

# What is maintaining variation in personalities in wild populations of great tits and blue tits?

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## Abstract

It is now commonly recognized that animals have different personalities and that these personalities are moderately heritable, repeatable, and may influence fitness components such as survival and reproduction. Much of this knowledge has been gained by studying birds, and in particular great tits *Parus major*. In nature, great variation in personalities seems to exist, from shy to bold individuals, i.e. a shy-bold continuum. It has been suggested that the various personalities have equal fitness over time because of environmental variation, and thus represent Evolutionary Stable Strategies (ESS). An alternative is that some individuals with low fighting ability, e.g. because of poor rearing conditions, play a shy personality (“Best of a bad job” strategy). I wanted to address this problem by studying anti-predator behaviour in great tits and blue tits *Cyanistes caeruleus* in a woodland area in Norway. A total of 107 great tit and 75 blue tit local recruits (grown up in the area) were caught in the autumn and several measures of anti-predator behaviour were recorded. Subsequent winter survival and reproductive success (i.e. laying date, clutch size, number of fledged and body mass on day 15) were observed. As the methods adopted in this study to measure personality traits were previously little used, analyses of repeatability was performed in order to determine whether the methods proved to be a reliable way of measuring personality. The results showed quite high repeatability within observers, but low repeatability between observers and within and between anti-predator variables in general. Possible explanations for this are discussed. Two significant relationships, both for great tits, were obtained between fitness measures and anti-predator behaviour (survivors screamed less than non-survivors, and birds with low breathing rate laid more eggs than birds with high breathing rate). However, due to the large number of tests, and data from one year only, no firm conclusions could be drawn. Improved methods and data from more years are needed.

## Introduction

Animal personality (Gosling 2001) is a subject that has steadily received an increasing amount of attention during the last decades. The study of animal personality is important for several reasons. The most significant one being that personality may affect a number of fitness traits (e.g. survival and reproduction). Second, it may influence how we analyse populations. In studies of population dynamics it is often assumed that all the individuals in a population behave the same way and therefore that the whole population will react in the same way to changes, such as climate change and human activity. The outcome of these analyses may be different if they account for the fact that individuals may react differently to environmental change (Dall et al. 2004; Sih et al. 2012). Third, personality may bias sampling, e.g. by never catching the most shy individuals (Wilson et al. 1994; Biro and Dingemanse 2009; Garamszegi et al. 2009). This can lead to errors when estimating population size, which is often based on the capture-recapture method, and thus relies on the assumption of equal probability of capture. Fourth, animal welfare can benefit from personality studies, as individuals may show differential vulnerability to stress and artificial housing conditions, which can be improved with increased knowledge (Carere and Eens 2005; Groothuis and Carere 2005). Finally, the interpretation and design of many animal experiments may benefit because individuals with different behavioural profiles may react differently to the same treatments (Carere and Eens 2005; Groothuis and Carere 2005).

It is well known that personality exists in captive animals, and there may be a heritable component, which can be used to develop individuals with special desired traits, like hunting dogs (Houpt 2007), or “tame” foxes (Belyaev 1979). It has also been shown that personality exists in many different taxa in the wild, such as fish (Wilson et al. 1993; Wilson et al. 2010), birds (Verbeek et al. 1994; van Oers et al. 2004), lizards (Cote et al. 2008; Carter et al. 2010) and mammals (Reale et al. 2000; Boon et al. 2007). These personality types have been shown to be repeatable (Reale et al. 2000; Dingemanse et al. 2002; Bell et al. 2009), moderately heritable (Benus et al. 1991; Dingemanse et al. 2002; Drent et al. 2003), and may be associated with components of fitness variation, such as survival (Dingemanse et al. 2004; Boon et al. 2008) and reproductive success (Both et al. 2005; Boon et al. 2007).

There is no clear consensus on the definition of personality, but it is often defined as consistent individual differences in behaviour across time and/or contexts (Dall et al. 2004; Reale et al. 2007; Stamps and Groothuis 2010). There are several other terms used, such as , temperament (Reale et al. 2007), behavioural syndromes (Sih et al. 2004a, b) and coping

styles (Koolhaas et al. 1999). In recent years several authors have tried to clarify the differences between these terms in order to avoid confusion (Reale et al. 2007; Stamps and Groothuis 2010; Herczeg and Garamszegi 2012). Some authors use the term personality and mention e.g. behavioural syndromes, temperament and coping styles as other terms used without any further discussion (Carere et al. 2005; Boon et al. 2008) while others argue for the use of one specific term, e.g. behavioural profiles (Groothuis and Carere 2005), personality differences (Dall et al. 2004) or temperament (Reale et al. 2000). I choose henceforth simply to use the term personality when referring to assumed consistent individual differences in animal behaviour across time and/or context.

When it comes to personality in birds, the great tit *Parus major* has been the most frequent model species. This is because it is abundant and breeds easily in nest boxes. It has therefore been extensively studied over the years, and it has been shown that, as for many other species, personality traits are repeatable, both in laboratory populations (van Oers et al. 2004; Fucikova et al. 2009; but see Carere et al. 2005) and in the wild (Dingemanse et al. 2002), moderately heritable (Dingemanse et al. 2002; Drent et al. 2003; van Oers et al. 2004), and may affect both survival (Dingemanse et al. 2004) and reproduction (Both et al. 2005).

Correlations have been found between a variety of different great tit personality traits, which can be separated into two broad categories: (1) Fast explorers, that are bold in exploration, aggressive, take more risks and have rigid foraging habits; and (2) slow explorers that are shy in exploration, relatively non-aggressive and more sensitive to external stimuli and quick to adjust to changes in their environment (Verbeek et al. 1994; Verbeek et al. 1996; Marchetti and Drent 2000; van Oers et al. 2004). A wide range of other personality traits have also been found to correlate with exploratory behaviour; e.g. territory defence (Amy et al. 2010), singing (Naguib et al. 2010), responses to lost contests/social defeat (Verbeek et al. 1999; Carere et al. 2001), dispersal (Dingemanse et al. 2003), and social learning (Marchetti and Drent 2000).

When it comes to possibly the two most common forms of personality measures, namely exploratory behaviour in a novel environment, devised by Verbeek et al. (1994) as a variant of the classical open field test of animal psychologists Walsh & Cummins (1976), and reaction to novel objects (Greenberg 1983), there has been found a correlation between the two (Verbeek et al. 1994).

Much debated is the role of plasticity in personality. There are many ways plasticity may affect personality, from permanent environmental effects taking place during

development (Dingemanse et al. 2010) to the extent that it may be debated whether it can be called personality anymore e.g. a day-by-day variation caused by changes in temperature and physical condition. The difference between fast and slow explorers' ability to adapt to changes may be called a difference in plasticity (Wolf et al. 2008), thereby making plasticity an inherent part of personality. Dingemanse et al. (2012) recently found that behaviour in populations of great tits were repeatable, but also plastic as shown by exploratory behaviour increasing with test sequence. The level to which plasticity affects personality is therefore dependent upon what kind of plasticity is involved. When it comes to measures of anti-predator behaviour with humans as predators (e.g. this study), plasticity in the form of learning may be involved. The birds may learn that this new predator will not kill or harm them, and thus adjust their behaviour appropriately in subsequent captures.

## Present study

The focus of this study will be on what is maintaining variation in personalities in a wild population of great tits and blue tits *Cyanistes caeruleus*; a so far little studied subject (Dingemanse et al. 2004). I measured the birds' anti-predator behaviour as a measure of personality in general and looked at subsequent survival and reproduction. Many studies have already been done on great tit personality (see above), but little has been done on blue tits. The blue tit has a different life history, being more r-selected with lower adult survival, but higher reproductive investment (Perrins 1979). Otherwise the two species have very similar ecology (e.g. same habitats, partially migratory, overlapping food niches in the spring). However, exploratory tendency and neophobia are not correlated in blue tits as opposed to great tits (Herborn et al. 2010).

I have chosen the names "bold" and "shy" to describe what I have measured in this study. This decision was based in part on Reale et al.'s (2007) definition of boldness-shyness as "an individual's reaction to any risky situation, but not new situations". Another deciding factor was that in the literature boldness, also called risk-taking behaviour (van Oers et al. 2004), is often measured as how an individual reacts to a predator or a scary situation in general, e.g. the distance at which an individual flees from a potential predator (Møller et al. 2008; Carter et al. 2010), behaviour when caught (Møller et al. 2011; Møller and Ibanez-Alamo 2012), tendency to group together (Wilson et al. 2010), latency to exit a refuge (Wilson et al. 2010) or latency to return after a startle (van Oers et al. 2004). When measuring personality traits it is common to separate the findings into two categories, such as

shy and bold, whereas in reality the trait will vary along a continuum with several individuals being rated in between the two extremes. The shy-bold axis, which is termed the shy-bold continuum, is well documented in several animal species such as mice and rats (Benus et al. 1991), lizards (Lopez et al. 2005), bighorn sheep *Ovis canadensis* (Reale et al. 2000) and fish (Wilson et al. 1993).

What interested me was to see how birds react to a predator, because predation is probably a main cause of death for tits during winter (Ekman 1986), and thus anti-predator behaviour will be under strong selection. I studied the scape behaviour of birds when held in the hand (methods modified from Møller et al. 2011), under the assumption that such behaviour would reflect anti-predator behaviour of birds when attacked by a real predator (Møller et al. 2011).

I therefore choose to term what I have measured as anti-predator behaviour and the individual measures anti-predator traits, or anti-predator variables, where birds may vary from shy to bold within each variable. I will assume that the anti-predator behaviour measured in this study correlates with other forms of anti-predator behaviour and other personality traits, allowing me to use the extensive research on personality in captive birds. However, as most of my measures have previously only been used by Møller et al. (2011, 2012), who did not test this; I have no way to determine if this assumption is true.

This thesis will consist of two parts. The first part presents a new method for measuring personality on tits' anti-predator response in nature. I will analyse how repeatable the different anti-predator variables are within and between observers; how repeatable the individual anti-predator variables are between first and second measurement of individual birds; and how strong the relationship is between the variables in order to determine if the respective measures are reliable ways of assessing personality. In the second part I will analyse whether survival and reproductive success are related to the observed measurements of anti-predator behaviour.

## Hypotheses, assumptions and predictions

I will assume that a bird that is bold in relation to a predator is aggressive in relation to a conspecific. In general there is a lot of evidence that suggests different personality traits are correlated (see above), but little research has been done, both for birds and in general, on the specific relationship between boldness towards a predator and aggression towards a conspecific. However, the research that has been done seems to indicate that there is a



correlation in species as diverse as spiders (Riechert and Hedrick 1993), fish (Huntingford 1976), and birds (Garamszegi et al. 2009; Cain et al. 2011). The findings of such similar behavioural complexes in such widely separated taxa suggests that these complexes may be found in many animal species (Riechert and Hedrick 1993).

In general, probability of survival is affected by the cost of reproduction, but from autumn to spring in their first year the birds' survival is not affected by this, and survival may therefore be determined by personality to a higher degree than later in life. By measuring survival from autumn to spring and using mainly juvenile tits in my analyses I therefore try to disentangle the cost of reproduction from personality when it comes to survival.

**Hypothesis I:** Best of a bad job. *An optimal behavioural phenotype exists, but it invokes costs of competition. Individuals with higher fighting abilities will have higher fitness than individuals with lower fighting ability, but all exhibit a behavioural type that is a best solution given the individual's state (Sih et al. 2004b).*

The hypothesis assumes that personality is a plastic trait (Sih et al. 2004b), where the difference between shy and bold is caused by differences in fighting ability. Such phenotypic variation in fighting ability can be caused by poor rearing conditions, aging, or sickness. The assumption is that some individuals will have a lower ability to win in competition and escape predators (e.g. because of shorter wings or less muscle-mass). They will therefore play a shy strategy by taking fewer risks in relation to conspecifics and predators, but will still suffer higher mortality than bold ones. Even though they avoid predators they may still be more likely to be caught by predators than the bold ones, because of presumably less ability to escape an attack.

#### Predictions:

- (1) When caught in the autumn, the smaller birds (shorter wings and tarsi, and lower body mass) will be shyer than larger birds.
- (2) The bold individuals will consistently do better than the shy when it comes to both survival and reproduction.

#### Tests:

I will test predictions (1) and (2).

**Hypothesis II:** Mixed ESS (Evolutionary stable strategy). *The different personalities constitutes a mixed ESS, meaning that short-term differences in fitness will balance out in the long run, giving the different personalities equal fitness over time* (Boon et al. 2007; Sih et al. 2012).

