Dim. 1	**Dim. 2**	**Dim. 3**	**Dim. 4**	**Dim. 5**
Variance	1.74	1.50	1.39	1.12	0.97
Percentage of variance	21.79	18.76	17.33	14.05	12.12
Cumulative percentage of variance	21.79	40.55	57.88	71.93	84.05

A variables factor map for the two first dimensions, which resumed ~ 41 % of the total variance, showed that predator response was moderately positively linked to dimension 2 (Figure 11, Appendix table 8.4b). Conspecific response was moderately negatively linked with dimension 1, but did not contribute a lot to the construction of the dimension. The supplementary variable, age, did not correlate with any of the first three dimensions (Appendix table 8.4b).

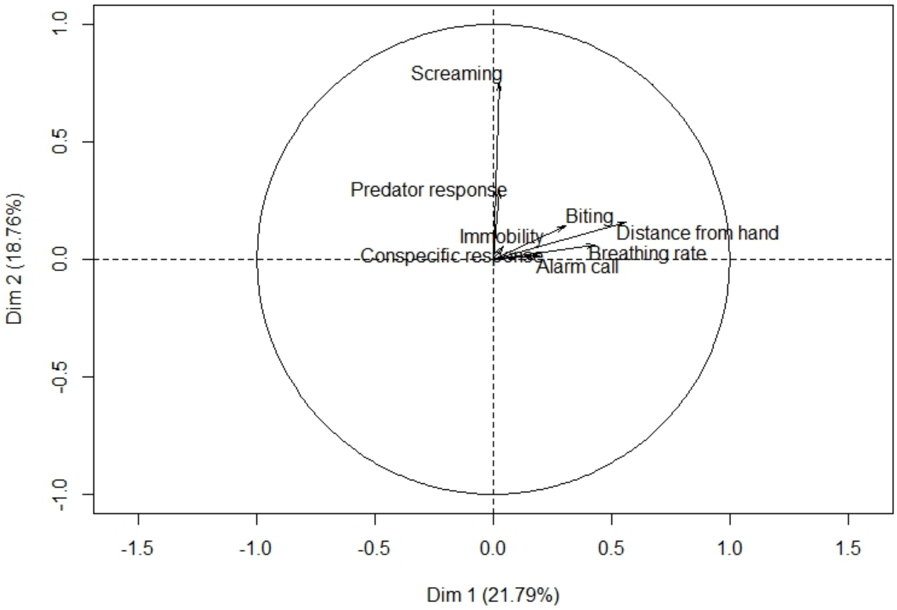

Figure 11. Variables factor map from separate FAMD-analysis on (all) behavioural traits measured on male great tits, showing how the traits align with dimension 1 (x-axis) and 2 (y-axis). Percentage indicate how much of the total observed variance the corresponding dimensions explain.

4 Discussion

This study found some evidence for repeatable behaviour within individuals within the study season. In general, few significant associations were found between different behavioural traits, and the correlations or differences between behavioural traits were often low, indicating that personality may not be best explained by a single personality axis. The most significant associations found will be discussed below in relation to the hypotheses addressed and also the literature on the shyness-boldness personality axis. Variation in behavioural response within traits as well as possible limitations of the study will also be addressed.

4.1 Repeatability in behavioural traits

Repeatability tests found some evidence of consistent behaviour within contexts (test scenarios). Breathing rate was strongly repeatable within in-hand test trials. There was a significant increase in individuals breathing rate from the first to second measurement, which may indicate an increased stress response to handling. However, the increase was only by one to two heartbeats. One measurement of breathing rate during the in-hand test may therefore be sufficient in future studies.

Distance from nest box and call when leaving the nest box measured for females in the incubation period was found to be repeatable across two trials and there was no difference in perch distance between the first and second measurement. This could indicate consistent behaviour, but it could also be due to habitat constraints. Available vegetation surrounding nest boxes varied across the study area.

There was also a tendency for individual repeatability in the attentiveness trait for females during incubation. Females were more persistent to stay on the nest during the second trial. The second trial was performed later in the incubation period (when some chicks had hatched), and the increase in attentiveness could be due to increased reproductive value of the clutch. Thorsteinsen (2015) found that attentiveness was positively associated with clutch size ($r_s = 0.23$, $N = 75$, $p = 0.045$) in the same great tit individuals used in the present study, which could indicate that females with larger clutches were more attentive than females with smaller clutches. Another explanation could be habituation to the human intruder, with females turning less fearful during the second test. Consistency were found in the call leaving variable, indicating that females that called when leaving the nest box after being disturbed by a human, also called when leaving during the second trial.

The attentiveness test was the only test with different observers, which could be a reason for the low repeatability of some traits. However, the measurement protocol of traits was well characterised and repeatability was found for some of the traits, indicating that measurement error was probably not the only reason for low repeatability. Another explanation could be that the behavioural responses were plastic and context dependent at the time of measurement. The birds' behaviour may for example be affected by local weather conditions (e.g. temperature), presence of conspecifics or heterospecifics, time since last incubation visit, and changes in physiological needs and states.

Unfortunately, due to time constraint during the fieldwork, repeatability could not be tested for all behavioural traits measured in this study. In a previous study on the same study population, repeatability was tested for the in-hand behavioural traits measured on individuals captured in autumn 2010 and 2011. Andersen (2012) found that screaming and breathing rate was significantly repeatable within seasons ($\chi^2 = 9.89$, N = 58, p = 0.002 and r = 0.50, N = 56, $p < 0.001$, respectively), and that breathing rate were almost repeatable across the two years (r = 0.43, N = 21, p = 0.06).

4.2 Relationship between traits

The main aim of the present study was investigate whether personality in great tits can be characterised by a small number of independent traits (predicted from H0), by a few groups of behavioural axes (predicted from H1), or by a single personality axis only going from shy to bold (predicted from H2). Some significant associations between traits were found, rejecting H0. However, as there were few, and in general weak associations between traits, a single personality axis could hardly explain the behavioural variation observed. Therefore, H2 is also rejected, making H1 most plausible, which means that the personality of individuals can only be explained by several dimensions, but not necessarily by an infinite number. This is in agreement with personality studies on other taxa (e.g. octopuses, fishes and many mammalian species), where more than one major personality axis is used to describe personality (reviewed in Gosling and John 1999).

In general, the FAMD-analyses did not show any clear construction of behavioural traits along dimensions and no dimension could explain more than 25 % of the total variance in the different analyses. However, the FAMD results were not surprising based on the findings in the prior two-by-two relationship analyses. In the in-hand test, breathing rate, biting, and distance from hand, stood out from the FAMD-analysis in explaining more of the variation across the traits. However, even these traits could only explain a small proportion of the total variance (~ 23 %). When traits from other tests were included in additional analyses, no clear link between these traits and the first three dimensions were found. The FAMD also failed in separating individuals based on the supplementary variables age and sex. This was neither surprising, as few differences in behaviour between age and sex categories were found in the previous tests.

4.3 Associations in relation to boldness

A second aim with the study was to try to find out which of the behavioural traits measured in the present study could be good indicators of personality for further studies. The traits measured were therefore evaluated based on their possible association to boldness (Table 9). Some associations between behavioural traits and boldness were a priori assumed: biting, and conspecific response are positively associated with boldness, whilst predator response and perch distance are negatively associated with boldness. Association with boldness for other traits measured were based on previous literature, and their association with the traits a priori assumed related to boldness.

Breathing rate was found to be highly repeatable within individuals in this study, and have also been found to be repeatable within two other seasons (repeated from above). Studies in captivity have found that slow explorers have higher breathing rate than fast explores (Carere *et al.* 2001, Carere and van Oers 2004). Therefore, breathing rate may be negatively associated with boldness. In support of this, breathing rate was found to be negatively associated with conspecific response, and positively associated with two perch distance traits (distance from hand, and distance from nest box) in this study. However, an association found that may contradict this was a positive association between breathing rate and biting.

In many small prey species, individuals produce vocal signals in the context of threat. Distress calls given when being captured by a predator or a human are hypothesised to confuse predators or to warn conspecifics and facilitate mobbing behaviour (Branch and Freeberg 2012). Alarm calls after being captured by a human has been proposed to be reciprocal altruism and a mate protection strategy (Krams *et al.* 2006). A study by Hollander *et al.* (2008) found that the intensity of alarm calling was positively associated with exploration in great tits and one may expect vocal signals to be bold as the birds may attract attention from predators. In this study, screamers bit more than non-screamers. The same relationship was found by Andersen (2012), who also found that alarm callers perched closer to the human. The same non-significant relationship was also found in the present study. This may indicate that screamers may be more aggressive, and screaming may be positively associated with boldness.

However, in this study, vocal behaviours were only measured as present or absent, and the number of times screaming individuals actually screamed were not accounted for. The association found by Hollander *et al.* (2008) between intensity of alarm calling and exploration may indicate that alarm calling (or other vocal traits) may not be a bold behaviour per se, but that it is bolder to have a higher calling intensity. Therefore, screamers and alarm callers in this study were not necessarily bold. This problem extend to all vocal behaviours measured in the study. Number or intensity of calls may be a better predictor of personality. Based on this, alarm call and screaming are considered positively associated with boldness because screaming was associated with biting, and alarm calling have been found to be associated with perch distance in a previous study (Andersen 2012).

The vocal behaviours measured during the attentiveness test did not show any significant association with the a priori assumed traits. Calling inside was positively associated with hissing (discussed below). It is hard to extrapolate the assumptions of the vocal traits measured in the in-hand test to the vocal traits from the attentiveness test as they were from two different contexts. Studies on vocal traits in titmice have shown that vocal signals may be context dependent. For instance, the level of risk of predation, if the threat is within the birds home range, and the presence of mate or conspecifics have been shown to affect vocal signals in titmice (Krams 2001, Krams *et al.* 2006). Association between boldness and vocal traits from the attentiveness test needs further study.

A high immobility score when leaving the hand may be considered a shy behaviour, as it may be because birds “freeze” as a response to high level of fear (Andersen 2012). However, it may also be bold behaviour, as the bird may show lower level of fear by not escaping the human "predator" at the first chance (Thorsteinsen 2015). In this study, no relationship was found between immobility and most of the other behavioural traits (Table 3). Immobility was associated with alarm call (discussed above), but the association differed between sexes, with screamers having lower immobility score than non-screamers in females, and an opposite result in males. Therefore, immobility is considered not to be associated with boldness.

Krams *et al.* (2014) studied great tit females' hissing behaviour towards predator intruders, when incubating in nest boxes, in relation to survival and found that hissing was highly repeatable, and that females could be divided into two types with regard to their propensity to give hissing calls. Krams *et al.* (2014) therefore suggested that hissing may be related to differences in personality and that giving hissing calls is a "risky" behaviour, which may therefore be considered a bold anti-predator response. In this study, hissing showed no or weak relationship with most of the other traits. Hissing was only significantly positively associated with call inside the nest box (discussed above), and it is therefore hard to state any relationship with boldness.

A high attentiveness score may be considered a bold behaviour, as the females do not try to escape the predator at first chance and instead try to protect their clutch (Thorsteinsen 2015). However, some birds did not voluntarily leave the nest box, and tried to hide in the nest by digging down in the nest material (pers. obs.). This could indicate that females with a high attentiveness score were shy and tried to hide from the predator. As attentiveness was not associated with any of the traits a priori assumed related to boldness, the trait is considered not to be associated with boldness.

No traits from the attentiveness test were strongly associated with the traits measured in other tests and significant association for these traits were only found within the test scenario. This may indicate that the females' response to human when incubation could represent behavioural variation along a different personality axis other than the shyness-boldness axis.

Table 9. Relationship between behavioural traits recorded in the present study and boldness in great tits. Traits 1-4 are a priori assumed to relate strongly to boldness. For the rest of the traits, the relationship with boldness is judged based on their individual association with traits 1-4 and previous literature (see main text).

No.	Behavioural trait	Association with boldness	Comments/Significant associations
1	Distance to predator	Negative	A priori assumed
2	Time on cage of intruder (females)	Positive	A priori assumed
3	Perch distance (all tests)	Negative	A priori assumed
4	Biting	Positive	A priori assumed
5	Breathing rate	Negative	Positively associated with distance from hand and distance from nest box (3) and negatively correlated with conspecific response (2). But, was positively associated with biting (4).
6	Screaming	Positive	Positively associated with biting (4).
7	Alarm call	Positive	Previously found to be associated with distance from hand (3). Same (non-significant) negative association with distance from hand (3) in the present study.
8	Immobility	None	No significant relationship with traits 1-4. Associated with alarm call, but the association pattern differed between sexes.
9	Attentiveness	None	No association with traits 1-4. Positively associated with calling inside (11).
10	Hissing	None	No association with traits 1-4. Positively associated with call inside (11)
11	Vocal traits (attentiveness test)	None	No association with traits 1-4. No association with other vocal traits (6-7). Call inside (the nest box) was positively associated with attentiveness (9).

Note: Please see Results (section 3.3) and Appendix 7 for details on the associations between traits.

4.4 Variation within behavioural traits

The study did not reveal any clear relationship between the behavioural traits measured and body measurements (body mass, wing and tarsus length) of individuals. Males with longer tarsus had a higher breathing rate, and females with a longer tarsus spent more time within a short distance to the caged conspecific intruder. Based on Table 9, these results may indicate that larger males were more shy when handled by a human than smaller birds, and larger females are bolder when being exposed to a conspecific intruder than smaller females. However, breathing rate and conspecific response to an intruder was not associated with any other body measurement in males and females, respectively. Males that screamed had a longer tarsus than males that did not scream, but even though statistically significant, the difference was so small (0.04 mm) that it is highly unlikely that this association was of biological relevance.

Males bit more and had a stronger response towards a predator model (an owl) than females. Therefore, males may be bolder than females when handled by a human and when facing a predator (Table 9).

More one-year old birds screamed compared with older birds and one-year old females were more attentive of their clutch than older females when disturbed by a human. Contrary, older birds had a stronger response towards the predator model than one-year old birds. Based on Table 9, this could indicate that younger birds may be bolder than older birds when handled by a human, and older birds are bolder than one-year old birds when exposed to a predator model. Other explanations to the behavioural difference between age categories could be that bold one-year olds have a lower survival, making the behaviour less bold among adults, or that the birds alter their behaviour as they age (e.g. by experience). These alternatives are not mutually exclusive.

FAMD-analyses did not reveal any significant differences between age and sex categories, which may indicate that, differences in behaviour between categories might be restricted to single behaviours and that there is no general pattern of one of the sexes or age category being bolder across different contexts (test scenarios) in the population. Further studies which follow individuals from their first year into adulthood is needed, to study if the behavioural differences in behavioural responses between age categories are consistent.

For the in-hand behavioural traits, there was some variation in behaviour between seasons (Appendix table 5.1). This study does not provide data on behaviour of the same individuals across seasons, making it difficult to state whether this indicate individual change of behaviour with seasons (e.g. due to different energy allocation) or if maybe some personality types are more prone to capture in for instance, the autumn, compared to spring. There were also a significant association between trial date and time of day for some of the behavioural traits (Appendix 6.1-6.5). However, because this study mostly measured individuals only once, it is not possible to know if there was a consistent change in behaviour with capture time at the individual level. Birds that were kept for a longer time in the bird bag before the in-hand test had a higher breathing rate, bit more and perched further away after leaving the hand than birds kept for a shorter time. This could indicate that birds that were kept for a longer time before tested were more stressed when handled than birds kept for a shorter time, and therefore that the behaviour may have to be adjusted according to time in bird bag. Further studies should test individuals more than once, for instance at different times in the season and keep them in different time intervals in the bird bag, to see if there is an effect on the behaviour at the individual level.

4.5 Limitations and future studies

Some limitations to the present study and suggestions to future work are already discussed above. As previously mentioned, repeatability was not tested for all behavioural traits, and should be a future aim to see if all the behaviours are repeatable, as it is a prerequisite of defining personality traits. Low repeatability for some traits could be due to measurement errors or behavioural plasticity, but the former was probably a minor problem as discussed above. However, reduction of observers in the attentiveness test could be of value to exclude possible inter-observer variation when measuring the belonging behavioural traits (cf. Andersen 2012). Further research, following individuals over more than one year, is needed to see if the behaviours are consistent over time and/or contexts.

Few significant associations between the behavioural traits measured were found in the pairwise relationship analyses and the FAMD failed to reduce the dimensionality. Even when associations were significant the correlations were in general low (r/r_s = 0.10-0.35). Sample size could be a reason to why some associations were not statistically significant. However, the study included more than 180 birds, indicating that this problem might be restricted to only a few behavioural traits with small sample size (e.g. call after 2 min and distance after 2 min measured during the attentiveness test). Hence, further studies on consistency in the behavioural traits seem necessary before any reduction of measurements can be carried out in future studies.

More possible confounding factors may have affected the results, such as local weather conditions, and time since last incubation, as already mentioned. The presence of mate or other conspecifics could also be important factors, as it is possible that individuals could be bolder in a situation, e.g., towards a predator, in the company of other individuals.

Lastly, this study did not have the opportunity to measure exploratory behaviour in captivity in the standardised way that has been frequently used in the literature. Comparing exploratory behaviour of the great tits in the Dæli population with the behavioural traits measured in this study could help to explain associations between behavioural traits, and to see which traits measured in the present study that are the best indicators of personality in great tits. Studies on exploratory and risk-taking behaviour on great tits in captivity have shown that behavioural traits can be heritable. Further studies on heritability of the traits measured in the present study would therefore be of interest.

5 Conclusion

Personality in great tits has often been explained by the use of a single, well-studied personality axis, known as the shyness-boldness continuum. This study shows that behaviour in wild great tits may be better explained by groups of behavioural traits, representing several (but not an indefinite number) of personality axes. Repeatability was found for some traits measured (breathing rate, distance from nest box, call when leaving, and tendencies for attentiveness). Several traits were also considered associated with boldness. These traits may therefore be predictors of personality in wild great tits. However, as repeatability was not tested for all traits and weak associations were found between traits, further studies seems necessary before any reduction of number of traits measured can be implemented in future studies. No strong association was found between behavioural and morphological traits. Furthermore, no general behavioural differences were found for different sex and age classes, with the exceptions that males bit more and approached the predator model more closely than the females. Further studies testing repeatability for all traits and following individuals over more than one year seems necessary to conclude which traits (and associations between traits) may be consistent within individuals. Additionally, comparative studies with exploration and investigation of trait heritability could help determine which of the measured traits may be good predictors of personality.

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Appendix

Note: The transformed behavioural traits used in statistical analyses were back-transformed in all tables in the Appendix for easier interpretation. This included: (mean) breathing rate from the in-hand test, and distance from nest box and distance from nest box after 2 minutes from the attentiveness test. Please see Material and Methods (part 2.2.3) for detailed description of all the behavioural traits.

Appendix 1. Effect of stimuli bird

Appendix table 1.1. Mann-Whitney U-test for differences in conspecific response between groups of great tits tested with two different stimuli birds (female great tits) during the conspecific intruder test. Females and males were analysed separately due to different measurements of the conspecific response trait.

Sex	**Stimuli bird 1 mean ± SD**	**N**	**Stimuli bird 2 mean ± SD**	**N**	**z**	**p**
Females	110.5 ± 116.4	46	156.9 ± 114.8	36	- 1.55	0.12
Males	1.8 ± 2.2	22	2.2 ± 2.2	26	- 0.74	0.46

Appendix 2. Consistency in behavioural traits measured twice

Appendix table 2.1. Pearson correlation tests between first and second measurement of breathing rate (from in-hand test) analysed separately for female and male great tits. Significant p-values ($p < 0.05$) are marked in bold.

	r	**N**	**p**
Females	0.91	95	< **0.001**
Males	0.89	86	< **0.001**

Appendix table 2.2. Comparison of behavioural trait values (given as mean ± SD), between first and second measurement of three quantitative behavioural traits taken on great tits that were consistent across the two measurements (see Table 2 in main text). Comparisons of breathing rate was done for all individuals (global analysis) and sexes separately.