Here the assumption is that personality can be genetic, plastic or a combination of both. According to this hypothesis variation in personality may occur even in constant environments e.g. by the hawk and dove game (Maynard Smith 1978). However, under natural conditions there will often be much variation in both competition (due to fluctuations in population size) and predation (due to fluctuations in predator population size). This may contribute to counteract selection towards a fixed behavioural type, but fitness may need to be monitored over a long period of time in order to see if the differences become balanced out. There are at least two different ways in which a mixed ESS can be achieved; (a) because of environmental variation or (b) from a life-history perspective.

**a) Environmental hypothesis:** *Variation in environmental conditions over time and between contexts will lead to variation in which personality achieves the highest fitness. This environmental variation will contribute to maintaining the variation in personalities* (Sih et al. 2004b).

Different personality traits may experience different fitness consequences with shifting environmental conditions such as food availability (Dingemanse et al. 2004), and predation pressure (Reale and Festa-Bianchet 2003). For instance, fast explorers may perform better in stable (predictable) environments, while slow explorers may benefit in unstable (unpredictable) environments where behavioural flexibility is favoured (Guillette et al. 2011).

The assumption here is that the fitness of the personality traits is dependent on climate, density and predators, that is, the environment fluctuates to such a degree that it affects survival and reproduction through personality.

Bad climate conditions, such as wind, rain and low temperatures, may increase the metabolic requirements of the birds and/or reduce the availability of food (e.g. snow cover). This may also increase the amount of time needed for foraging (Clobert et al. 1988) and thus affect competition for food. Density of both conspecifics and competing species may also affect the level of competition (Clobert et al. 1988). Aggressive individuals should have access to more resources at high densities when the level of conflict is high, and non-aggressive individuals should find more resources at low densities when aggressiveness is a

wasted and costly effort (Sih et al. 2012). These assumptions can be applied to both survival and reproduction, because resources can represent both food and territories. Predation risk may depend on both predator density and food availability i.e. when food is scarce the birds will need to spend more time foraging, exposing themselves to predation for a greater amount of time. If in addition to this, predator density is high, the birds will need to scan more, losing foraging time. During the breeding season the birds may need to forage for their young in addition to themselves, and will therefore face similar difficulties as during the winter.

When trying to combine all of these factors it becomes rather complex, but some assumptions can be formulated: In severe winters with low food availability and high population density, bold individuals will have an advantage by being aggressive in confrontations and thereby getting more food. In severe winters with low food availability and low population density, shy individuals will have an advantage as they are well adapted at foraging under changing feeding conditions (Verbeek et al. 1994). In mild winters with high densities bold individuals may have higher survival, because they will win in competitions for food. In mild winters with low densities there will be no major difference in survival between the personalities.

In the assumptions above risk of predation was not taken into account, a factor that may severely influence the outcome of the different behaviours. If we assume that bold individuals are more vulnerable to predation (because they take greater risks), the predicted outcome may be quite opposite depending on the risk of predation.

#### Predictions:

(1) Assuming a low risk of predation:

- (i) At high levels of competition for food, bold individuals will get access to more food.
- (ii) At low levels of competition for food, shy individuals will get access to more food.

(2) Assuming a high risk of predation:

Bold individuals will suffer higher mortality and thus lower fitness than shy individuals independent of food level.

#### Tests:

The predictions cannot be directly tested with my data as I only have data from one year and lack information on predator density. In the particular year of the study winter survival was

below average (Slagsvold unpublished data), which in combination with the low temperatures indicates a severe winter. However, it will be impossible to decide whether the low survival was caused by starvation, predation or a combination of the two. I may use population size in spring as a measure of competition for high quality territories. Population size of great tits and blue tits was above average in spring 2011 (Slagsvold unpublished data) and thus I can test the prediction that bold individuals have better territories than shy when density is high i.e. bold have higher reproduction success.

**b) Life history trade-off hypothesis:** *There is a trade-off between survival and reproduction. The bold individuals have higher reproductive success than shy, but live shorter and vice versa.*

This hypothesis is supported by a meta-analysis done across species, where it was found that bolder individuals had increased reproductive success, especially in males, but incurred a survival cost (Smith and Blumstein 2008). This might be caused by a context dependency, for instance a bold individual may be at an advantage when it comes to competing with conspecifics for mates, and thus have high reproductive success, but if they maintain this behavioural pattern when encountering a predator, it may decrease survival (Smith and Blumstein 2008; Garamszegi et al. 2009).

The assumption here is that mortality during winter is caused by predation and/or by a shortage of food when density is high, and that bold birds will take more risks in order to obtain food, leading to a higher mortality rate than shy. Both food availability and predation risk are factors that will vary over time, and therefore fitness of the different personalities will also vary over time. When it comes to reproduction the assumption is that bold individuals will do better as they have higher parental investment, that is, they invest more time and energy in obtaining a mate and fight more to obtain better territories leading to raising their offspring in higher quality areas, i.e. areas that offer more resources or lower predation risk. But as they take more risks they have a smaller chance of surviving the breeding season, and because they invest more energy they have a smaller chance of surviving the following winter (Zera and Harshman 2001).

#### Prediction:

The personalities reflect different life history strategies. Birds with low survival will have high reproductive rate (i.e. the bold individuals) and vice versa. If we assume that adult

mortality in spring is mainly caused by predation, the prediction becomes that bold individuals will have lower survival than shy, but that those who survive will have higher reproductive success than shy, if they survive reproducing.

Test:

I will test if there is a difference in winter survival between bold and shy that is counteracted by an inverse difference in reproductive success.

## **Materials and methods**

### **Study area and study species**

The study was undertaken at Dæli (60 00 °N, 10 38 °E), an area of approximately 1.6 km<sup>2</sup> near Oslo, Norway. The study area consists of a mixture of deciduous and coniferous woodland area provided with about 500 nest boxes and about 25 capture sites scattered over the area. The boxes are regularly distributed 40-50 m apart, with one large for every two small.

The study species in this study are the great tit and the blue tit. They breed easily in nest boxes and are only partially migratory and can therefore be caught until late autumn (when the weather becomes the restricting factor). The species are territorial songbirds that live in forests in Europe and Asia (Hoyo et al. 2007). The birds forage in flocks in the winter (Slagsvold and Wiebe 2011). However, they have different foraging strategies that might influence their survival in a harsh winter. Blue tits forage mainly above ground high in trees (Suhonen et al. 1994), and may be less affected by snowfall than great tits, which feed mainly on the ground or on the trunks and thicker branches of trees (Slagsvold and Wiebe 2007). Their prey items may also differ, leading to even greater chances for difference in survival (Slagsvold and Wiebe 2011).

### **Capture and measurements**

In this study the birds are classified as either local recruits or immigrants, with local recruit being every bird that has grown up in the area independent of its age. About 1200 nestlings were ringed in the spring of 2010 (487 great tits, 710 blue tits; see Appendix 1 for details).

#### ***Autumn 2010***

Mist nets were used to capture the birds, and food was put out in the days before capture took place to accustom birds to visit the capture site. The net was checked regularly in order to avoid leaving the birds there for too long. While waiting to be measured the birds were kept in cloth bags hung on branches and the like.

The juvenile local recruits were given rings with unique colour combinations in addition to their unique aluminium rings. All the immigrants were given immigrant colour codes according to age (juvenile or adult) based on the colour of their greater coverts, and uniquely numbered aluminium rings.

During the autumn season 107 local great tits (76 juvenile, 31 adults) and 75 local blue tits (41 juvenile, 34 adults) were captured and anti-predator behaviour was measured.

Six different measures of anti-predator behaviour were used and modified from Møller et al. (2011).

(1) Biting: An index finger was moved towards the bird's beak three times and it was recorded if the bird bit once or more (a score of 1) or did not attempt to bite (a score of 0). The assumption was that a bird that bites will have a higher probability of escaping the predator, and is therefore considered as bold (Møller et al. 2011).

(2) Fear scream: Whether the bird gave a fear scream (also called a distress call) while being handled (a score of 1) or not (a score of 0). Loud fear screams have been shown to attract the attention of a secondary predator and may therefore increase the probability of escape, but it might also alert the predator that the prey is still alive (Perrone 1980). Silent and motionless prey can cause the predator to loosen its grip or shift its attention elsewhere, thus allowing the prey to escape (Perrone 1980). Screaming is therefore considered as bold behaviour.

(3) Alarm call: Whether the bird gave an alarm call while flying away or directly after it landed (a score of 1) or was silent (a score of 0). The alarm call has been hypothesized to be a distraction of the predator or a warning signal for kin or mates (Marler 1955; Platzen and Magrath 2004). Giving the call while departing is considered as bold behaviour, as this will keep the predator's attention on the bird.

(4) Breathing rate: The number of breaths taken in 30 seconds was measured by watching the chest movements while holding the bird on its back. It has been found that bolder birds have a lower breathing rate, and that breathing rate in general is lower during resting (Carere and van Oers 2004). A low breathing rate is therefore considered as bold behaviour.

(5) Tonic immobility: The bird was placed on its back in a flat palm and held there for a couple of seconds, or until it stopped wriggling and/or biting. Then the bird was slowly tipped to the side and over to the other hand, by tilting the hand that held it. How many degrees it had been tilted when it flew were noted down (between 0° and 180°, ending the right way up in the other hand). Tonic immobility was measured by Møller et al. (2011) as the "time until the bird righted itself and flew away". They allowed the bird 30 seconds. It quickly became apparent that most of the tits in this study stayed for 30 seconds, and I therefore needed to alter the method in order to separate the shy from the bold. The assumption is the same for both methods: the longer the bird stayed, the higher its level of fear is considered to be (Forkman et al. 2007).

(6) Flight distance: The linear distance to first perching site after release was noted (categories: <5m, 5-10m and >10m). The assumption is that the more frightened a bird is, the longer it will fly.

I decided to exclude two of Møller et al.'s (2011) measures, wriggle and feather loss, and added breathing rate and flight distance. Feather loss is a measure of susceptibility to predation (Møller et al. 2011), and not considered to be a measure of anti-predator behaviour per se. Very few of our birds lost feathers during handling and so this measure was not used. Wriggle was deemed too difficult to standardize, and therefore not a reliable measure.

In addition, morphological traits were recorded: body mass using a Pesola 50g spring balance, wing length (flattened, straightened wing) using a ruler with a zero-stop, tarsus length (with bent toes) with calipers, and skull width and length, also using calipers.

I have chosen to only use the local recruits in the second part of my study as (1) that makes it more standardized because immigrants may lack knowledge of the area (e.g. predators) and therefore behave in a different way, (2) they have all been handled by humans before as fledglings, which may contribute to standardizing, and (3) exact age is known.

### ***Spring 2011***

Birds observed after 1 March were classified as having survived the winter, whereas the missing birds were assumed to have died. I base this on the fact that in general the survival is around 60-70% between autumn and spring, leading to the highly likely scenario that at least 30-40% have died during the winter (Slagsvold unpublished). The survival of our birds over the winter was 59% for great tits (females 54%, males 62%) and 48% for blue tits (females 39% , males 51%), most likely a result of the very cold winter.

The birds were followed closely from March to the end of June, to document their reproductive success. Owners of the different nest boxes were registered, and their mating success and reproductive success was recorded, that is: (1) the date of the first egg laid, (2) number of eggs laid, (3) the date the first egg hatched, (4) the number of eggs that hatched, (5) the number of fledglings at day 15, (6) the number of fledglings that died after day 15 but before fledging, (7) the number of young that fledged, and (8) the body mass at day 15 of the young that fledged. Nests were inspected every second day starting 14 days after the final egg was laid. Date of first egg laid was estimated by the number of eggs when inspecting the box (as tits will lay one egg per day on average). Hatching date of the first egg was estimated from nestling body mass (using a 5 g or 10 g Pesola spring balance). Both date of the first egg laid



and date the first egg hatched was calculated with 1 April as day one. A total of 1227 fledglings were ringed during 2011 (553 great tits, 674 blue tits). In total there were 141 blue tit and 133 great tit nests being monitored, and 49 blue tit and 62 great tit local recruits with nests that got at least as far as laying their first egg. For a detailed account of the number and mean of each reproductive statistic separated by sex and rearing condition see Appendix 2a and b. Anti-predator measurements of breeding local recruits that had not been caught during the autumn were taken during the nestling period.

The birds that were recorded as dead will be assumed to have been sexed correctly due to the observation that in spring 79% of the blue tits ( $n = 36$ ) and 92% of the great tits ( $n = 63$ ) were shown to have been correctly sexed in the autumn. These numbers differ from number of local recruits with nests because here only local recruits measured in autumn are taken into account.

### *Autumn 2011*

I did not take part in the field work in the autumn of 2011, but the two main observers were the same as in 2010. This provides the opportunity of including data from this season in the first part of my analyses when assessing the repeatability of the measurements both within and between the observers and between first and second measurement of individual birds; and when analysing the relationship between the variables. All measuring techniques were the same as autumn 2010. I included 158 great tits from this season in my analyses, of which 87 were local recruits (48 juvenile, 39 adult).

### Statistical analyses

The first part of this thesis presents a new method for measuring anti-predator behaviour. Due to time constraints I have focused only on great tits, except when assessing the relationship between the years where I wanted to study whether annual variation existed and whether it was similar for both species. For the second part both species were used to analyse whether survival and reproduction are related to anti-predator behaviour.

The first tests conducted were normality analyses for all the continuous variables, with the Shapiro-Wilk p-value as the deciding factor. Breathing rate for both species was not normally distributed and so was log-transformed (test results not shown). Values given in tables are back-transformed for easy interpretation. Despite non-normality, immobility data did not benefit from transformation so it was kept untransformed for both species, and

statistics are therefore given as median and range in the tables. Flight distance was measured as either <5m, 5-10m or >10m, but was converted to two categories,  $\leq 10\text{m}$  and  $>10\text{m}$ , in the statistical tests, as there were so few birds that flew less than five meters.

Three of the reproduction variables for great tits (number of eggs that hatched, number of young that fledged and mean body mass at day 15 of the young that fledged ) and one for blue tits (mean body mass at day 15 of the young that fledged) were not normal, and transformations did not help, despite attempts using different functions. Three of these four variables (number of fledged and mean body mass for great tits, and mean body mass for blue tits) had a more or less bimodal distribution, and initial values were therefore used. The fourth variable (number of eggs hatched for great tits) was also used untransformed.

Except for the analyses looking for repeatability between the years all the repeatability analyses were done using birds measured twice within the same season. For the tests of repeatability within and between observers in part one, I have used the index of concordance formula  $A / (A+D)$ , where A is the total number of agreements of measured and D is the total number of disagreements (Martin and Bateson 1993). All values are given as percentage agreement (PA) values. I will regard values equal to or greater than 70% as biologically significant cf. (Martin and Bateson 1993).

Due to the lack of correlation between the anti-predator variables (See results, Table 8) each one was tested separately rather than being combined for a principal component analysis (PCA). In addition, the decision to remove flight distance as a variable in the second part of the analysis was made based on the fact that I consider the variable to be highly inconsistent due to the variance in habitat at the different measuring sites, with some sites being located in open areas with a considerable distance to the trees whereas others were in the middle of the forest. The variable was retained for the first part, as its repeatability was of interest.

Only the main observers, observer 1 (Tore Slagsvold) and 2 (Jan Husek), provided large enough sample sizes of anti-predator variables to test for repeatability within and between observers. In general, when comparing anti-predator variables within observer, the first and second measurements of the birds were used, and when comparing between observers, the first measurement taken by each observer was used. However, due to some incomplete first measurements, later measurements were used in a few cases. For the subsequent analyses all of the observers (1-5) were used in order to gain maximum sample size. Despite the inexperience of observers 3-5 (Merethe Andersen, Jason Whittington and Anders Herland), the measurements (percentages, means or medians) provided by them fell

acceptably within the range of the experienced observers (see Appendix 3). I considered using the mean for birds that had been measured more than once, but decided that it would make these numbers statistically more accurate than the rest.

The datasets from autumn 2010 and spring 2011 include only local recruits. The dataset from autumn 2011 includes all the local recruits and some immigrants to increase sample size. The latter dataset was only used to increase the sample size in the first part of the analyses. A total of 19 birds were excluded from autumn 2011 and two from 2010 (because of insufficient data) to avoid pseudoreplication because they had been measured both years, but were included when comparing anti-predator behaviour between the years. The anti-predator measures taken during spring 2011 on the previously uncaught local recruits were only used in the analyses of reproductive success, in order to increase sample size. For part one, this information was not used as there may have been a difference in anti-predator behaviour between autumn and spring that could confound the results. For further information on which dataset was used when, see the relevant table text.

In the analyses of reproductive success I have included nests with total breeding failure (e.g. due to predation or abandoning of nest) in order to gain maximum sample size. For the analyses of rearing condition I have only used two categories (reared by great tit and reared by blue tit), but I chose to also make a table for each species including three separate categories in a hope to obtain more insight (see Appendix 2a and b). This table also includes (1) the number of fledglings at day 15 (2) the number of fledglings that died after day 15 but before fledging and (3) the number of birds that had one or more young that successfully fledged. These variables were deleted from the analyses as they were deemed redundant. For the variables (1) date of the first egg laid and (2) number of eggs laid only females were used in the analyses ( $n = 18$  for great tits,  $n = 6$  for blue tits), as this was considered more biologically relevant. As a result sample size was reduced to only  $n = 6$  for blue tits and so these variables were excluded from the blue tit analyses. For all the other variables both males and females were used ( $n = 50$  for great tits,  $n = 40$  for blue tits), but because of breeding failures sample size was not the same in all cases. In five of the cases for great tits, and one for blue tits, the male and female were both local recruits for which anti-predator behaviour had been measured, which were so few that all were included.

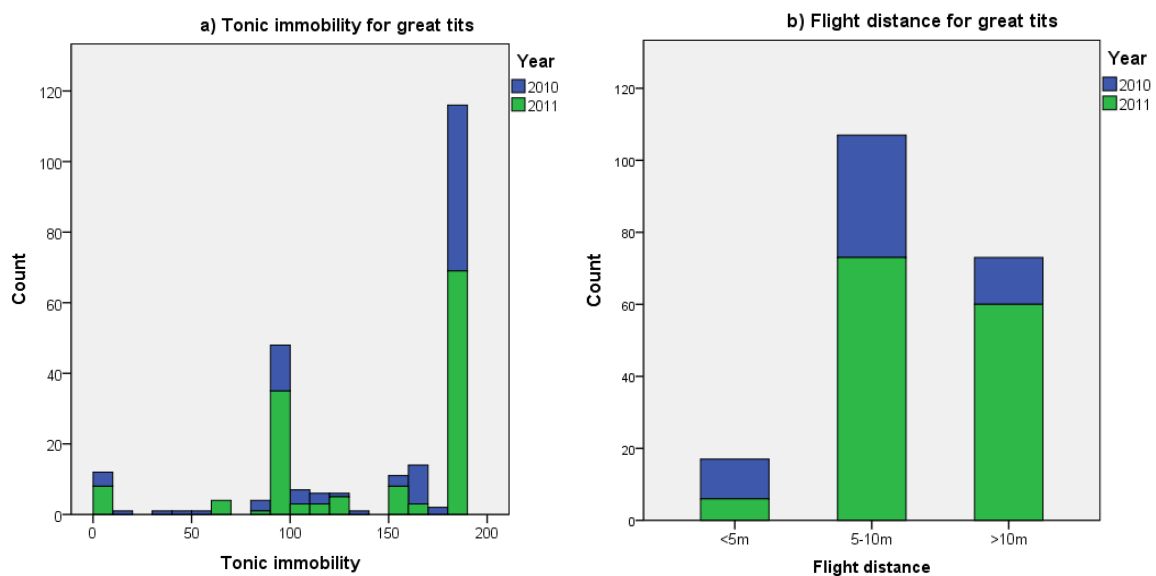
Datasets were made in Excel (Excel® 2010 for Windows). All statistical analyses were done with SPSS (SPSSStatistics® version 19). For all tests with interactions, only two-

way interactions were included, because of low sample size. All statistical tests are two-tailed and chi-square values are given with continuity correction.

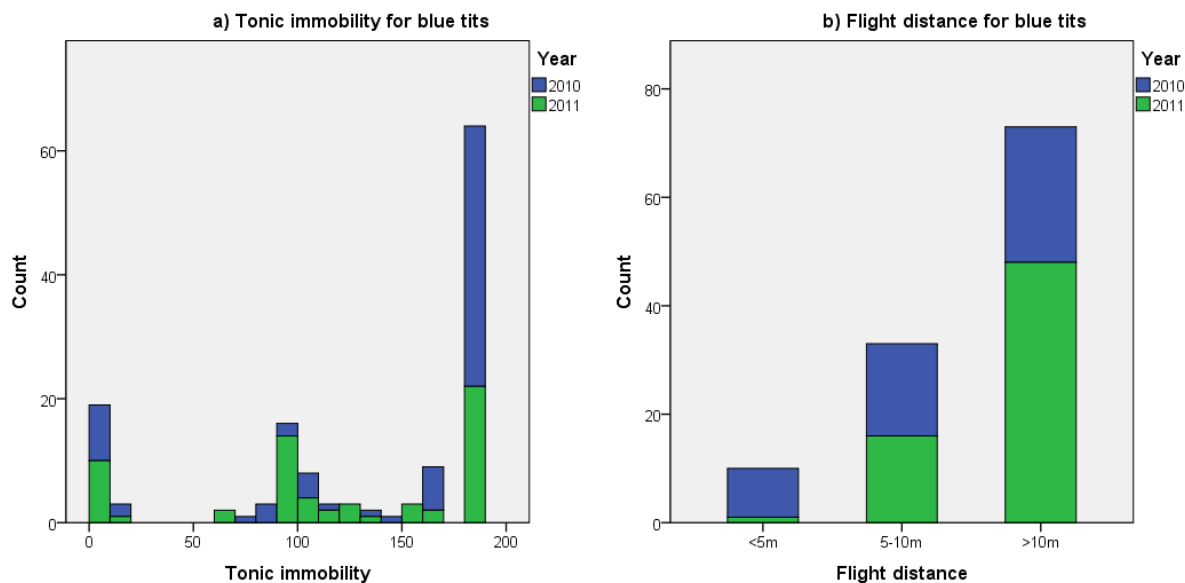
# Results

## Descriptive statistics

A figure for tonic immobility and flight distance is included to show the distribution for both years (Figure 1a, b and 2a, b). Flight distance is only given with two groups in subsequent analyses ( $\leq 10\text{m}$  and  $>10\text{m}$ ). For the remaining variables, see Table 7 for a summary of the values in both years, and individual tables for more details. For both species, level of both tonic immobility and flight distance were high and level of screaming was low in both years, indicating a majority of shy birds. But for great tits, level of biting and calling was high, indicating a majority of bold birds. For blue tits, both biting and calling varied much between the years, but the average indicates a high level of both. Mean breathing rate was approximately the same in both years for great tit, and was significantly reduced in the second year for blue tits.



**Figure 1:** Great tit frequency distributions of a) tonic immobility (from 0° to 180°, n = 254) and b) flight distance (n = 216). Data from autumn 2010 and 2011.



**Figure 2:** Blue tit frequency distributions of for a) tonic immobility (from 0° to 180°, n = 137) and b) flight distance (n = 116). Data from autumn 2010 and 2011.

## Part one

### *Repeatability within and between observers*

Analyses were run separately for each observer comparing individual birds to determine the repeatability of the behaviours between the first and second measurement within the same season (Table 1). Fear scream and flight distance were significantly repeatable for observer 2 (Table 1), and there was a significant positive correlation between the first and second measurement of breathing rate for both observers (Table 1, Figure 3a and b).

**Table 1:** Repeatability within observers for anti-predator variables of great tits measured within the same season. Data from autumn 2010 and 2011.