Analysis	**Behavioural trait**	**First measurement**	**N**	**Second measurement**	**N**	**t[1]/V[2]**	**p**
Females	Breathing rate	66.4 ± 1.2	95	67.7 ± 1.2	95	-2.31[1]	**0.023**
	Attentiveness	1.9 ± 1.2	29	2.5 ± 1.3	29	24[2]	**0.041**
	Distance box	7.7 ± 1.5	72	7.2 ± 1.8	29	-0.08[1]	0.94
Males	Breathing rate	64.1 ± 1.2	86	66.6 ± 1.2	86	-3.86[1]	< **0.001**
Global	Breathing rate	66.1 ± 1.2	181	67.6 ± 1.2	181	-4.36[1]	< **0.001**

[1]t: Student's paired t-test

[2]V: Wilcoxon signed rank test

Appendix 3. Relationships between behavioural- and morphological traits

Appendix table 3.1. Correlation between numeric behavioural traits and body measurements. Females and males were analysed separately. "-" indicates behavioural traits not measured for males. Significant p-values (< 0.05) are marked in bold.

Behavioural traits	**Morphological traits**	**Females** r^1/r_s^2	**N**	**p**	**Males** r^1/r_s^2	**N**	**p**
Breathing rate	Body mass	0.06^1	95	0.54	0.25^1	86	**0.019**
	Wing length	-0.07^1	95	0.48	0.03^1	86	0.76
	Tarsus length	0.12^1	94	0.24	-0.10^1	85	0.32
Biting	Body mass	0.03^2	95	0.77	0.05^2	86	0.62
	Wing length	-0.01^2	95	0.89	0.02^2	86	0.79
	Tarsus length	0.01^2	94	0.90	0.07^2	85	0.52
Immobility	Body mass	0.01^2	95	0.91	0.01^2	86	0.96
	Wing length	0.11^2	95	0.30	-0.10^2	86	0.38
	Tarsus length	-0.13^2	94	0.22	0.00^2	85	0.98
Distance hand	Body mass	0.08^2	95	0.41	0.17^2	86	0.099
	Wing length	0.06^2	95	0.54	0.04^2	86	0.70
	Tarsus length	0.08^2	94	0.44	-0.06^2	85	0.57
Attentiveness	Body mass	-0.03^2	76	0.77	-	-	-
	Wing length	-0.18^2	76	0.13	-	-	-
	Tarsus length	0.13^2	75	0.28	-	-	-
Distance box	Body mass	-0.09^1	68	0.45	-	-	-
	Wing length	0.00^1	68	0.99	-	-	-
	Tarsus length	-0.14^1	67	0.25	-	-	-
Distance 2min	Body mass	-0.02^1	62	0.90	-	-	-
	Wing length	-0.00^1	62	0.97	-	-	-
	Tarsus length	-0.11^1	61	041	-	-	-
Conspecific response	Body mass	-0.09^1	66	0.45	0.09^2	59	0.49
	Wing length	-0.13^1	66	0.30	-0.19^2	59	0.14
	Tarsus length	-0.33^1	65	**0.008**	-0.09^2	58	0.46
Predator response	Body mass	0.01^2	78	0.96	0.05^2	48	0.71
	Wing length	-0.05^2	78	0.64	0.05^2	48	0.70
	Tarsus length	-0.05^2	77	0.69	0.08^2	48	0.56

[1]: Pearson correlation test, [2]: Spearman's rank correlation

Appendix table 3.2. Student's two sample t-tests for morphological differences between categories of dichotomous behavioural traits. Females and males are analysed separately. Significant p-values (< 0.05) are marked in bold.

	Behavioural traits					
	No		**Yes**			
Morphological traits	**mean ± SD**	**N**	**mean ± SD**	**N**	**t**	**p**
Females			**Screaming**			
Body mass (g)	170.8 ± 7.6	70	172.1 ± 8.3	25	-0.71	0.48
Wing length (mm)	746.9 ± 16.2	70	742.5 ± 12.9	25	1.21	0.23
Tarsus length (mm)	221.6 ± 6.7	69	222.2 ± 6.8	25	-0.39	0.70
			Alarm call			
Body mass (g)	171.5 ± 7.4	26	171.0 ± 7.9	69	0.27	0.78
Wing length (mm)	743.3 ± 16.0	26	746.6 ± 15.3	69	-0.95	0.35
Tarsus length (mm)	221.8 ± 6.1	26	221.9 ± 6.6	68	0.08	0.94
			Hissing			
Body mass (g)	170.4 ± 7.8	53	172.2 ± 8.2	23	-0.90	0.37
Wing length (mm)	746.6 ± 14.9	53	746.2 ± 14.7	23	0.10	0.92
Tarsus length (mm)	221.8 ± 6.6	52	222.4 ± 4.8	23	-0.41	0.69
			Call inside			
Body mass (g)	171.5 ± 8.3	53	169.7 ± 6.8	23	0.90	0.37
Wing length (mm)	746.0 ± 14.8	53	747.6 ± 14.8	23	-0.43	0.67
Tarsus length (mm)	222.1 ± 6.1	52	221.6 ± 6.1	23	0.37	0.71
			Call leaving			
Body mass (g)	168.9 ± 7.1	8	171.3 ± 8.2	60	-0.80	0.43
Wing length (mm)	750.6 ± 15.7	8	746.6 ± 14.5	60	0.74	0.46
Tarsus length (mm)	220.8 ± 6.5	8	221.6 ± 6.0	60	-0.38	0.71
			Call 2min			
Body mass (g)	171.2 ± 6.9	6	171.0 ± 8.1	57	0.06	0.95
Wing length (mm)	749.2 ± 17.4	6	746.1 ± 14.1	57	0.50	0.62
Tarsus length (mm)	220.5 ± 7.9	6	221.7 ± 6.0	56	-0.46	0.65
Males			**Screaming**			
Body mass (g)	181.6 ± 8.3	60	180.4 ± 7.3	26	0.60	0.55
Wing length (mm)	780.0 ± 15.7	60	774.4 ± 16.5	26	1.49	0.14
Tarsus length (mm)	222.8 ± 6.6	59	226.8 ± 7.9	26	0.57	0.57
			Alarm call			
Body mass (g)	180.5 ± 8.2	28	181.6 ± 7.9	58	-0.57	0.57
Wing length (mm)	778.4 ± 19.4	28	778.3 ± 14.3	58	0.03	0.97
Tarsus length (mm)	224.9 ± 8.4	28	228.7 ± 5.9	57	-2.40	**0.019**

Appendix 4. Comparisons of behaviour between sex- and age categories

Appendix table 4.1. Comparisons of behavioural trait values between one year old and older great tits, measured during the in-hand-(1), conspecific intruder-(2), predator model-(3) and attentiveness test (4). Both global and separate analyses were ran for behavioural traits measured the same way for both females and males. Significant p-values (< 0.05) are marked in bold.

	Age categories					
	One year old		Older			
Behavioural trait (test)	**mean ± SD**	**N**	**mean ± SD**	**N**	**Test statistic**	**p-value**
Global						
Breathing rate (1)	66.4 ± 1.2	87	66.4 ± 1.2	94	0.02[1]	0.98
Biting (1)	1.9 ± 1.7	87	2.0 ± 1.7	94	-0.29[2]	0.77
Screaming (1)*	39 %	87	18 %	94	8.83[3]	**0.003**
Immobility (1)	126 ± 61.1	87	109.8 ± 62.6	94	1.82[2]	0.069
Alarm call (1)*	71 %	87	68 %	94	0.02[3]	0.88
Distance hand (1)	8.3 ± 2.8	87	9.1 ± 4.3	94	-0.43[2]	0.67
Predator response (3)	3.9 ± 3.8	87	2.6 ± 2.5	94	-1.99[2]	**0.047**
Females						
Breathing rate (1)	67.6 ± 1.2	50	66.1 ± 1.2	45	0.27[1]	0.78
Biting (1)	1.2 ± 1.5	50	1.3 ± 1.7	45	0.01[2]	0.99
Screaming (1)*	38 %	50	13 %	45	6.21[3]	**0.012**
Immobility (1)	127.8 ± 60.6	50	111.3 ± 64.2	45	1.35[2]	0.18
Alarm call (1)*	72 %	50	73 %	45	0[3]	1
Distance hand (1)	8.4 ± 3.0	50	9.2 ± 4.2	45	-0.39[2]	0.70
Conspecific response (2)	160.6 ± 117.9	46	93.03 ± 106.5	36	2.51[2]	0.13
Predator response (3)	5.0 ± 4.8	37	3.3 ± 3.1	29	1.24[2]	0.21
Hissing (4)*	30 %	44	31 %	36	0[3]	1
Attentiveness (4)	2.3 ± 1.3	44	1.8 ± 1.1	36	2.09[2]	**0.037**
Call inside (4)*	32 %	44	28 %	36	0.02[3]	0.88
Call leaving (4)*	90 %	38	88 %	34	0.88[4]	1
Distance box (4)	8.1 ± 1.6	38	7.4 ± 1.6	34	0.66[1]	0.51
Call 2min (4)*	91 %	35	88 %	32	0.66[4]	0.70
Distance 2min (4)	8.0 ± 0.9	34	8.2 ± 0.6	31	0[1]	1
Males						
Breathing rate (1)	64.6 ± 1.2	37	66.1 ± 1.2	49	-0.38[1]	0.70
Biting (1)	3.0 ± 2.1	37	2.7 ± 1.8	49	0.75[2]	0.46
Screaming (1)*	40 %	37	22 %	49	2.47[3]	0.12
Immobility (1)	124.1 ± 62.5	37	108.4 ± 61.8	49	1.14[2]	0.25
Alarm call (1)*	70 %	37	65 %	49	0.06[3]	0.80
Distance hand (1)	8.1 ± 2.6	37	9.1 ± 4.4	49	-0.17[2]	0.86
Conspecific response (2)	2.5 ± 2.3	22	1.6 ± 2.0	26	1.48[2]	0.13
Predator response (3)	2.5 ± 1.9	25	2.1 ± 1.6	35	1.17[2]	0.24

[1]: Student's two-sample t-test (t) [2]: Mann-Whitney U test (z) [3]: Chi-square test (χ^2) [4]: Fisher's exact test (odds ratio)
*dichotomous variables: percentage of individuals screaming or giving alarm calls etc. within each age category

Appendix table 4.2. Comparison of the behavioural traits measured in the in-hand (1) test and predator model test (2) between female and male great tits. Significant p-values (< 0.05) are marked in bold.