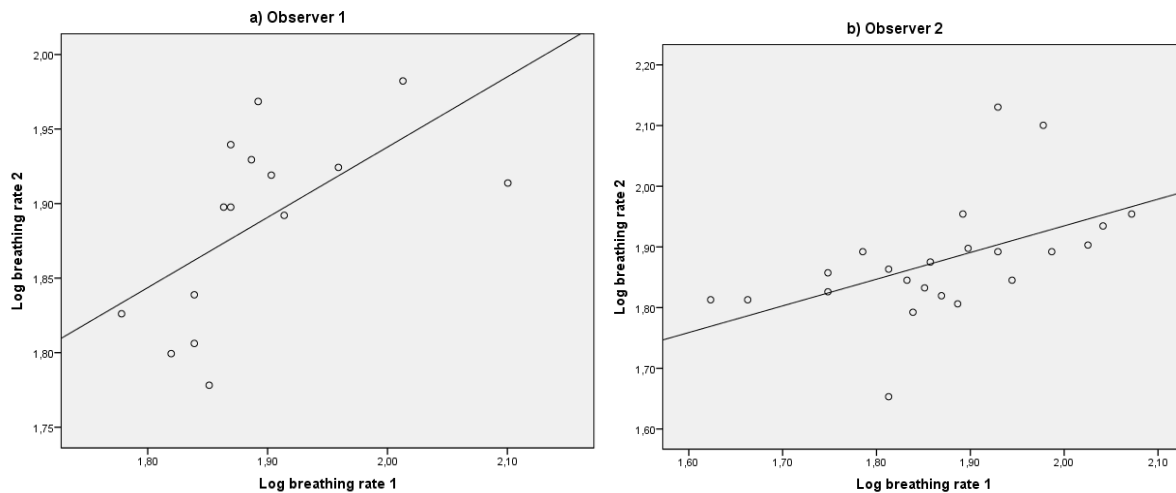
Variable	Observer 1 Measurement				Percentage agreement	Observer 2 Measurement				Percentage agreement
	1	2		n		1	2		n	
		No	Yes			No	Yes			
Biting	No	2	3	16	69	No	5	5	25	68
	Yes	2	9			Yes	3	12		
Fear scream	No	12	2	16	<b>81</b>	No	10	3	25	<b>76</b>
	Yes	1	1			Yes	3	9		
Alarm call	No	4	5	15	67	No	3	1	25	<b>72</b>
	Yes	0	6			Yes	6	15		
Flight distance <sup>1</sup>	≤10m	6	3	12	67	≤10m	5	1	10	<b>70</b>
	>10m	1	2			>10m	2	2		

Variable	Observer 1			Observer 2		
	n	Test-value*	p	n	Test-value*	p
Breathing rate	15	r = 0.60	<b>0.018</b>	23	r = 0.51	<b>0.013</b>
Tonic immobility	12	r <sub>s</sub> = 0.28	0.39	25	r <sub>s</sub> = 0.01	0.97

\* r-value refers to Pearson correlation test and r<sub>s</sub>-value refers to Spearman rank correlation test

<sup>1</sup>“No” represents values ≤10m and “Yes” represents values >10m for measurement 2 by observer 1 and 2 respectively

**Note:** For explanation of variables, see main text



**Figure 3:** Log breathing rate for the first and second measurement of the same individual great tits measured by a) observer 1 (n = 15, R<sup>2</sup> = 0.36) and b) observer 2 (n = 23, R<sup>2</sup> = 0.26). All measurements were done on the same individual birds on two separate occasions within the same season. Data from autumn 2010 and 2011.

In addition to repeatability analyses, test were also run to determine if the measurements of the observers were consistently decreasing or increasing between the two separate trapping occasions within a season. Only tonic immobility was shown to change (decrease) for both observers (Table 2 and 3).

**Table 2:** Comparison of anti-predator variables for two measurements of the same great tit taken within the same season by observer 1 (paired tests)\*. Data from autumn 2010 and 2011.

Variable	Measurement		n	Test-value*	p
	1	2			
Biting	69% <sup>1</sup>	75% <sup>1</sup>	16	$\chi^2 = 0.00$	1.00
Fear scream	13% <sup>1</sup>	19% <sup>1</sup>	16	$\chi^2 = 0.00$	1.00
Alarm call	40% <sup>1</sup>	73% <sup>1</sup>	15	$\chi^2 = 2.2$	0.14
Flight distance	75% <sup>1</sup>	58% <sup>1</sup>	12	$\chi^2 = 0.19$	0.67
Breathing rate	78.2 (1.2) <sup>2</sup>	77.2 (1.2) <sup>2</sup>	15	t = 0.33	0.75
Tonic immobility	170 (90) <sup>3</sup>	97.5 (180) <sup>3</sup>	12	z = -2.0	<b>0.044</b>

\*  $\chi^2$  values refer to chi-square test, t-value refers to paired t-test and z-value refers to Wilcoxon paired-test.

<sup>1</sup> Per cent of individuals biting/screaming/calling/flying  $\leq 10$ m.      <sup>2</sup> Mean (SD).      <sup>3</sup> Median (Range).

**Note:** For explanation of variables, see main text.

**Table 3:** Comparison of anti-predator variables for two measurements of the same great tit taken within the same season by observer 2 (paired tests)\*. Data from autumn 2010 and 2011.

Variable	Measurement		n	Test-value*	p
	1	2			
Biting	60% <sup>1</sup>	68% <sup>1</sup>	25	$\chi^2 = 0.09$	0.77
Fear scream	48% <sup>1</sup>	48% <sup>1</sup>	25	$\chi^2 = 0.00$	1.00
Alarm call	84% <sup>1</sup>	64% <sup>1</sup>	25	$\chi^2 = 1.66$	0.20
Flight distance	70% <sup>1</sup>	60% <sup>1</sup>	10	$\chi^2 = 0.00$	1.00
Breathing rate	74.2 (1.3) <sup>2</sup>	75.5 (1.3) <sup>2</sup>	23	t = -0.33	0.75
Tonic immobility	180 (180) <sup>3</sup>	90 (180) <sup>3</sup>	25	z = -2.5	<b>0.013</b>

\*  $\chi^2$  values refer to chi-square test, t-value refers to paired t-test and z-value refers to Wilcoxon paired-test.

<sup>1</sup> Per cent of individuals biting/screaming/calling/flying  $\leq 10$ m.      <sup>2</sup> Mean (SD).      <sup>3</sup> Median (Range).

**Note:** For explanation of variables, see main text.



Analyses were also run to look for repeatability between the observers and differences in the anti-predator measurements between the observers, for great tits measured twice within the same season. Alarm call was found to be significantly repeatable (Table 4). The anti-predator measurements were not significantly different (Table 5), showing that neither of the observers consistently measured above or below the other.

**Table 4:** Repeatability between observers for anti-predator variables measured within the same season of great tits. Data from autumn 2010 and 2011.

Variable	Observer 1	Observer 2		n	Percentage agreement
		No	Yes		
Biting	No	1	5	26	46
	Yes	9	11		
Fear scream	No	13	2	26	65
	Yes	7	4		
Alarm call	No	4	4	23	<b>70</b>
	Yes	3	12		
Flight distance <sup>1</sup>	≤10m	4	4	13	62
	>10m	1	4		

Variable	n	Test-value*	p
Breathing rate	23	r = 0.31	0.14
Tonic immobility	18	r <sub>s</sub> = -0.11	0.67

\* r-value refers to Pearson correlation test and r<sub>s</sub>-value refers to Spearman rank correlation test.

<sup>1</sup> “No” represents values ≤10m and “Yes” represents values >10m for observer 2.

**Note:** For explanation of variables, see main text.

**Table 5:** Comparison of anti-predator variables between observers (paired tests)\*. Only great tits measured by both observers within the same season are used. Data from autumn 2010 and 2011.

Variable	Observer 1	Observer 2	n	Test-value*	p
Biting	77% <sup>1</sup>	62% <sup>1</sup>	26	$\chi^2 = 0.81$	0.37
Fear scream	42% <sup>1</sup>	23% <sup>1</sup>	26	$\chi^2 = 1.40$	0.24
Alarm call	65% <sup>1</sup>	70% <sup>1</sup>	23	$\chi^2 = 0.00$	1.00
Flight distance	38% <sup>1</sup>	62% <sup>1</sup>	13	$\chi^2 = 0.62$	0.43
Breathing rate	76.0 (1.2) <sup>2</sup>	75.4 (1.2) <sup>2</sup>	23	t = 0.19	0.85
Tonic immobility	115 (90) <sup>3</sup>	100 (180) <sup>3</sup>	18	z = -1.1	0.29

\*  $\chi^2$  values refer to chi-square test, t-value refers to paired t-test and z-value refers to Wilcoxon paired-test.

<sup>1</sup> Per cent of individuals biting/screaming/calling/flying ≤10m.

<sup>2</sup> Mean (SD).

<sup>3</sup> Median (Range).

**Note:** For explanation of variables, see main text.

### ***Influence of sex, age, and rearing condition***

All analyses below include all observers. Initial analyses were run for sex, age, and rearing condition to determine if all the birds could be used in the subsequent analyses (Appendix 4a, b and c). Significant interactions were found for flight distance with age ( $n = 197$ ,  $\chi^2 = 7.3$ ,  $p = 0.007$ ; Appendix 4b), and tonic immobility and flight distance with rearing condition (tonic immobility:  $n = 230$ ,  $z = -2.3$ ,  $p = 0.020$ ; flight distance:  $n = 192$ ,  $\chi^2 = 6.5$ ,  $p = 0.011$ ; Appendix 4c).

### ***Repeatability within the anti-predator variables***

To test for repeatability of the anti-predator variables within individual birds, analyses were run between the first and second measurement of all the birds that were measured twice or more within one season. A significant positive relationship was found for fear scream and breathing rate (Table 6, Figure 4). Because flight distance was significantly influenced by age, and tonic immobility and flight distance were significantly influenced by rearing condition, the dataset was separated by age (juvenile and adult) and rearing condition (reared by great tits [control] and reared by blue tits [cross-fostered]) respectively. Correlation analyses were run again, with the first and second measurements of flight distance analysed for the juveniles and adults separately, and the first and second measurements of tonic immobility and flight distance analysed for control and cross-fostered separately (flight distance within juveniles:  $n = 22$ ,  $\chi^2 = 0.00$ ,  $p = 1.00$ , flight distance within adults:  $n = 9$ ,  $\chi^2 = 1.41$ ,  $p = 0.24$ , tonic immobility within control:  $n = 34$ ,  $r_s = 0.10$ ,  $p = 0.57$ , tonic immobility within cross fostered:  $n = 18$ ,  $r_s = 0.21$ ,  $p = 0.41$ , flight distance within control:  $n = 19$ ,  $\chi^2 = 0.05$ ,  $p = 0.83$ , flight distance within cross fostered:  $n = 12$ ,  $\chi^2 = 0.00$ ,  $p = 1.00$ ). This resulted in mostly lower  $r$ -values and only higher  $p$ -values, indicating that the variables were not affected by age or different rearing conditions despite the results of the initial analyses. Because of this, all the birds were used in the subsequent analyses.

**Table 6:** Repeatability within great tit anti-predator variables between first and second measurement of each variable within the same season. Data from autumn 2010 and 2011.

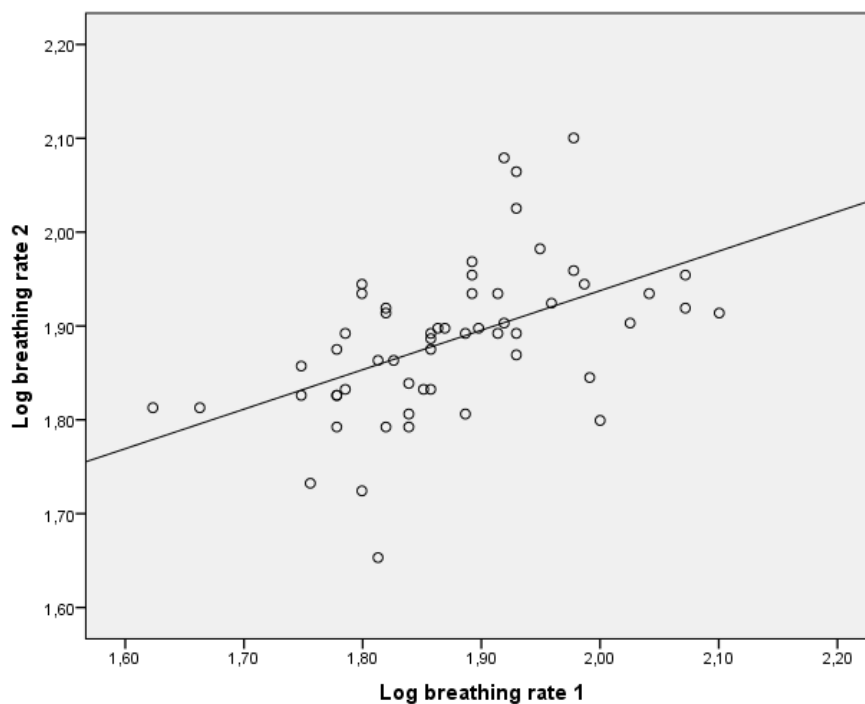
Variable	Measurement 2				Test-value*	p
	Measurement 1	No	Yes	n		
Biting	No	12	9	58	$\chi^2 = 2.43$	0.12
	Yes	12	25			
Fear scream	No	29	6	58	$\chi^2 = 9.89$	<b>0.002</b>
	Yes	9	14			
Alarm call	No	10	7	56	$\chi^2 = 1.69$	0.19
	Yes	14	39			
Flight distance <sup>1</sup>	≤10m	13	6	31	$\chi^2 = 0.42$	0.52
	>10m	6	6			

Variable	n	Test-value*	p
Breathing rate	56	$r = 0.50$	<b>&lt;0.001</b>
Tonic immobility	52	$r_s = 0.14$	0.32

\* r-value refers to Pearson correlation test and  $r_s$ -value refers to Spearman rank correlation test.

<sup>1</sup>“No” represents values ≤10m and “Yes” represents values >10m for the second measurement.

**Note:** For explanation of variables, see main text.



**Figure 4:** Log breathing rate for the first and second measurement taken within the same season of the same individual great tits ( $n = 56$ ,  $R^2 = 0.25$ ). Data from autumn 2010 and 2011.

For great tits there was moderate variation between the anti-predator variables between the years; biting increased and flight distance decreased between years (Table 7). For blue tits the variation was high between the years, with some variables increasing and some decreasing in a rather inconsistent way, with fear scream being the only variable that did not change significantly (Table 7). There were only 21 great tits caught both years. Correlation analyses were run on the 21 great tits to look for repeatability between the years (Appendix 5). No significance was found except a marginal tendency for breathing rate ( $n = 21$ ,  $r = 0.43$ ,  $p = 0.06$ ).

**Table 7:** Variation between the two years for the different anti-predator variables, separated by species. Data from autumn 2010 and 2011, including 21 birds measured both years.

Species	Variable	2010	n	2011	n	Test-value*	p
Great tit	Biting	58% <sup>1</sup>	106	73% <sup>1</sup>	158	$\chi^2 = 5.77$	<b>0.016</b>
	Fear scream	36% <sup>1</sup>	104	42% <sup>1</sup>	158	$\chi^2 = 0.77$	0.38
	Alarm call	72% <sup>1</sup>	105	62% <sup>1</sup>	158	$\chi^2 = 2.56$	0.11
	Flight distance	56% <sup>1</sup>	58	78% <sup>1</sup>	158	$\chi^2 = 7.3$	<b>0.007</b>
	Breathing rate	76.6 (1.3) <sup>2</sup>	104	73.0 (1.2) <sup>2</sup>	158	$t = 1.90$	0.06
	Tonic immobility	170 (180) <sup>3</sup>	96	160 (180) <sup>3</sup>	158	$z = -0.73$	0.46
Blue tit	Biting	79% <sup>1</sup>	75	54% <sup>1</sup>	65	$\chi^2 = 8.63$	<b>0.003</b>
	Fear scream	20% <sup>1</sup>	75	31% <sup>1</sup>	65	$\chi^2 = 1.62$	0.20
	Alarm call	36% <sup>1</sup>	74	66% <sup>1</sup>	65	$\chi^2 = 11.03$	<b>0.001</b>
	Flight distance	51% <sup>3</sup>	51	35% <sup>1</sup>	65	$\chi^2 = 6.5$	<b>0.01</b>
	Breathing rate	93.0 (1.3) <sup>2</sup>	74	78.8 (1.3) <sup>2</sup>	65	$t = 3.63$	<b>&lt;0.001</b>
	Tonic immobility	180 (180) <sup>3</sup>	73	110 (180) <sup>3</sup>	64	$z = -2.59$	<b>0.010</b>

\*  $\chi^2$  values refer to chi-square test, t-values refer to unpaired t-test and z-values refer to Mann-Whitney U-test.

<sup>1</sup> Per cent of individuals biting/screaming/calling/flying  $\leq 10$ m. <sup>2</sup> Mean (SD). <sup>3</sup> Median (Range).

**Note:** For explanation of variables, see main text.

### ***Relationship between the anti-predator variables***

Analyses were run between pairs of anti-predator variables from the first measurement of all birds (Table 8). A significant negative relationship was found between alarm call and flight distance (callers flew shorter than non-callers), and a significant positive relationship was found between biting and fear scream (biters had higher probability of screaming than non-biters), and tonic immobility and fear scream (screamers had higher immobility values than non-screamers, see Table 8).

**Table 8:** Relationship between anti-predator variables for individual great tits. Data from first capture of birds in autumn 2010 and 2011.

	Fear scream		Alarm call		Flight distance		Breathing rate		Tonic immobility	
	No	Yes	No	Yes	≤10m	>10m	Mean	SD	Median	n
Biting	No	54	22	20	35	18	74.8	1.24	175	76
	Yes	87	78	62	89	55	74.7	1.22	165	165
	p	<b>0.011<sup>a</sup></b>		0.12 <sup>a</sup>	0.71 <sup>a</sup>		0.98 <sup>b</sup>		0.72 <sup>c</sup>	
Fear scream	No	-	-	53	65	45	75.3	1.23	160	139
	Yes	-	-	29	58	27	73.6	1.22	180	100
	p	-	-	0.20 <sup>a</sup>	0.25 <sup>a</sup>		0.40 <sup>b</sup>		<b>0.024<sup>c</sup></b>	
Alarm call	No	-	-	-	37	33	73.6	1.19	160	82
	Yes	-	-	-	87	40	75.4	1.24	180	159
	p	-	-	-	<b>0.043<sup>a</sup></b>		0.38 <sup>b</sup>		0.25 <sup>c</sup>	
Flight distance	≤10m	-	-	-	-	-	75.8	1.22	180	124
	>10m	-	-	-	-	-	73.7	1.22	160	73
	p	-	-	-	-	-	0.34 <sup>b</sup>		0.14 <sup>c</sup>	
Breathing rate		-	-	-	-	-	-	-	r = 0.039	234
	p								0.55 <sup>d</sup>	

<sup>a</sup>Chi-square test. <sup>b</sup>Unpaired t-test. <sup>c</sup>Mann-Whitney U-test. <sup>d</sup>Spearman rank correlation test.

**Note:** For explanation of variables see main text.

## Part two

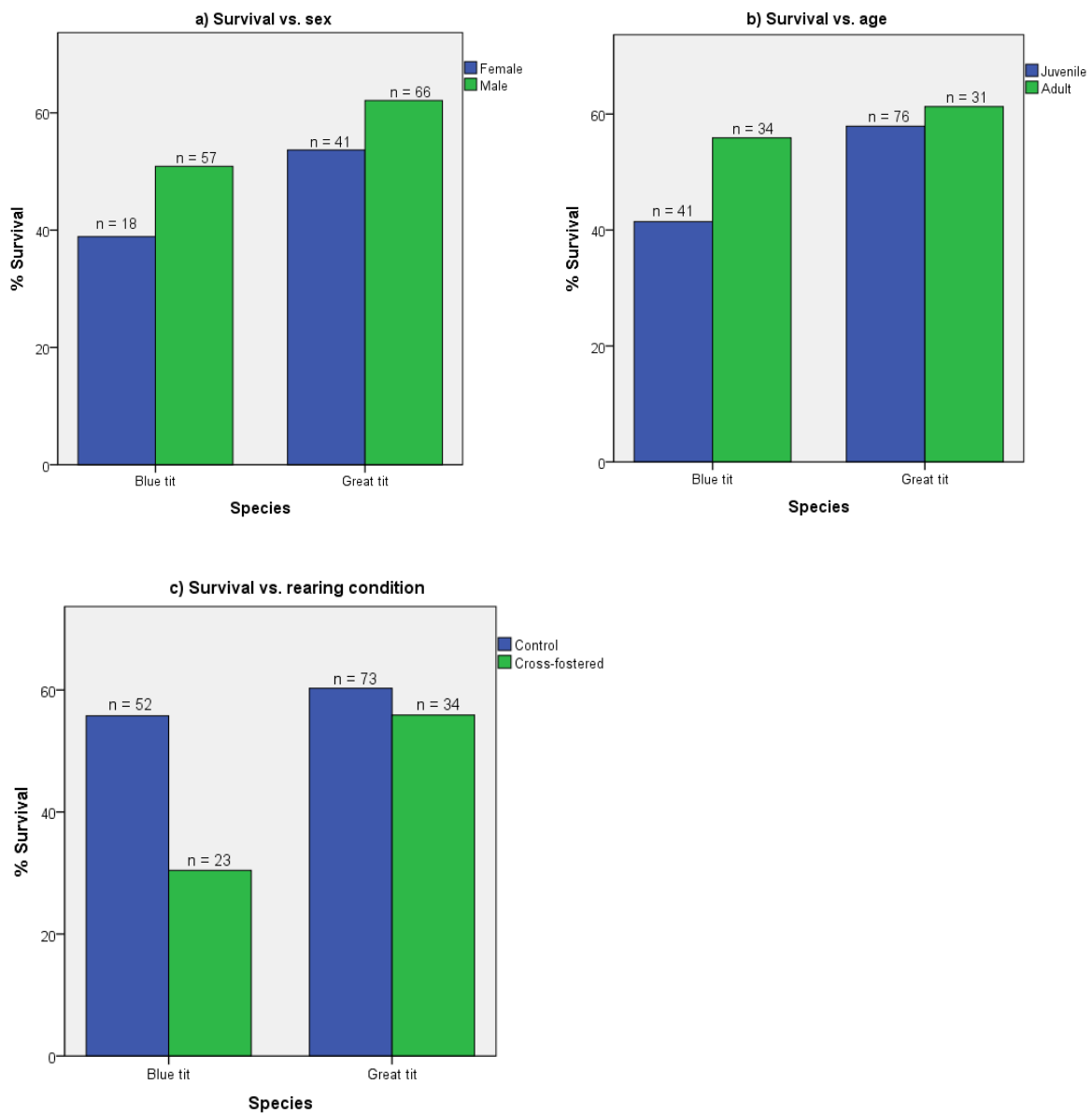
### *Morphology and anti-predator behaviour*

Due to sexual dimorphism, the morphological variables from females and males were tested separately (Appendix 6a, b and 7a, b). For great tit females there was a significant negative relationship between breathing rate and tarsus length ( $n = 40$ ,  $r = -0.39$ ,  $p = 0.012$ ; Appendix 6b), and for males there was a significant negative relationship between tonic immobility and wing length ( $n = 59$ ,  $r = -0.34$ ,  $p = 0.008$ ; Appendix 6b). For blue tit females there was a significant positive relationship between fear scream and tarsus length i.e. screamers had longer tarsi ( $t = -2.8$ ,  $p = 0.013$ ; Appendix 7a) and between tonic immobility and tarsus length ( $n = 18$ ,  $r_s = 0.49$ ,  $p = 0.041$ ; Appendix 7b), whereas no significant relationships were found for males.

### *Winter survival*

Initially, analyses were run to see if great tit and blue tit survival was affected by sex, age, and rearing condition (Figure 5a, b and c). No significant results emerged (see Appendix 8 for details), allowing me to use all the birds in the subsequent analyses. However, as tit winter survival may quite possibly differ with sex, age and rearing condition, I will also do multivariate analyses.

Except for fear scream in great tits (Figure 6), no relationship between survival and anti-predator behaviour was found for either great tits (Table 9) or blue tits (Table 10). When accounting for sex, age, and rearing condition with individual logistic regression analyses; and with a combined logistic regression with backwards selection and all anti-predator variables included, no effect was found for great tits. However, an effect of rearing condition was found for each blue tit anti-predator variable (all  $p < 0.063$ ). Why this was not discovered in the initial analyses may be because continuity correction was used for the chi-test (original  $p$ -value = 0.043). However, no anti-predator variables were found to be significant when accounting for rearing condition with the logistic regression analyses (all  $p > 0.11$ ). The correlation between survival and fear scream was not significant after a Bonferroni correction ( $p = 0.05/5 = 0.01$ ).



**Figure 5:** Percentage of blue tits and great tits that survived the winter 2010/2011 according to a) sex, b) age, and c) rearing condition (control = reared by same species, cross-fostered = reared by opposite species).



**Table 9:** Comparison of anti-predator variables recorded in autumn 2010 of great tits that survived or did not survive the subsequent winter.