	Females		**Males**			
Behavioural Trait (test)	**mean ± SD**	**N**	**mean ± SD**	**N**	**Test statistic**	**p-value**
Breathing rate (1)	67.1 ± 1.2	95	65.5 ± 1.2	86	0.93[1]	0.35
Biting (1)	1.2 ± 1.6	95	2.8 ± 1.9	86	-5.65[2]	**< 0.001**
Screaming (1)*	26 %	95	30 %	86	0.18[3]	0.67
Immobility (1)	120.0 ± 62.5	95	115.1 ± 62.2	86	0.49[2]	0.62
Alarm call (1)*	73 %	95	67 %	86	0.36[3]	0.55
Distance hand (1)	8.8 ± 3.6	95	8.7 ± 3.7	86	0.27[2]	0.79
Predator response (2)	4.3 ± 4.2	66	2.3 ± 1.7	60	2.56[2]	**0.010**

[1]: Student's two-sample t-test (t) [2]: Mann-Whitney U test (z) [3]: Chi-square test (χ^2)

*dichotomous variables: percentage of individuals screaming or giving alarm calls etc. within sexes

Appendix 5. Comparisons of trait values between seasons when captured

Appendix table 5.1. Comparisons of behavioural trait values between individuals captured during spring and autumn for traits measured in the in-hand test. Both global and separate analyses were ran. Significant p-values (< 0.05) are marked in bold.

Behavioural trait	Autumn		Spring		Test statistic	p-value
	mean ± SD	N	mean ± SD	N		
Global						
Breathing rate	70.4 ± 1.1	61	64.4 ± 1.2	120	3.36[1]	**< 0.001**
Biting	2.5 ± 2.1	61	1.7 ± 1.8	120	2.37[2]	**0.018**
Screaming*	39 %	61	23 %	120	4.83[3]	**0.027**
Immobility	130.3 ± 57.2	61	111.3 ± 64.0	120	1.94[2]	0.053
Alarm call*	69 %	61	71 %	120	0.01[3]	0.92
Distance hand	9.9 ± 4.2	61	8.2 ± 3.2	120	2.74[2]	**0.006**
Females						
Breathing rate	72.1 ± 1.1	29	65.1 ± 1.2	66	2.80[1]	**0.006**
Biting	1.7 ± 1.8	29	1.0 ± 1.5	66	1.69[2]	0.091
Screaming*	45 %	29	18 %	66	6.07[3]	**0.014**
Immobility	133.3 ± 60.3	29	114.1 ± 63.0	66	1.41[2]	0.16
Alarm call*	69 %	29	74 %	66	0.08[3]	0.78
Distance hand	10.0 ± 4.4	29	8.2 ± 3.1	66	1.84[2]	0.066
Males						
Breathing rate	68.9 ± 1.1	32	63.7 ± 1.2	54	2.07[1]	**0.041**
Biting	3.2 ± 2.0	32	2.5 ± 1.8	54	1.56[2]	0.12
Screaming*	34 %	32	28 %	54	0.16[3]	0.69
Immobility	127.5 ± 55.0	32	107.8 ± 65.6	54	1.40[2]	0.16
Alarm call*	69 %	32	67 %	54	0[3]	1
Distance hand	9.8 ± 4.1	32	8.1 ± 3.4	54	2.04[2]	**0.041**

[1]: Student's two-sample t-test (t) [2]: Mann-Whitney U test (z) [3]: Chi-square test (χ^2)

*dichotomous variable: percentage of individuals screaming or giving alarm calls for each season (i.e. percentage of individuals in the yes-category of the variable)

Note: for explanation of variables, see main text

Appendix 6. Effect of capture time

Appendix table 6.1. Association between trial date (within seasons when captured), time of day and time spent in bird bag and all the quantitative behavioural variables measured on female and male great tits during the in-hand test. r_s = Spearman's rank correlation coefficient. Significant p-values (< 0.05) are marked in bold.

Time variable	**Behavioural variable**	**Global**			**Females**			**Males**		
		r_s	**N**	**p**	**r_s**	**N**	**p**	**r_s**	**N**	**p**
Trial date[1] (autumn)	Breathing rate	0.33	61	**0.009**	0.03	29	0.86	0.60	32	**< 0.001**
	Biting	0.08	61	0.50	-0.07	29	0.70	0.15	32	0.42
	Immobility	0.08	61	0.54	-0.02	29	0.90	0.19	32	0.31
	Distance hand	0.24	61	0.058	0.33	29	0.08	0.19	32	0.29
Trial date[1] (spring)	Breathing rate	-0.43	120	**< 0.001**	-0.42	66	**< 0.001**	-0.48	54	**< 0.001**
	Biting	-0.25	120	**0.007**	-0.35	66	**0.004**	-0.10	54	0.48
	Immobility	-0.00	120	0.93	-0.12	66	0.33	0.12	54	0.37
	Distance hand	-0.00	120	0.99	0.10	66	0.41	-0.12	54	0.37
Time of day[2]	Breathing rate	-0.11	181	0.13	-0.11	95	0.27	-0.12	86	0.29
	Biting	-0.17	181	**0.034**	-0.12	95	0.26	-0.23	86	**0.036**
	Immobility	-0.08	181	0.27	-0.09	95	0.36	-0.07	86	0.50
	Distance hand	-0.02	181	0.77	0.08	95	0.45	-0.12	86	0.27
Time in bird bag[3]	Breathing rate	0.18	181	**0.014**	0.16	95	0.12	0.22	86	**0.043**
	Biting	0.30	181	**< 0.001**	0.20	95	**0.047**	0.37	86	**< 0.001**
	Immobility	0.01	181	0.86	0.01	95	0.93	0.02	86	0.86
	Distance hand	0.18	181	**0.014**	0.14	95	0.19	0.25	86	**0.019**

[1]Date when captured in mist net measured as number of days after the last day in February (i.e. 1. March = 1) for birds caught during the spring, and number of days after 31st of August (i.e. 1. September = 1), for birds caught during the autumn.

[2]Time of day when captured measured in hours.

[3]Time spent in the bird bag measured in minutes between time when captured in mist net and start time of behavioural test.

Appendix table 6.2. Comparisons of trial date (within season when captured), time of day and time spent in bird bag between groups (No/Yes) for two binary variables measured on female and male great tits during the in-hand test. Z = test statistic from Mann-Whitney U-test. Significant p-values ($p < 0.05$) are marked in bold.

	Behavioural variable					
	Screaming					
	No		**Yes**			
Time variable	**mean ± SD**	**N**	**mean ± SD**	**N**	**Z**	**p**
Global						
Trial date (autumn)[1]	35.0 ± 19.6	37	44.0 ± 22.6	24	-1.24	0.21
Trial date (spring) [1]	77.8 ± 35.1	93	77.8 ± 37.2	27	-0.13	0.90
Time of day[2]	10.7 ± 2.3	130	9.6 ± 1.5	51	3.09	**0.002**
Time in bird bag[3]	16.1 ± 12.4	130	17.4 ± 12.8	51	-0.87	0.38
Females						
Trial date (autumn)[1]	32.3 ± 19.0	16	46.2 ± 20.2	13	-1.80	0.071
Trial date (spring) [1]	83.0 ± 33.8	54	61.6 ± 42.1	12	1.86	0.063
Time of day[2]	10.7 ± 2.2	70	9.8 ± 1.6	25	1.67	0.095
Time in bird bag[3]	15.5 ± 13.2	70	16.1 ± 11.5	25	-0.96	0.34
Males						
Trial date (autumn)[1]	37.1 ± 20.2	21	41.0 ± 25.9	11	-0.08	0.94
Trial date (spring) [1]	70.7 ± 36.0	39	90.8 ± 27.7	15	-2.09	**0.036**
Time of day[2]	10.8 ± 2.3	60	9.45 ± 1.5	26	2.63	**0.008**
Time in bird bag[3]	16.8 ± 11.5	60	18.7 ± 14.1	26	-0.24	0.81
	Alarm call					
Global						
Trial date (autumn)[1]	43.2 ± 21.8	19	36.5 ± 20.7	42	0.93	0.35
Trial date (spring) [1]	74.5 ± 36.9	35	79.2 ± 34.9	85	-0.73	0.47
Time of day[2]	10.6 ± 2.2	54	10.3 ± 2.1	127	1.16	0.24
Time in bird bag[3]	15.6 ± 11.4	54	16.9 ± 13.0	127	-0.37	0.71
Females						
Trial date (autumn)[1]	32.3 ± 19.0	16	46.6 ± 20.2	13	-0.21	0.83
Trial date (spring) [1]	61.0 ± 39.3	17	85.4 ± 33.0	49	-2.31	**0.021**
Time of day[2]	10.3 ± 1.6	26	10.6 ± 2.3	69	0.18	0.86
Time in bird bag[3]	16.0 ± 12.3	26	15.6 ± 12.7	69	0.29	0.77
Males						
Trial date (autumn)[1]	48.3 ± 24.2	10	33.9 ± 19.8	22	1.32	0.19
Trial date (spring) [1]	87.2 ± 30.3	18	70.9 ± 36.1	36	1.78	0.075
Time of day[2]	10.9 ± 2.6	28	10.9 ± 2.0	58	1.47	0.14
Time in bird bag[3]	15.2 ± 10.7	28	18.4 ± 12.9	58	-1.02	0.31

[1]Date when captured in mist net measured as number of days after the last day in February (i.e. 1. March = 1) for birds caught during the spring, and number of days after 31st of August (i.e. 1. September = 1), for birds caught during the autumn.