Variable	Survived		n	Test-value*	p
	No	Yes			
Biting	63% <sup>1</sup>	43	56% <sup>1</sup>	63	$\chi^2 = 0.29$ 0.59
Fear scream	49% <sup>1</sup>	41	27% <sup>1</sup>	63	$\chi^2 = 4.24$ <b>0.039</b>
Alarm call	71% <sup>1</sup>	42	73% <sup>1</sup>	63	$\chi^2 = 0.00$ 1.00
Breathing rate	76.5 (1.3) <sup>2</sup>	41	76.7 (1.3) <sup>2</sup>	63	t = -0.04 0.97
Tonic immobility	170 (135) <sup>3</sup>	40	172.5 (180) <sup>3</sup>	56	z = -0.86 0.39

\*  $\chi^2$  values refer to chi-square test, t-value refers to unpaired t-test and z-value refers to Mann-Whitney U-test.

<sup>1</sup> Per cent of individuals biting/screaming/calling. <sup>2</sup> Mean (SD). <sup>3</sup> Median (Range).

**Note:** For explanation of variables, see main text.

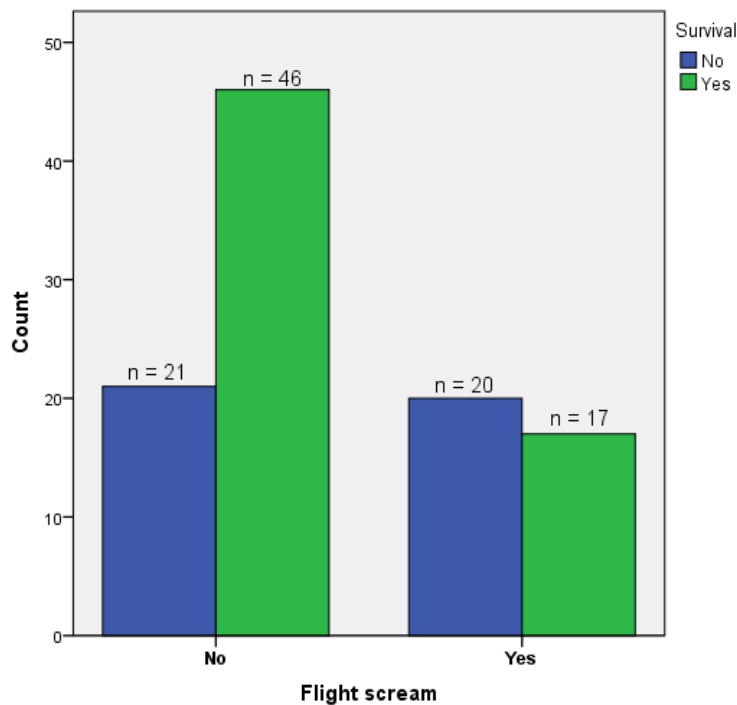
**Table 10:** Comparison of anti-predator variables recorded in autumn 2010 of blue tits that survived or did not survive the subsequent winter.

Variable	Survived		n	Test-value*	p
	No	Yes			
Biting	79% <sup>1</sup>	39	78% <sup>1</sup>	36	$\chi^2 = 0.00$ 1.0
Fear scream	23% <sup>1</sup>	39	17% <sup>1</sup>	36	$\chi^2 = 0.16$ 0.69
Alarm call	33% <sup>1</sup>	39	40% <sup>1</sup>	35	$\chi^2 = 0.13$ 0.72
Breathing rate	90.8 (1.3) <sup>2</sup>	39	95.6 (1.3) <sup>2</sup>	35	t = -0.78 0.44
Tonic immobility	180 (180) <sup>3</sup>	38	180 (180) <sup>3</sup>	35	z = 0.96 0.34

\*  $\chi^2$  values refer to chi-square test, t-value refers to unpaired t-test and z-value refers to Mann-Whitney U-test.

<sup>1</sup> Per cent of individuals biting/screaming/calling. <sup>2</sup> Mean (SD). <sup>3</sup> Median (Range).

**Note:** For explanation of variables, see main text.



**Figure 6:** Number of great tits that did or did not give a fear scream during measuring in autumn 2010, separated by whether they survived the subsequent winter.

### *Reproductive success*

Analyses were run between each reproductive variable and the anti-predator variables (Table 11 and 12). Number of eggs laid was negatively correlated with breathing rate for great tits (Table 11). No significant relationships were found for blue tits (Table 12). When p-values were less than 0.10, a general linear model (GLM) analysis with stepwise backwards elimination was run, including the confounding variables sex, age and rearing condition as independent variables in addition to the anti-predator variable (sex was excluded for the first two reproductive variables as only females were used). The choice to analyse p-values below 0.10 was made because of the low sample size. In four of the cases there was a non-normally distributed reproductive variable (3 for great tits, 1 for blue tits). Normality was therefore assumed in order to run the GLM.

For both great tits and blue tits none of the anti-predator variables with  $p < 0.10$  retained p-values less than 0.10 when taking sex, age and rearing condition into account in a GLM. Only number of eggs laid vs. breathing rate for great tits, (initial  $p = 0.036$ ) remained significant after taking rearing condition and age into account (rearing condition  $p = 0.005$ , breathing rate  $p = 0.03$ ), but not after a Bonferroni correction ( $p = 0.05/30 = 0.0016$ ).

**Table 11:** Relationship between reproductive variables and anti-predator variables of great tits. Data from autumn 2010 and spring 2011.

Variable	Biting		Fear scream		Alarm call		Breathing rate		Tonic immobility		
	No	Yes	No	Yes	No	Yes	No	Yes	r-value	n	
Date first egg laid <sup>a</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	r-value	n	r <sub>s</sub> -value	n
	28.3 (3.9) <sup>1</sup>	26.1 (2.5) <sup>1</sup>	27.3 (3.7) <sup>1</sup>	27.0 (1.8) <sup>1</sup>	26.2 (1.6) <sup>1</sup>	27.6 (3.8) <sup>1</sup>	27.6 (3.8) <sup>1</sup>	0.39 <sup>3</sup>	13	0.21 <sup>4</sup>	15
No. of eggs laid <sup>a</sup>	7.3 (1.6) <sup>1</sup>	7.3 (1.7) <sup>1</sup>	<b>7.7 (1.4)<sup>1*</sup></b>	<b>6.0 (1.6)<sup>1*</sup></b>	8.2 (0.8) <sup>1</sup>	7.0 (1.7) <sup>1</sup>	7.0 (1.7) <sup>1</sup>	<b>-0.50<sup>3**</sup></b>	13	<b>-0.39<sup>4</sup></b>	15
Date 1. egg hatched	48.6 (4.5) <sup>1</sup>	48.4 (3.3) <sup>1</sup>	48.4 (3.9) <sup>1</sup>	48.6 (3.7) <sup>1</sup>	48.7 (3.4) <sup>1</sup>	48.4 (4.0) <sup>1</sup>	48.4 (4.0) <sup>1</sup>	0.03 <sup>3</sup>	37	0.05 <sup>4</sup>	43
No. of eggs hatched	7.5 (7) <sup>2</sup>	7.0 (8) <sup>2</sup>	7.0 (7) <sup>2</sup>	7.0 (8) <sup>2</sup>	7.0 (8) <sup>2</sup>	7.0 (7) <sup>2</sup>	7.0 (7) <sup>2</sup>	0.02 <sup>4</sup>	37	<b>-0.28<sup>4*</sup></b>	43
No. of fledged	4.0 (9) <sup>2</sup>	5.5 (3) <sup>2</sup>	5.0 (9) <sup>2</sup>	5.5 (3) <sup>2</sup>	6.0 (3) <sup>2</sup>	5.0 (9) <sup>2</sup>	5.0 (9) <sup>2</sup>	0.13 <sup>4</sup>	35	0.15 <sup>4</sup>	38
Mean body mass d15	16.0 (11.6) <sup>2</sup>	16.2 (8.3) <sup>2</sup>	15.9 (11.6) <sup>2</sup>	17.4 (8.3) <sup>2</sup>	16.2 (6.9) <sup>2</sup>	16.0 (11.6) <sup>2</sup>	16.0 (11.6) <sup>2</sup>	<b>-0.26<sup>4*</sup></b>	35	<b>0.17<sup>4</sup></b>	38

\* p<0.10, \*\* p<0.05.

<sup>1</sup> Unpaired t-test.

<sup>2</sup> Mann-Whitney U-test.

<sup>3</sup> Pearson correlation test.

<sup>4</sup> Spearman rank correlation test.

<sup>a</sup> Only females included.

<sup>b</sup> Mean (SD) given for date first egg laid, number of eggs laid, date first egg hatched. Median (Range) given for number of eggs that hatched, number of young that fledged and mean body mass at day 15 of the young that fledged.

**Note:** For explanation of variables see main text.

**Table 12:** Correlations analyses between fitness variables and anti-predator variables of blue tits. Data from autumn 2010 and spring 2011.

Variable	Biting		Fear scream				Alarm call		Breathing rate		Tonic Immobility	
	No	Yes	No	Yes	No	Yes	No	Yes	r-value	n		
Date first egg laid <sup>a</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	Mean (SD)/ Median (Range) <sup>b</sup>	r-value	n	r <sub>s</sub> -value	n
	N.A.	1 N.A.	5 N.A.	6 N.A.	0 N.A.	3 N.A.	3 N.A.	3 N.A.	N.A.	3	6 N.A.	6
No. of eggs laid <sup>a</sup>	N.A.	1 N.A.	5 N.A.	6 N.A.	0 N.A.	3 N.A.	3 N.A.	3 N.A.	N.A.	3	6 N.A.	6
Date 1. egg hatched	50.1 (4.0) <sup>1</sup>	14 48.4 (3.4) <sup>1</sup>	26 49.0 (3.9) <sup>1</sup>	32 49.3 (2.7) <sup>1</sup>	8 49.2 (3.7) <sup>1</sup>	24 48.6 (3.8) <sup>1</sup>	15 0.05 <sup>3</sup>	39 -0.25 <sup>4</sup>	0.05 <sup>3</sup>	15	39	39
No. of eggs hatched	7.1 (2.5) <sup>1</sup>	14 7.7 (2.4) <sup>1</sup>	24 7.2 (2.3) <sup>1</sup>	30 8.6 (2.4) <sup>1</sup>	8 7.0 (2.5) <sup>1*</sup>	23 8.3 (2.0) <sup>1*</sup>	15 0.20 <sup>3</sup>	38 0.14 <sup>4</sup>	0.20 <sup>3</sup>	15	38	38
No. of fledged	5.5 (2.7) <sup>1</sup>	13 6.8 (1.9) <sup>1</sup>	21 6.5 (2.3) <sup>1</sup>	27 5.4 (2.1) <sup>1</sup>	7 6.1 (2.1) <sup>1</sup>	19 6.5 (2.5) <sup>1</sup>	15 0.27 <sup>3</sup>	34 0.17 <sup>4</sup>	0.27 <sup>3</sup>	15	34	34
Mean body mass d15	11.4 (8.3) <sup>2</sup>	13 11.0 (8.9) <sup>2</sup>	21 11.0 (8.9) <sup>2</sup>	27 11.2 (7.1) <sup>2</sup>	7 11.4 (8.7) <sup>2*</sup>	19 10.6 (8.0) <sup>2*</sup>	15 -0.20 <sup>4</sup>	34 -0.19 <sup>4</sup>	-0.20 <sup>4</sup>	15	34	34

\* p<0.10, \*\* p<0.05.

<sup>1</sup> Unpaired t-test.

<sup>a</sup> Only females included

<sup>b</sup> Mean (SD) given for date first egg laid, number of eggs laid, date first egg hatched, number of eggs that hatched and number of young that fledged. Median (Range) given for mean body mass at day 15 of the young that fledged.

**Note:** For explanation of variables see main text.

<sup>2</sup> Mann-Whitney U-test.

<sup>3</sup> Pearson correlation test.

<sup>4</sup> Spearman rank correlation test.

## Discussion

An essential part of personality is that behaviour is repeatable. Over all the present results indicate that the repeatability within anti-predator variables measured twice in the same birds in the same season was quite low. However, the repeatability within observers was quite high, and there were some significantly repeatable variables both between observers (alarm call and to some extent breathing rate) and within the individual anti-predator variables measured twice (fear scream and breathing rate). I will therefore discuss the results as if the anti-predator behaviour measured in this study reflects a bird's personality.

### Part one

#### *Repeatability within and between observers*

Within observers, the variables fear scream and breathing rate were significantly repeatable for both observers. Alarm call and flight distance were significantly repeatable within observer 2, and biting was almost significantly repeatable within both observers. Between observers alarm call was the only significantly repeatable variable. The relationship between anti-predator measures was good both within and between observers, showing that both observers measured consistently the first and the second time, and that there was no pattern of one observer consistently measuring above or below the other.

The low repeatability within birds of the anti-predator responses measured once by each observer compared to the rather high repeatability within observers could be due to poor standardization. For example, the speed with which the hand was turned to measure tonic immobility could vary between the two observers. This may explain why within observer repeatability was higher than between observer repeatability. Observer experience level cannot explain the lack of repeatability between observers, as only data from experienced observers were used for this part. Small sample sizes may have had an effect, and it should be noted that even though breathing rate was not significantly repeatable between the observers, it had a rather high r-value (0.30), indicating that breathing rate may have become significantly repeatable with a larger sample size. Alternatively, variation in anti-predator measurements within individuals may simply reflect variation in the response of the focal bird itself, i.e. anti-predator behaviour is too plastic to be repeatable.

### *Repeatability within the anti-predator variables*

The results for repeatability within anti-predator variables measured twice in the same birds in the same season suggest that fear scream and breathing rate were the two most repeatable variables. The variation between the years was moderate for great tits, and high for blue tits. For the 21 great tits measured both years analyses were run, but yielded no significant results. However, breathing rate had a high r-value ( $r = 0.43$ ).

A factor that could influence both the repeatability within and between observers and the repeatability between the first and second measurement of the anti-predator variables is the possibility that personality may change with time of year. For instance, closer to the winter the birds may weigh more and have different priorities than in early fall (e.g. because of stronger competition for roosting sites). First and second measurement may therefore not be repeatable because of this change in state. In a meta-analysis across vertebrate taxa, Bell et al. (2009) found that the overall repeatability was higher when the interval between the observations was shorter. In my case, the interval varied with individual birds and it may therefore be interesting to look at repeatability using only birds measured within a certain timespan. Due to time constraints of the study this, unfortunately, was not done.

If time influences repeatability, I would expect to find low repeatability within individual birds and a high variation in the anti-predator measurements between the years. The 21 great tits measured both years did have low repeatability, but this could also be because of the low sample size. It is interesting that breathing rate was the most repeatable variable between the years, as it was one of only two variables, the other being fear scream, with high repeatability overall. Concerning the relationship between the years for the anti-predator measures, it should be noted that different birds were being analysed in the two seasons (except for the 21 great tits). It could therefore be that the variation in both species was caused by a shift in the means of populations (assuming that the subset of the population I measured are representative for the whole population), caused by high mortality because of directional selection. If this was the case, I would expect to see a trend in the data towards either more shy or bold. It is not definitively clear whether this was the case or not. For blue tits, the level of biting went down and flight distance increased in the second year, indicating a trend towards more shy birds. However, the level of screaming and calling went up, and breathing rate and tonic immobility went down, which indicates a shift towards bolder birds. As flight distance is probably an unreliable measure, the data support a shift towards more bold blue tits. If the reliance on significance is relaxed, great tits also appear to be trending

towards more bold birds, as biting and fear scream went up while breathing rate and tonic immobility went down. This was not as dramatic as for blue tits however. One reason for the less clear shift could be because winter survival for great tits was higher than for blue tits, leading to a weaker selection on personality. As a high winter density is assumed, due to high autumn and spring densities, it is possible that the cold winter favoured the bolder birds, as suggested by the environmental hypothesis. However, as previously mentioned, knowledge of the predation pressures would influence predictions based on this hypothesis. Another possible explanation for the shift is that there has been no selection, but rather that the shy birds simply became bolder over time, as has been previously documented in great tits (Carere et al. 2005).

Low observer standardization between the years can most likely be ruled out as a reason for the inconsistent results, as one would expect a high variation for both species if the observers had changed their methods, and this was not the case. Also, the trends for the variables that do show high variation for both species seem to go in opposite directions, e.g. level of biting went up for great tits and down for blue tits. A consistent change in either direction would be expected if observers had somehow changed their methods between the years. The low sample size in general, may explain the varying results.

### ***Relationship between the anti-predator variables***

A significant negative relationship was found between alarm call and flight distance (callers flew shorter than non-callers), and a significant positive relationship between biting and fear scream (biters had higher probability of screaming than non-biters), and tonic immobility and fear scream (screamers had higher immobility values than non-screamers). But significance in itself is irrelevant if the correlation is the opposite of what is expected (expected trends were decided by the assumptions in the Methods, e.g. a bird that bites [considered bold] is expected to have low breathing rate [considered bold]). A way of comparing expected and actual trends is by comparing them in a table (see Appendix 9). Results with p-values up to  $p = 0.20$  were included in order to ensure that all possible trends were accounted for. Raw numbers were included for the categorical variables, and the r-values for the continual, in case the sample size was too low to give a trend a p-value less than 0.20. The result was rather inconsistent, with equal amounts of support for and against the expected trends. Without taking the strength of the trends into consideration there were three trends that matched the expected trends and four trends that went in the opposite direction of the expected. Eight variable pairs

showed no trends. All in all there was little correlation between the anti-predator variables, which is why I chose to analyse the variables separately instead of doing a PCA.

Møller has used his anti-predator measures in two separate papers (Møller et al. 2011; Møller and Ibanez-Alamo 2012). In both cases, repeatability analyses were not performed within or between the two observers used, or within the anti-predator variables. Relationship between the anti-predator variables, on the other hand, was analysed, but yielded only three and one significant relationships (all positive) between pairs of variables in 2011 and 2012, respectively. In the first study only one of the three significant variable pairs contained two of the same variables that I have used, namely biting and fear scream. It is interesting to note that I only found three significant relationships between anti-predator variables as well, and one of them was biting and fear scream. In the second study (2012) the only significant relationship between variables were between wriggle and feather loss. This study used 1132 birds from 15 different species, and the first used 2105 birds from 80 species, making it difficult to properly compare those and the current study.

The low repeatability between observers may have affected all the subsequent analyses and may therefore explain the lack of significant results. It is noteworthy that the only two variables that were repeatable between the first and second measurement when all the birds were used, namely fear scream and breathing rate, also scored very well both within and between observers. This suggests that the repeatability between the first and second measurement of the other variables may have been higher if only observer repeatability was higher. This raises once again the issue of the low repeatability between observers. If it was due to poor standardization between the observers the possibility of a high repeatability between all variables is still there, but it could also be due to the fact that the other anti-predator measures are inherently not very repeatable.

The fact that both breathing rate and fear scream had rather high repeatability within and between observers and was repeatable between first and second measurement where all the birds were used could lead to the assumption that the relationship between them should be significant. This was not the case, which indicates that high repeatability in itself does not predict a strong relationship between the relevant variables.

### ***Improvement of methods***

There are several ways in which I think the present methods could be improved. Better standardization may be required, especially for tonic immobility. For instance, how long the



bird is held on its back before release, how quickly the hand is tilted and how cold the bird is, could all impact tonic immobility measurements. It has also been found that staring the bird in the eyes induces immobility to a higher degree (Forkman et al. 2007), and I would therefore suggest that this be implemented. Flight distance may, as mentioned, be affected by the fact that the surroundings vary from open areas to rather dense forest, and may therefore not give an accurate measure of how fear level in the bird, as it sometimes can seek refuge in a dense thicket close by and other times has to fly a distance before reaching a tree. These two measures, tonic immobility and flight distance, were the least repeatable of all variables.

Breathing rate was highly repeatable, likely due to being easy to measure and standardize. Fear scream was also rather repeatable overall, and was easy to measure as the bird was in the hand and it was clear if it screamed or not. Biting comes somewhat in between, as it had high repeatability within observers, was not significant in the other repeatability analyses, but had a significant relationship with fear scream. It turned out to be harder to standardize than originally thought, as there is a difference in the strength with which a bird bites, and it was hard to decide what constituted a real bite and what did not. In addition, some birds bit only once, while others would snap several times for each of the three instances the finger was moved towards it. A better measure might be to count the number of bites out of a certain number of finger approaches.

When using risk-taking behaviour as a way of measuring anti-predator behaviour in great tits, van Oers et al. (2004) found that the behaviour was repeatable. Bell et al. (2009) found in a meta-analysis across vertebrate taxa that within the different types of behaviour, anti-predator behaviour scored intermediately high on repeatability. This indicates that anti-predator behaviour in general is repeatable, but gives no suggestion as to why my measures were not repeatable.

The main goal of this part of the analyses was to determine if my way of measuring anti-predator behaviour is a reliable one. Mainly due to lack of data and the possibility that the low repeatability between observers could affect the subsequent results, this issue is still unresolved.

### ***Confounding factors***

I have already mentioned some confounding factors specific to certain analyses, but there are also factors that can affect my results as a whole. In studies conducted in the wild such as this there will be a large number of factors that are not possible to control or standardize such as

time of day, light, temperature, disturbance by other people/observers, amount of time birds spend in the bag and trouble extricating the birds from the nets. Amount of time spent in the bag could lead to differences in stress level, leading to differences that would not have been there had they all been measured immediately after capture. Landys et al. (2011) showed that cross fostered tits became more stressed from spending time in the bag than did control birds (measured as rate of corticosteroid increase). Unfortunately, time spent in the bag was not recorded for this study and could therefore not be taken into account in the analyses.

## Part two

### *Winter survival and reproductive success*

When it comes to how survival and reproduction were related to anti-predator behaviour there were two significant results, both for great tits (survivors screamed less and slow breathers laid more eggs), but because of the high number of analyses Bonferroni tests were run, rendering both the results non-significant.

There were no significant differences in survival between the sexes, ages, or rearing conditions giving me the opportunity to use all the birds in the analyses. Despite this there were no significant relationships between survival and anti-predator behaviour for either species, except for fear scream for great tits. The difference here was noteworthy; half the birds that died were screamers, whereas only 27% of the survivors gave a fear scream. If we look at this as an indicator of personality in general, it would suggest that being shy was advantageous during the winter. However, as this was the only significant result, it is premature to draw this conclusion. The total number of surviving birds could explain the lack of significant results if the number was higher than usual, as one would expect the differences in personality to become less clear when mortality is low e.g. selection is weak. However, both species had slightly lower winter survival (59% and 48% respectively) than average (60-70%) in the study period, and the survival rate is therefore not a possible explanation for the lack of significance.

When analysing the relationships between reproductive success and anti-predator behaviour there were several p-values less than 0.10, but all but one increased to over 0.10 when a GLM including the confounding variables sex, age, and rearing conditions was run. I will assume that early laying and hatching, large clutch size, high hatching success, high number of fledged young and high mean body mass are all positively correlated with

reproductive success (Perrins 1965; Perrins and McCleery 1989; Tinbergen and Boerlijst 1990; Naef-Daenzer et al. 2001).

Out of the four great tit reproductive variables that tended to correlate with anti-predator behaviour, one was in favour of the shy birds (the non-screamers laid more eggs) and three were in favour of the bold birds (the slow breathers laid more eggs and had fledglings with higher mean body mass at day 15, birds with low tonic immobility had a higher number of hatched young). For blue tits, there were two correlations with  $p < 0.10$ , i.e. those that gave an alarm call had a higher number of hatched young, but they had young with lower day 15 body mass than those who did not call. More data is therefore needed before any conclusions can be drawn, but it is still possible to discern some trends from the data. All variable pairs with p-values less than 0.20 were included in two tables, one for each species (Table 13a and b), to more easily spot possible patterns. Even when accounting for trends there seems to be no clear relationship between neither survival and anti-predator behaviour nor reproduction and anti-predator behaviour. There was about equal support for both bold and shy birds having highest reproductive success in blue tits. For great tits, the majority of trends indicated that bold birds have the highest reproductive success. However, there were several contradictions, e.g. for number of eggs laid, two trends indicated that shy had the highest reproductive success, and two others indicated bold behaviour was more successful. Both et al. (2005) found that neither laying date, clutch size nor number of fledglings were related to exploratory behaviour, which could indicate that there was in fact no relationship between reproductive success and personality. However, there was conflicting evidence here as well, as fledgling size correlated negatively with female exploratory behaviour. It therefore seems that reproductive success has a complex relationship with personality when it comes to both anti-predator behaviour and exploratory behaviour.