[2]Time of day when captured measured in hours.

[3]Time spent in the bird bag measured in minutes between time when captured in mist net and start time of behavioural test.

Appendix table 6.3. Relationship between test time (trial date and time of day) and the quantitative behavioural variables measured on great tit females during the attentiveness test. r_s = Spearman rank correlation coefficient. Significant p-values ($p < 0.05$) are marked in bold.

Trial time	Behavioural trait	r_s	N	p
Trial date[1]	Attentiveness	-0.02	77	0.84
	Distance box	-0.25	69	**0.040**
	Distance 2min	-0.11	63	0.40
Time of day[2]	Attentiveness	-0.10	80	0.37
	Distance box	0.16	72	0.17
	Distance 2min	0.34	65	**0.005**

[1]Date when the attentiveness test was conducted measured as number of days after 30th of April (i.e. 1. May = 1)
[2]Time of day when the test began measured in hours.

Appendix table 6.4. Comparison of test time (date and time of day) between groups (No/Yes) for four binary variables measured on great tit females during the attentiveness test. Z = test statistic from Mann-Whitney U-test. Significant p-values ($p < 0.05$) are marked in bold.

			Behavioural trait			
			Hissing			
	No		**Yes**			
Time variable	**mean ± SD**	**N**	**mean ± SD**	**N**	**Z**	**p**
Trial date[1]	13.39 ± 5.26	56	15.04 ± 4.57	24	-1.79	0.073
Time of day[2]	10.61 ± 1.58	56	10.60 ± 1.53	24	0.12	0.90
			Call inside			
Trial date[1]	13.73 ± 5.29	56	14.24 ± 4.64	24	-0.70	0.49
Time of day[2]	10.53 ± 1.46	56	10.53 ± 1.78	24	0.72	0.47
			Call leaving			
Trial date[1]	13.73 ± 5.29	56	14.25± 4.64	24	-0.67	0.50
Time of day[2]	10.64 ± 1.46	56	10.53 ± 1.78	24	-1.02	0.31
			Call after 2min			
Trial date[1]	20.86 ± 5.11	7	12.98 ± 4.62	60	3.29	**< 0.001**
Time of day[2]	10.65 ± 0.73	7	10.64 ± 0.71	60	0.34	0.74

[1]Date when the attentiveness test was conducted measured as number of days after 30th of April (i.e. 1. May = 1)
[2]Time of day when the test began measured in hours.

Appendix table 6.5. Relationship between test time (date and time of day) and great tits response to conspecific intruder and to a predator model owl. r_s = Spearman rank correlation coefficient. Significant p-values ($p < 0.05$) are marked in bold.

Confounding variable	**Behavioural variable**	**Global**			**Females**			**Males**		
		r_s	**N**	**p**	**r_s**	**N**	**p**	**r_s**	**N**	**p**
Trial date[1]	Conspecific response	na	na	na	-0.15	82	0.17	-0.20	48	0.17
	Predator response	0.19	118	**0.039**	0.08	66	0.55	0.37	60	**0.003**
Time of day[2]	Conspecific response	na	na	na	0.16	82	0.16	0.02	48	0.86
	Predator response	0.03	118	0.75	0.09	66	0.47	-0.03	60	0.79

na = not applicable due to different measurements for females and males

[1]Date when the conspecific intruder/predator model test was conducted measured as number of days after 30. of April (i.e. 1. May = 1).

[2]Time of day when the test began measured in hours.

Appendix 7. Relationships between pairs of behavioural traits

Appendix table 7.1. Table a shows correlation between quantitative behavioural traits measured during the in-hand-(1), conspecific intruder-(2) and predator model test (3) on female and male great tits Table b shows association between quantitative and qualitative (dichotomous) behavioural traits measured during the same tests. Results from both global and separate analyses and uncorrected p-values are shown in both tables. Significant p-values ($p < 0.05$) are marked in bold, and an asterisk (*) indicates significant p-values robust to correction for multiple testing.

a)

Behavioural trait 1	Behavioural trait 2	Global			Females			Males		
		r	**N**	**p**	**r**	**N**	**p**	**r**	**N**	**p**
Breathing rate (1)	Biting (1)	0.12[1]	181	0.12	0.22[1]	95	**0.029**	0.08[1]	86	0.46
	Immobility (1)	-0.02[1]	181	0.76	-0.08[1]	95	0.42	0.05[1]	86	0.67
	Distance hand (1)	0.25[1]	181	**< 0.001***	0.29[1]	95	**0.003***	0.19[1]	86	0.082
	Conspecific response (2)	na	na	na	-0.19[1]	75	0.098	-0.19[1]	45	0.21
	Predator response (3)	0.09[1]	117	0.31	-0.07[2]	62	0.60	0.25[1]	55	0.062
Biting (1)	Immobility (1)	-0.07[1]	181	0.32	-0.15[1]	95	0.14	0.05[1]	86	0.67
	Distance hand (1)	0.04[1]	181	0.58	-0.14[1]	95	0.17	0.26[1]	86	**0.014**
	Conspecific response (2)	na	na	na	0.15[1]	75	0.20	0.10[1]	45	0.53
	Predator response (3)	-0.11[1]	117	0.22	-0.09[1]	62	0.50	0.06[1]	55	0.65
Immobility (1)	Distance hand	0.09[1]	181	0.22	0.09[1]	95	0.36	0.10[1]	86	0.34
	Conspecific response (2)	na	na	na	0.05[1]	75	0.67	0.21[1]	45	0.16
	Predator response (3)	0.09[1]	117	0.33	0.20[1]	62	0.13	-0.07[1]	55	0.59
Distance hand (1)	Conspecific response (2)	na	na	na	-0.34[1]	75	**0.003***	-0.16[1]	45	0.29
	Predator response (3)	0.13[1]	117	0.16	0.17[1]	62	0.18	0.12[1]	55	0.40
Conspecific response (2)	Predator response (3)	na	na	na	-0.14[1]	62	0.26	-0.19[1]	35	0.26

[1]: Spearman Rank Correlation test (r_s)

[2]: Pearson Correlation test (r)

na: not applicable, due to different measurement of conspecific response for females and males

Quantitative behavioural traits	**Dichotomous behavioural traits**											
	Screaming						**Alarm call**					
	No		**Yes**				**No**		**Yes**			
	mean ± SD	**N**	**mean ± SD**	**N**	**Test statistic**	**P-value**	**mean ± SD**	**N**	**mean ± SD**	**N**	**Test statistic**	**P-value**
Global												
Breathing rate (1)	67.0 ± 1.2	130	64.9 ± 1.2	51	1.13[1]	0.26	67.4 ± 1.2	54	66.0 ± 1.2	127	0.74[1]	0.46
Biting (1)	1.7 ± 1.8	130	2.6 ± 2.0	51	-2.65[2]	**0.008***	2.1 ± 2.0	54	1.9 ± 1.9	127	0.54[2]	0.59
Scream (1)*	-	-	-	-	-	-	33 %	54	25 %	127	0.68[3]	0.41
Immobility (1)	112.9 ± 61.4	130	130.0 ± 63.4	51	-1.94[2]	0.05	122.2 ± 64.9	54	115.8 ± 61.3	127	1.02[2]	0.31
Alarm call (1)*	72 %	130	65 %	51	0.68[3]	0.41	-	-	-	-	-	-
Distance hand (1)	8.8 ± 3.7	130	8.7 ± 3.4	51	-0.07[2]	0.94	9.5 ± 3.9	54	8.4 ± 3.5	127	1.77[2]	0.08
Conspecific response (2)	na	na	na	na	na	na	na	na	na	na	na	na
Predator response (3)	2.3 ± 2.4	79	2.2 ± 2.0	38	0.40[2]	0.69	2.8 ± 2.3	37	2.1 ± 2.2	80	1.38[2]	0.17
Females												
Breathing rate (1)	66.5 ± 1.2	70	68.9 ± 1.0	25	-0.88[1]	0.38	70.3 ± 1.2	26	66.0 ± 1.2	69	1.62[1]	0.11
Biting (1)	1.0 ± 1.5	70	1.8 ± 1.7	25	-2.75[2]	**0.012**	1.0 ± 1.6	26	1.3 ± 1.6	69	-0.81[2]	0.42
Scream (1)*	-	-	-	-	-	-	35 %	26	23 %	69	0.75[3]	0.37
Immobility (1)	115.3 ± 62.3	70	133.2 ± 62.5	25	-1.36[2]	0.17	146.5 ± 54.6	26	110.0 ± 62.7	69	2.80[2]	**0.005***
Alarm call (1)*	76 %	70	64 %	25	0.75[3]	0.37	-	-	-	-	-	-
Distance hand (1)	8.83 ± 3.58	70	8.64 ± 3.66	25	0.03[2]	0.98	9.6 ± 3.5	26	8.5 ± 3.6	69	1.88[2]	**0.061**
Conspecific response (2)	119.5 ± 114.2	55	151.0 ± 118.1	20	-1.17[2]	0.24	99.3 ± 117.1	22	139.8 ± 113.5	53	-1.13[2]	0.26
Predator response (3)	2.8 ± 2.7	44	2.6 ± 2.1	18	0.36[1]	0.72	3.4 ± 2.6	19	2.5 ± 2.5	43	1.25[1]	0.22
Males												
Breathing rate (1)	67.5 ± 1.2	60	61.2 ± 1.2	26	2.48[1]	**0.015**	64.7 ± 1.2	28	67.5 ± 1.2	58	-0.46[1]	0.65
Biting (1)	2.6 ± 1.8	60	3.3 ± 2.1	26	-1.60[2]	0.11	3.0 ± 1.8	28	2.7 ± 2.0	58	0.83[2]	0.40
Scream (1)*	-	-	-	-	-	-	32 %		29 %		0[3]	0.99
Immobility (1)	110.0 ± 60.7	60	126.9 ± 65.4	26	-1.42[2]	0.16	99.6 ± 66.4	28	122.6 ± 59.3	58	-1.35[2]	0.18
Alarm call (1)*	68 %	60	65 %	26	0[3]	0.99	-	-	-	-	-	-
Distance hand (1)	8.7 ± 4.0	60	8.7 ± 3.1	26	-0.27[2]	0.79	9.4 ± 4.4	28	8.3 ± 3.3	58	0.77[2]	0.44
Conspecific response (2)	1.9 ± 2.1	31	2.1 ± 2.4	14	-0.26[2]	0.79	2.2 ± 2.3	17	1.8 ± 2.1	28	0.77[2]	0.44
Predator response (3)	1.8 ± 1.8	35	1.9 ± 2.0	20	0.18[2]	0.86	2.2 ± 2.0	18	1.7 ± 1.8	37	1.09[2]	0.27

[1]: Student's Two-Sample t-test (t) [2]: Mann-Whitney U test (z) [3]: Chi-square test (χ^2)

*dichotomous variables: instead of mean (± SD), percentage of individuals screaming or giving alarm calls (i.e. yes) of each group is given

na: not applicable, due to different measurement of conspecific response for females and males

Appendix table 7.2. Relationship between behavioural traits measured during the in-hand-(1), conspecific intruder-(2), predator model-(3) and attentiveness test (4) on female great tits. Table a shows correlation between quantitative traits, table b shows comparisons of means of quantitative traits for each level of dichotomous traits. Significant p-values ($p < 0.05$) are marked in bold, and an asterisk (*) indicates significant great titp-values robust to correction for multiple testing.

a)

		Females		
Behavioural trait 1	**Behavioural trait 2**	r^1/r_s^2	**N**	**p**
Breathing rate (1)	Attentiveness (4)	-0.00[1]	74	1.00
	Distance box (4)	0.26[2]	66	**0.038**
	Distance 2min (4)	0.08[2]	60	0.53
Biting (1)	Attentiveness (4)	0.09[1]	74	0.46
	Distance box (4)	0.12[1]	66	0.33
	Distance 2min (4)	-0.04[1]	60	0.79
Immobility (1)	Attentiveness (4)	-0.18[1]	74	0.12
	Distance box (4)	-0.04[1]	66	0.73
	Distance 2min (4)	0.06[1]	60	0.65
Distance hand (1)	Attentiveness (4)	0.16[1]	74	0.17
	Distance box (4)	0.11[1]	66	0.37
	Distance 2min (4)	0.15[1]	60	0.25
Conspecific response (2)	Attentiveness (4)	0.06[1]	77	0.60
	Distance box (4)	0.00[1]	69	0.97
	Distance 2min (4)	0.07[1]	62	0.57
Predator response (3)	Attentiveness (4)	0.04[1]	60	0.76
	Distance box (4)	0.24[2]	54	**0.086**
	Distance 2min (4)	0.19[2]	49	0.20
Attentiveness (4)	Distance box (4)	-0.09[1]	70	0.48
	Distance 2min (4)	-0.15[1]	63	0.23
Distance box (4)	Distance 2min (4)	0.74[2]	63	**< 0.001***

[1]: Spearman Rank Correlation test (r_s)
[2]: Pearson Correlation test (r)

b)

	Dichotomous traits											
	Screaming (1)						Alarm call (1)					
	No		Yes				No		Yes			
Females	**mean ± SD**	**N**	**mean ± SD**	**N**	**Test statistic**	**P-value**	**mean ± SD**	**N**	**mean ± SD**	**N**	**Test statistic**	**P-value**
Hissing (4)	26 %	54	35 %	20	0.23[3]	0.63	33 %	21	26 %	53	0.10[3]	0.76
Attentiveness (4)	1.9 ± 1.2	54	2.40 ± 1.27	20	-1.39[2]	0.16	2.0 ± 1.3	21	2.1 ± 1.2	53	-0.56[2]	0.57
Call inside (4)	24 %	54	45 %	20	2.14[3]	0.14	29 %	21	30 %	53	0[3]	1
Call leaving (4)	86 %	49	95 %	17	2.63[4]	0.67	75 %	16	92 %	50	3.74[4]	0.090
Distance box (4)	7.4 ± 1.7	49	8.5 ± 1.6	17	-0.95[1]	0.34	7.5 ± 1.7	16	7.7 ± 1.7	50	-0.11[1]	0.91
Call after 2min (4)	91 %	45	88 %	16	0.69[4]	0.65	100 %	13	88 %	48	0[4]	0.33
Distance 2min (4)	7.8 ± 0.7	44	8.8 ± 1.1	16	-0.67[1]	0.50	8.3 ± 1.2	13	8.0 ± 0.7	47	0.21[1]	0.84
	Hissing (4)						**Call inside (4)**					
Breathing rate (1)	65.5 ± 1.2	53	69.5 ± 1.2	23	-1.33[1]	0.19	66.6 ± 1.2	53	66.6 ± 1.2	23	-0.00[1]	1
Biting (1)	1.3 ± 1.5	53	1.9 ± 1.6	23	1.73[2]	**0.085**	1.2 ± 1.5	53	1.1 ± 1.7	23	0.02[2]	0.98
Scream (1)*	25 %	53	33 %	21	0.23[3]	0.63	21%	52	41 %	22	2.14[3]	0.14
Immobility (1)	114.3 ± 63.9	53	143.5 ± 51.1	23	-1.82[2]	**0.069**	125.1 ± 59.6	53	118.7 ± 66.8	23	0.49[2]	0.62
Alarm call (1)*	74 %	53	67 %	21	0.10[3]	0.76	71 %	52	73 %	22	0[3]	1
Distance hand (1)	8.6 ± 3.5	53	8.8 ± 3.0	23	-0.32[2]	0.75	8.7 ± 2.2	53	8.7 ± 3.6	23	0.13[2]	0.90
Conspecific response (2)	139.1 ± 116.9	55	109.2 ± 115.2	22	0.88[2]	0.38	121.7 ± 116.6	54	151.4 ± 115.9	23	-1.18[2]	0.24
Predator response (3)	2.8 ± 2.7	45	3.1 ± 0.9	16	-0.62[1]	0.54	2.9 ± 2.7	44	2.5 ± 2.2	17	0.58[1]	0.56
Hissing (4)*	-	-	-	-	-	-	80 %	55	48 %	23	4.90[3]	**0.027**
Attentiveness (4)	2.1 ± 1.3	56	2.1 ± 1.2	22	0.08[2]	0.93	1.8 ± 1.2	55	2.7 ± 1.2	23	-3.10[2]	**0.002***
Call inside (4)*	21 %	56	50 %	22	4.90[3]	**0.027**	-	-	-	-	-	-
Call leaving(4)*	88 %	49	90 %	21	1.32[4]	1	88 %	52	89 %	18	1.04[4]	1
Distance box (4)	7.8 ± 1.7	49	7.5 ± 1.7	21	0.24[1]	0.81	7.7 ± 1.7	52	7.7 ± 1.7	18	-0.00[1]	1
Call after 2min (4)*	91 %	46	84 %	19	0.51[4]	0.41	90 %	49	88 %	16	0.80[4]	1
Distance 2min (4)	8.1 ± 0.8	45	7.9 ± 0.8	18	-0.01[1]	0.99	8.3 ± 0.9	47	7.4 ± 0.5	16	0.52[1]	0.60
	Call leaving(4)						**Call after 2min (4)**					
Breathing rate (1)	67.8 ± 1.2	8	65.4 ± 1.2	60	0.56[1]	0.58	66.5 ± 1.2	6	65.3 ± 1.2	57	0.24[1]	0.81
Biting (1)	0.5 ± 0.8	8	1.2 ± 1.7	60	-0.89[2]	0.37	1.3 ± 1.5	6	1.1 ± 1.6	57	0.36[2]	0.72
Scream (1)*	13 %	8	28 %	58	2.63[4]	0.67	33 %	6	25 %	55	0.69[4]	0.65
Immobility (1)	127.5 ± 65.6	8	123.0 ± 61.9	60	0.22[2]	0.83	130.0 ± 41.0	6	120.5 ± 65.0	57	0.13[2]	0.90
Alarm call (1)*	50 %	8	79 %	58	3.74[4]	0.090	100 %	6	76 %	55	0[4]	0.33
Distance hand (1)	6.9 ± 2.0	8	8.7 ± 3.2	60	-1.79[2]	**0.073**	8.5 ± 3.2	6	8.5 ± 3.2	57	0.18[2]	0.85
Conspecific response (2)	206.5 ± 99.4	8	122.3 ± 118.7	61	1.92[2]	**0.055**	148.3 ± 136.0	7	127.5 ± 119.4	57	0.45[2]	0.66
Predator response (3)	3.1 ± 2.4	6	2.7 ± 2.5	48	0.28[1]	0.78	2.2 ± 2.4	4	2.7 ± 2.5	46	-0.37[1]	0.71
Hissing (4)*	25 %	8	31 %	62	1.32[4]	1	43 %	7	28 %	58	0.51[4]	0.41

(Table 7.2b continued)

Attentiveness (4)	1.5 ± 0.9	8	1.9 ± 1.1	62	-1.00[2]	0.32	2.0 ± 1.2	7	1.9 ± 1.1	58	0.44[2]	0.66
Call inside (4)*	25 %	8	26 %	62	1.04[4]	1	29 %	7	25 %	58	0.80[4]	1
Call leaving (4)*	-	-	-	-	-	-	100 %	7	93 %	58	0[4]	1
Distance box (4)	6.9 ± 2.8	8	7.8 ± 1.6	62	-0.66[1]	0.51	7.4 ± 1.4	7	7.6 ± 1.7	58	-0.09[1]	0.93
Call after 2min (4)*	100 %	4	89 %	61	0[4]	1	-	-	-	-	-	-
Distance 2min (4)	5.1 ± 0.8	4	8.3 ± 0.8	59	-1.41[1]	0.16	9.7 ± 1.4	5	8.0 ± 0.8	58	0.68[1]	0.50

[1]: Student's Two-Sample t-test (t) [2]: Mann-Whitney U test (z) [3]: Chi-square test (χ^2), 4: Fisher's Exact test (odds ratio)

*dichotomous variables: instead of mean (± SD), percentage of females showing the behaviour (i.e. the percentage "yes") of each group (no/yes) of the other variable is given

na: not applicable, due to different measurement of conspecific response for females and males

Appendix table 7.3. Table a shows logistic regression for dichotomous dependent behavioural traits with other behavioural traits and sex as independent variables. Table b shows analyses of (co)variance for quantitative behavioural traits with other behavioural traits and sex as independent variables. All traits are measured during the in-hand test. Only models with in-hand traits that were significant associated after correcting for multiple testing in pairwise analyses are included. Sex had a significant main effect in all models with biting or predator response as dependent variables, in agreement with previous findings (Appendix table 4.2). Significant p-values (< 0.05) are shown. N = 181 for all analyses.

a)

Dependent variable	**Independent variables**	**z**	**p**
Screaming	Biting	2.70	**0.007**
	Sex (male)	-0.60	0.55
Alarm call	Immobility	-1.62	0.10
	Sex(male)	-2.11	**0.035**
	Immobility:Sex(male)	2.27	**0.023**

b)

Dependent variable	**Independent variables**	**F**	**p**
Breathing rate[1]	Distance hand	12.26	**<0.001**
	Sex	1.39	0.24
Biting[2]	Screaming	1.79	**0.010**
	Sex	46.62	**<0.001**
Immobility[2]	Alarm call	0.01	0.92
	Sex	5.00	**0.027**
	Alarm:Sex	5.40	**0.022**
Distance hand[1]	Breathing rate	12.27	**<0.001**
	Sex	0.46	0.50

[1]: Analysis of covariances (ANCOVA)
[2]: Analysis of variances (ANOVA)

Appendix 8. FAMD-analyses

Appendix table 8.1. Global analysis on behavioural traits measured on great tits during the in-hand test. Table a shows the summary output from the FAMD-analysis, and table b shows calculation of correlation coefficients between variables and dimensions for both active (behavioural traits) and supplementary (sex and age) variables. Only correlations significant at the 0.05 level are included. Table c contains supplementary descriptions of table a and b.

a) FAMD summary output

	Dim 1				Dim 2				Dim 3			
	coord	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**
Quantitative var.												
Breathing rate	0.49	17.80	0.24		0.57	26.64	0.32		-0.12	1.42	0.02	
Biting	0.52	19.88	0.27		-0.30	7.44	0.09		-0.62	36.54	0.39	
Immobility	0.26	4.77	0.07		-0.28	6.74	0.08		0.75	52.61	0.56	
Distance from hand	0.67	32.97	0.45		0.33	9.16	0.11		0.13	1.67	0.02	
Categories												
Not Screaming	-0.24	2.36	0.14	-4.43	0.53	14.07	0.67	10.38	0.05	0.17	0.01	1.07
Screaming	0.62	5.75	0.14	4.43	-1.35	35.86	0.67	-10.38	-0.13	0.42	0.01	-1.07
Not Alarming	0.85	11.63	0.30	6.38	-0.06	0.07	0.00	-0.48	0.43	5.03	0.08	3.71
Alarming	-0.36	4.95	0.30	-6.38	0.03	0.03	0.00	0.48	-0.19	2.14	0.08	-3.71

b) Results

	Dim 1		Dim 2		Dim 3	
Quantitative variables	**correlation**	**p.value**	**correlation**	**p.value**	**correlation**	**p.value**
Breathing rate	0.49	< 0.001	0.57	< 0.001	-	-
Biting	0.52	< 0.001	-0.30	< 0.001	-0.62	< 0.001
Immobility	0.26	< 0.001	-0.28	< 0.001	0.75	< 0.001
Distance from hand	**0.67**	**< 0.001**	-0.33	< 0.001	-	-
Qualitative variables	**R^2**	**p.value**	**R^2**	**p.value**	**R^2**	**p.value**
Alarm	0.23	< 0.001	-	-	0.08	< 0.001
Scream	0.11	< 0.001	0.60	< 0.001	-	-
Sex	0.02	< 0.001	0.02	0.033	0.06	< 0.001
SexAge	-	-	0.07	0.003	0.07	0.007
Age	-	-	0.04	0.006	-	-
Categories	**estimate**	**p.value**	**estimate**	**p.value**	**estimate**	**p.value**
Not alarming	0.61	< 0.001	-	-	0.312	< 0.001
Alarming	-0.61	< 0.001	-	-	-0.312	< 0.001
Screaming	0.43	< 0.001	-0.942	< 0.001	-	-
Not screaming	-0.43	< 0.001	0.942	< 0.001	-	-
Male	0.18	0.044	-0.173	0.031	-0.260	< 0.001
Female	-0.18	0.044	0.174	0.031	0.260	< 0.001
Older	-	-	0.224	0.006	-	-
One-year old	-	-	-0.224	0.006	-	-
FemaleOlder	-	-	0.432	0.003	-	-
FemaleOneyear	-	-	-	-	0.334	0.010
MaleOlder	-	-	-	-	-0.255	0.032
MaleOneyear	-	-	-0.451	0.003	-	-

c) Supplementary description of FAMD summary output and results, based on Husson (2013).

	FAMD-summary output
Abbreviations	**Description**
coord	Variables' coordinates on the dimensions.
ctr	Variables' contribution to the construction of the dimension.
cos2	A measure of the variables' quality of representation on the dimension, measured by the squared cosine. Cos2-value near 1 indicates that the variable is well-projected on the dimension.
v.test	Only for categories. The v.test takes a value between [-2, 2] if on average the coordinates of samples that take the category is not significant different from zero. The v.test is smaller than -2, or greater than 2, if, on average, the coordinates of samples which take the category is significant lesser or greater than zero, respectively.
	Results
correlation	Correlation coefficient between quantitative variables and the dimension.
R^2	Square correlation ratio between the coordinates of the individuals and the qualitative variable. R^2 is the indicator in a one-way ANOVA to see if there is a link between the dimension and the categorical variable.
estimate	An estimate on whether the individuals belonging to the category have on average higher (positive value) or lower coordinates (negative value). The coefficient is the hat alpha_i in a one-way ANOVA of the model: dimension explained by the category. Sum of the estimate coefficients of categories of the same variable is equal to zero.

Appendix table 8.2. Separate analyses on behavioural traits measured on female and male great tits during the in-hand test. Table a and b shows the summary output from the FAMD-analysis. Table c and d shows calculation of correlation coefficients between variables and dimensions for both active variables (behavioural traits) and supplementary variable (age). Only correlations significant at the 0.05 level are included. Please see Appendix table 8.1c for supplementary description of tables.

a) FAMD-summary output: Females

	Dim 1				Dim 2				Dim 3			
Quantitative var.	**coord**	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**
Breathing rate	0.65	28.81	0.43		0.34	8.78	0.12		0.35	10.59	0.12	
Biting	0.39	10.04	0.15		0.67	33.80	0.44		-0.33	9.17	0.11	
Immobility	0.30	6.23	0.09		-0.68	35.36	0.46		-0.33	9.45	0.11	
Distance from hand	0.48	15.54	0.23		-0.05	0.17	0.00		0.62	33.17	0.38	
Categories												
Not Screaming	-0.36	4.21	0.32	-4.73	-0.08	0.29	0.02	-1.16	0.42	0.87	0.46	6.38
Screaming	1.00	11.79	0.32	4.73	0.23	0.81	0.01	1.16	-1.18	27.65	0.46	-6.38
Not Alarming	1.17	16.99	0.46	5.72	-0.97	15.10	0.33	-5.05	0.06	0.079	0.00	0.34
Alarming	-0.44	6.40	0.46	-5.72	0.37	5.69	0.31	5.05	-0.02	0.03	0.00	-0.34

b) FAMD-summary output: Males

	Dim 1				Dim 2				Dim 3			
Quantitative var.	**coord**	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**
Breathing rate	0.22	3.48	0.05		0.79	46.97	0.62		-0.01	0.00	0.00	
Biting	0.71	35.99	0.10		0.08	0.51	0.01		-0.12	1.20	0.01	
Immobility	0.32	7.50	0.10		0.08	0.52	0.01		0.76	48.17	0.58	
Distance from hand	0.76	41.77	0.58		0.26	5.29	0.07		-0.06	0.33	0.00	
Categories												
Not Screaming	-0.23	1.86	0.11	-2.70	0.56	12.55	0.64	6.81	-0.20	2.00	0.09	-2.60
Screaming	0.52	4.29	0.11	2.70	-1.20	28.97	0.64	-6.81	0.47	4.62	0.09	2.60
Not Alarming	0.45	3.45	0.09	2.46	-0.34	2.11	0.05	-1.87	-1.14	29.46	0.59	-6.67
Alarming	-0.22	1.67	0.09	-2.46	0.16	1.02	0.05	1.87	0.55	14.22	0.59	6.67

c) Results: Females

	Dim 1		Dim 2		Dim 3	
Quantitative variables	**correlation**	**p.value**	**correlation**	**p.value**	**correlation**	**p.value**
Breathing rate	0.65	< 0.001	0.34	< 0.001	0.35	< 0.001
Biting	0.39	< 0.001	0.67	< 0.001	-0.32	0.001
Immobility	0.30	< 0.001	-0.68	< 0.001	-0.33	0.001
Distance from hand	0.48	< 0.001	-	-	0.62	< 0.001
Qualitative variables	**R^2**	**p.value**	**R^2**	**p.value**	**R^2**	**p.value**
Alarm call	0.35	< 0.001	0.27	< 0.001	-	-
Screaming	0.24	< 0.001	-	-	0.43	< 0.001
Age	-	-	-	-	0.05	0.023
Categories	**estimate**	**p.value**	**estimate**	**p.value**	**estimate**	**p.value**
Not alarming	0.81	< 0.001	-0.67	< 0.001	-	-
Alarming	-0.81	< 0.001	0.67	< 0.001	-	-
Screaming	0.68	< 0.001	-	-	-0.80	< 0.001
Not screaming	-0.68	< 0.001	-	-	0.80	< 0.001
Older	-	-	-	-	0.25	0.023
One-year old	-	-	-	-	-0.25	0.023

d) Results: Males

	Dim 1		Dim 2		Dim 3	
Quantitative variables	**correlation**	**p.value**	**correlation**	**p.value**	**correlation**	**p.value**
Breathing rate	0.22	0.042	0.79	< 0.001	-	-
Biting	0.71	< 0.001	-	-	-	-
Immobility	0.32	0.002	-	-	0.76	< 0.001
Distance from hand	0.76	< 0.001	0.26	0.014	-	-
Qualitative variables	**R^2**	**p.value**	**R^2**	**p.value**	**R^2**	**p.value**
Alarm call	0.07	0.013	-	-	0.52	< 0.001
Screaming	0.09	0.006	0.55	< 0.001	0.08	< 0.001
Age	-	-	-	-	-	-
Categories	**estimate**	**p.value**	**estimate**	**p.value**	**estimate**	**p.value**
Not alarming	0.34	0.013	-	-	-0.84	< 0.001
Alarming	-0.34	0.013	-	-	0.84	< 0.001
Screaming	0.38	0.006	-0.92	< 0.001	0.33	< 0.001
Not screaming	-0.38	0.006	0.92	< 0.001	-0.33	< 0.001
Older	-	-	-	-	-	-
One-year old	-	-	-	-	-	-

Appendix table 8.3. Separate analyses on all behavioural traits measured on female great tits during the in-hand-(1), attentiveness-(2), conspecific intruder-(3), and predator model test (4). Table a shows the summary output from the FAMD-analysis. Table b shows calculation of correlation coefficients between variables and dimensions for both active variables (behavioural traits) and the supplementary variable (age). Only correlations significant at the 0.05 level are included. Please see Appendix table 8.1c for supplementary description of tables.

a)

	Dim 1				Dim 2				Dim 3			
Quantitative var.	**coord**	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**
Breathing rate (1)	-0.26	3.53	0.07		0.49	14.08	0.24		0.33	7.13	0.11	
Biting (1)	0.45	10.03	0.20		0.49	13.92	0.24		0.39	9.75	0.15	
Immobility (1)	-0.42	8.73	0.17		-0.27	4.15	0.07		0.29	5.28	0.08	
Distance from hand (1)	-0.56	15.92	0.32		0.46	12.44	0.21		-0.13	1.07	0.02	
Attentiveness (2)	0.51	13.10	0.26		0.26	3.98	0.07		-0.31	6.03	0.09	
Distance nest box (2)	0.19	1.73	0.03		0.47	13.04	0.22		0.38	9.39	0.15	
Conspecific resp. (3)	0.58	16.85	0.33		-0.37	8.07	0.14		0.44	12.59	0.19	
Predator resp. (4)	-0.11	0.56	0.01		0.03	0.04	0.00		0.05	0.18	0.00	
Categories												
Not Screaming (1)	-0.11	0.20	0.02	-0.88	-0.37	3.45	0.29	-3.33	-0.29	2.50	0.18	-2.71
Screaming (1)	0.27	0.53	0.02	0.88	0.96	8.98	0.29	3.33	0.75	6.49	0.18	2.71
Not Alarming (1)	-1.30	11.10	0.46	-3.96	-0.23	0.46	0.01	-0.75	0.91	8.94	0.22	3.14
Alarming (1)	0.45	3.88	0.46	3.96	0.08	0.16	0.01	0.75	-0.32	3.13	0.22	-3.14
Not hissing (2)	0.35	2.15	0.24	2.76	0.01	0.00	0.00	0.09	0.12	0.40	0.03	1.05
Hissing (2)	-0.82	5.10	0.24	-2.76	-0.03	0.01	0.00	-0.09	-0.28	0.95	0.03	-1.05
Not calling inside (2)	-0.28	1.49	0.21	-2.55	0.02	0.02	0.00	0.24	0.23	1.69	0.15	2.40
Calling inside (2)	0.88	4.71	0.21	2.55	-0.08	0.05	0.00	-0.24	-0.73	5.33	0.15	-2.40
Not calling leaving (2)	0.35	0.35	0.01	0.64	-1.98	15.23	0.39	-3.92	1.19	17.04	0.36	3.96
Calling leaving (2)	-0.04	0.04	0.01	-0.64	0.25	1.90	0.39	3.92	-0.24	2.13	0.36	-3.96

b)

	Dim 1		Dim 2		Dim 3	
Quantitative variables	**correlation**	**p.value**	**correlation**	**p.value**	**correlation**	**p.value**
Breathing rate (1)	-	-	0.49	< 0.001	0.33	0.01
Biting (1)	0.45	< 0.001	0.48	< 0.001	0.39	0.003
Immobility (1)	-0.41	< 0.001	-	-	0.29	0.036
Distance from hand (1)	-0.56	< 0.001	0.46	< 0.001	-	-
Attentiveness (2)	0.51	< 0.001	-	-	-0.31	0.025
Distance from nest box (2)	-	-	0.47	< 0.001	0.38	0.004
Conspecific response (3)	0.58	< 0.001	-0.37	0.006	0.44	< 0.001
Predator response (4)	-	-	-	-	-	-
Qualitative variables	**R^2**	**p.value**	**R^2**	**p.value**	**R^2**	**p.value**
Alarm call (1)	0.30	< 0.001	-	-	0.19	0.001
Screaming (1)	-	-	0.21	< 0.001	0.14	0.006
Hissing (2)	0.14	0.005	-	-	-	-
Call inside (2)	0.12	0.009	-	-	-	-
Call leaving (2)	-	-	0.29	< 0.001	0.30	< 0.001
Age	-	-	-	-	-	-
Categories	**estimate**	**p.value**	**estimate**	**p.value**	**estimate**	**p.value**
Not alarming (1)	-0.87	< 0.001	-	-	0.61	0.001
Alarming (1)	0.87	< 0.001	-	-	-0.61	0.001
Screaming (1)	-	-	0.66	< 0.001	0.52	0.006
Not screaming (1)	-	-	-0.66	< 0.001	-0.52	0.006
Hissing (2)	-0.58	0.005	-	-	-	-
Not hissing (2)	0.58	0.005	-	-	-	-
Calling inside (2)	0.58	0.009	-	-	-0.48	0.015
Not calling inside (2)	-0.58	0.009	-	-	0.48	0.015
Calling leaving (2)	-	-	1.11	< 0.001	-1.08	< 0.001
Not calling leaving (2)	-	-	-1.11	< 0.001	1.08	< 0.001
Older	-	-	-	-	-	-
One-year old	-	-	-	-	-	-

Appendix table 8.4. Separate analyses on all behavioural traits measured on male great tits during the in-hand-(1), conspecific intruder-(2), and predator model test (3). Table a shows the summary output from the FAMD-analysis. Table b shows calculation of correlation coefficients between variables and dimensions for both active variables (behavioural traits) and supplementary variable (age). Only correlations significant at the 0.05 level are included. Please see Appendix table 8.1c for supplementary description of tables.

a)

	Dim 1				**Dim 2**				**Dim 3**			
Quantitative var.	**coord**	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**	**coord**	**ctr**	**cos2**	**v.test**
Breathing rate (1)	0.66	24.58	0.43		-0.25	4.13	0.06		0.43	13.17	0.18	
Biting (1)	0.55	17.47	0.30		0.38	9.49	0.14		0.22	3.50	0.05	
Immobility (1)	0.20	2.38	0.04		0.24	3.80	0.06		0.68	33.44	0.46	
Distance from hand (1)	0.75	32.18	0.56		-0.40	10.63	0.16		-0.06	0.22	0.00	
Conspecific resp. (2)	-0.41	9.65	0.17		-0.12	0.91	0.01		0.43	13.06	0.19	
Predator resp. (3)	0.15	1.26	0.02		0.54	19.74	0.30		-0.36	9.48	0.13	
Categories												
Not Screaming (1)	-0.15	0.46	0.31	-0.90	-0.77	17.20	0.86	-5.06	-0.01	0.00	0.00	-0.06
Screaming (1)	0.28	0.89	0.31	0.90	1.47	32.98	0.86	5.06	0.02	0.01	0.00	0.06
Not Alarming (1)	0.76	7.00	0.27	2.57	-0.21	0.70	0.02	-0.75	-0.93	16.74	0.41	-3.54
Alarming (1)	-0.45	4.14	0.27	-2.57	0.12	0.41	0.02	0.75	0.55	9.88	0.41	3.54

b)

	Dim 1		Dim 2		Dim 3	
Quantitative variables	**correlation**	**p.value**	**correlation**	**p.value**	**correlation**	**p.value**
Breathing rate (1)	0.65	< 0.001	-	-	0.43	0.010
Biting (1)	0.55	< 0.001	0.38	0.025	-	-
Immobility (1)	-	-	-	-	0.68	< 0.001
Distance from hand (1)	0.75	< 0.001	-0.40	0.017	-	-
Conspecific response (2)	-0.41	0.014	-	-	0.43	0.009
Predator response (3)	-	-	0.54	< 0.001	-0.36	0.032
Qualitative variables	**R^2**	**p.value**	**R^2**	**p.value**	**R^2**	**p.value**
Alarm call (1)	0.19	0.008	-	-	0.37	< 0.001
Screaming (1)	-	-	0.75	< 0.001	-	-
Age	-	-	-	-	-	-
Categories	**estimate**	**p.value**	**estimate**	**p.value**	**estimate**	**p.value**
Not alarming (1)	0.60	0.008	-	-	-0.74	< 0.001
Alarming (1)	-0.60	0.008	-	-	0.74	< 0.001
Screaming (1)	-	-	1.12	< 0.001	-	-
Not screaming (1)	-	-	-1.12	< 0.001	-	-
Older	-	-	-	-	-	-
One-year old	-	-	-	-	-	-