**Table 13:** Overview of analyses between survival and anti-predator behaviour, and reproduction and anti-predator behaviour of a) great tits and b) blue tits. All results with p-values less than 0.20 included. Direction of correlation (bold or shy) indicated in parenthesis, with lower case letters indicating trends (p-values  $\geq 0.10$ ) and upper case letters indicating p-values  $< 0.10$ . Categorical variables always analysed with “no” as the lowest value, e.g. the negative relationship between scream and number of eggs for great tits indicate that the non-screamers laid the highest no. of eggs.

**a)**

Anti-predator variable	Survival	Date first egg laid	Number of eggs laid	Day first egg hatched	Number of eggs that hatched	No. of young that fledged	Mean body mass day 15
Biting		- (b)					
Fear scream	--- (S)		-- (S)				+ (b)
Alarm call			- (s)				
Breathing rate		+ (b)	--- (B)				- (B)
Tonic immobility			- (b)		-- (B)		

+++/-- p<0.05, ++/-- p<0.10, +/- p<0.20, blank: p>0.20.  
**Note:** For explanation of variables, see main text.

**b)**

Anti-predator variable	Survival	Date first egg laid	Number of eggs laid	Day first egg hatched	Number of eggs that hatched	No. of young that fledged	Mean body mass day 15
Biting		N.A	N.A	- (b)		+ (b)	
Fear scream		N.A	N.A		+ (b)		
Alarm call		N.A	N.A		++(B)		-- (S)
Breathing rate		N.A	N.A			+ (s)	
Tonic immobility		N.A	N.A	- (s)			

+++/-- p<0.05, ++/-- p<0.10, +/- p<0.20, blank: p>0.20.  
**Note:** For explanation of variables see main text.

## The hypotheses

*Best of a bad job hypothesis.* This hypothesis had two predictions. I found no support for the first prediction, namely that the shy birds would be smaller (i.e. shorter wings and tarsi and lower body mass) in the autumn. There were two significant relationships between great tit anti-predator variables and morphological variables (birds with short tarsi and wings had high breathing rate and tonic immobility [considered shy behaviour] respectively). There were also two significant blue tit relationships (birds with short tarsi screamed less [considered shy behaviour] and had lower immobility [considered bold behaviour]). Despite a trend towards shy birds being smaller, taking the high number of tests in total into account suggests that body size, as an indicator of rearing condition, did not affect anti-predator behaviour.

The second prediction, that bold birds would do consistently better than shy ones when it came to both survival and reproduction, did not receive any support either. The only significant relationship between survival and anti-predator behaviour was between survival and alarm call for great tits. The relationship indicates that the shy great tits had higher survival. There was one significant relationship between reproduction and anti-predator behaviour for great tits (slow breathers [considered bold behaviour] laid more eggs) and, in addition, three p-values less than 0.10. Three of these relationships indicated that the bold birds had higher reproductive success. For blue tits, there were two variable pairs with p-values less than 0.10 that opposed each other (birds that gave an alarm call had more eggs that hatched, but lower mean body mass of the fledglings at day 15), but no significant relationships. It would therefore be premature to make conclusions concerning this hypothesis.

*ESS: Environmental hypothesis.* This hypothesis included many predictions, of which I could only test one: that bold individuals had higher reproductive success. I found no support for this prediction for blue tits, and only weak support for great tits (see discussion above and Table 13a and b).

*ESS: Trade-off hypothesis.* This hypothesis predicted that the bold birds would have lower survival, but higher reproductive success, than shy birds. The one significant result for survival indicated that shy great tits had higher survival, which is in concordance with the prediction, but as survival seemed not to be influenced by any of the other anti-predator variables I will not make any conclusions. There was only weak support for bold great tits having higher reproductive success (see discussion above and Table 13b).

The different hypotheses give rather similar predictions under the conditions experienced in the study period. All three of them predicted that the bold individuals would have higher reproductive success. Had there been a greater number of significant relationships between survival and anti-predator behaviour I could have tried to separate the best of a bad job hypothesis and the trade-off hypothesis, as their predictions are opposite for survival. The environmental hypothesis, on the other hand, needs data from at least two years and more information on predator density before it is possible to make any conclusions about it.

### What is maintaining variation in personalities?

When it comes to the hypotheses in this study the literature seems to favour the ESS hypothesis. The best of a bad job hypothesis is for the most part not mentioned in the literature on personality. It has been argued that fast exploring and aggressive phenotypes have an advantage over slow exploring and more docile phenotypes (Krebs 1978 in Both et al. 2005). However, in light of the recent findings of how slow-exploring individuals may have an advantage by quickly adapting to changes in the environment (see Introduction), it seems that most researchers have discarded this hypothesis. Verbeek et al. (1994, 1996) found that variation in exploratory behaviour was unrelated to current body condition (body mass/tarsus length). As exploratory behaviour and boldness have been shown to correlate (see Introduction), this indicates that variation in boldness, and by extension variation in the present measures, are also unrelated to current condition, which slightly discredits prediction 1 of hypothesis 1 that is, that the smaller birds play a shy strategy. Poor rearing conditions in the form of large brood size was found to actually increase exploration scores in great tits, most likely as a result of increased sibling competition (Groothuis and Carere 2005).

When it comes to the ESS hypotheses much research has been done on both trade-offs and environmental influences (Dingemanse et al. 2004; Boon et al. 2007; Smith and Blumstein 2008) . The problem with many of the trade-off hypotheses is that they focus on trade-offs that are irrelevant to this study, such as trade-offs between early and late fecundity (Nussey et al. 2006) or between growth and survival in indeterminate growers (Biro et al. 2004). In addition, there is rarely any focus on the personality aspect. A trade-off between reproduction and survival was found in great tits (McCleery et al. 1996), but the reduction in survival was attributed to the cost of reproduction and only happened late in life. Boon et al. (2008) found that increasing activity was associated with an increasing tendency to bequeath territories, leading to higher offspring survival but a reduction in adult survival. However, the

study was done with North American red squirrels *Tamiasciurus hudsonicus*, and the patterns may not apply to birds. As mentioned earlier, Smith and Blumstein (2008) conducted a meta-analysis on the fitness consequences of personality and found a trade-off between survival and reproduction in relation to boldness. They did not, however, include any studies measuring both survival and reproduction. They analysed survival against boldness separately from reproduction against boldness, and found that bolder individuals exhibited higher reproductive success and shorter life span. To the best of my knowledge, no studies looking at both survival and reproduction in relation to boldness in the same individuals have been conducted.

The environmental hypothesis is also difficult to find support for as most researchers have only tested parts of it, e.g. how exploratory behaviour relates to survival and reproduction under different levels of food-availability (Dingemanse et al. 2004), how selection on temperament is affected by predation pressure (Reale and Festa-Bianchet 2003) or how variation in personality may be maintained by changing selection pressures acting via reproductive traits and fluctuations in food-abundance (Boon et al. 2007). Seeing as how there was a lack of significant results in my study, there are two main explanations. Either, as discussed, personality may be plastic to the extent that no repeatability can be found, rendering my hypotheses irrelevant, or there are consistent differences in anti-predator behaviour, but the methods were not designed well enough to show them. If the former explanation is the case, then no further discussion on how anti-predator behaviour influences fitness is possible, as it would be too varying to have any significant influence on fitness. However, the literature does indicate that personality is moderately heritable so I will therefore continue my discussion as if the latter possibility is the case.

In general, researchers seem to focus mainly on frequency-dependent selection, density-dependent selection or fluctuating environmental conditions as possible explanations for the maintenance of different personality types (Dingemanse et al. 2004; Guillette et al. 2009; Sih et al. 2012). The environmental hypothesis in this study includes both density dependent selection and effects of fluctuating environment. Negative frequency dependent selection may occur when one personality phenotype is rare and has higher fitness compared with alternate personality phenotypes (Guillette et al. 2009). Both et al. (2005) showed that fast-exploring males monopolized the best quality territories, but that slow-exploring great tit males were able to gain high reproductive success on their low quality territories. If fast explorers are rare, they may occupy only the best territories and hence have higher

reproductive success on average than slow explorers. In contrast, if fast-explorers are common, some will have to settle for low-quality territories and their average reproductive success may be lower than that of the few slow-explorers who do well with their low quality territories (Both et al. 2005).

This frequency-dependent form of selection is not one I have addressed in the hypotheses, but I would suggest including it in future work, especially as it may work in concert with temporal variation in environmental conditions. The reason for not addressing frequency-dependent selection in the present study is both because of the lack of correlation between anti-predator variables and a lack of data. The lack of correlation between anti-predator variables inhibited me from doing a PCA to look at the general distribution of shy and bold birds. However, it is possible to look at the individual variables. For both great tits and blue tits there was support for both a majority of shy and bold birds depending on which variable that was assessed (see Results). But even if there had been a clear trend in either direction it would still not have been enough to analyse the frequency distribution because of the lack of data. The study period was only one season (two if 2011 is included), which is not enough to get a clear picture how the frequencies vary. I may interpret a level of biting at e.g. 25% as low, suggesting that selection would favour bold birds in the following year, when in fact the average level was around 20% and bold birds were more common than usual.

The three different forms of selection pressures suggested here may all contribute to maintaining variation in personalities by exerting differential selection over time. It is possible to attempt to disentangle these, but it would require long-term studies in multiple populations in order to understand both the immediate consequences (within year) and long term effects (across several generations) of selection on populations i.e. to obtain data under different selection pressures and several estimates of fitness (survival and lifetime reproductive success) and the trade-off between these fitness measures (Dingemanse and Reale 2005; Groothuis and Carere 2005; Archard and Braithwaite 2010).



## Conclusion

Within observer repeatability was found to be good, whereas repeatability between observers was low. Some repeatability between the first and second measurement of individual birds was found, and a few significant relationships between the variables. The low repeatability between observers calls for better standardisation of the anti-predator measures, to determine if repeatability can be improved.

Several hypotheses may explain why personalities are maintained in wild populations, and these are not mutually exclusive. However, it was not possible to disentangle the different hypotheses in the present study, as data from different environmental conditions are needed i.e. different densities of conspecifics and predators under different food and temperature conditions. This study is therefore seen as an effort to develop a method to determine the true mechanism maintaining variation in personalities in nature.

The present study has illustrated many of the issues associated with personality research. Despite a relatively large sample size and several measures of anti-predator behaviour it was not possible to find any clear relationships between fitness measures and anti-predator behaviour. Several important assumptions were made that could not be tested: that the anti-predator measures correlate with anti-predator behaviour in general, and in extension, that the measures correlate with other personality traits, such as aggression towards conspecifics and exploratory behaviour. In order to determine if the anti-predator measures can be used as a proxy for personality, I would suggest taking some of the measured birds back to the lab in order to perform different tests to evaluate the different assumptions. As so many different measures of boldness already exist it would be difficult to determine which one I should use to determine if the present anti-predator measures correlates with boldness in general. I would therefore suggest focusing on how the anti-predator measures correlates with exploratory behaviour. Should they be shown to correlate it would then be possible to use the anti-predator measures as a proxy for personality. However, in order to do this, the measurements need first to be improved in order to combine the variables (e.g. in a PCA) to reduce the number of tests.

In conclusion, data from more years are needed both in order to determine if anti-predator behaviour is repeatable, and if so, to determine how it affects both survival and reproduction under varying environmental conditions.

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## Appendix

**Appendix 1:** Rearing condition and number of fledglings in 2010.

<b>Nestling</b>	<b>Host</b>	<b>Number of fledglings</b>
Cross fostered (between species)		
Blue tit	Great tit	163
Great tit	Blue tit	179
Great tit	Coal tit	18
Total		360
Controls (not manipulated)		
Blue tit	Blue tit	547
Great tit	Great tit	290
Total		837
Total number of nestlings		1197

**Appendix 2a:** Great tit fitness data, separated by sex and rearing condition (C1 = reared by great tits, OCF = reared by parents reared by blue tits, CF = reared by blue tits). First clutches only unless specified. Data from 2011.

Variable	Rearing condition	Female		Male		Total	
		Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
Date first egg laid	C1	26.7 (2.7)	9	27.5 (3.3)	20	27.2 (3.19)	29
	OCF	29.3 (4.7)	3	30.3 (3.8)	4	29.9 (3.8)	7
	CF	28.6 (3.0)	10	26.1 (2.7)	9	27.4 (3.0)	19
Number of eggs laid	C1	8.7 (1.1)	9	7.7 (1.5)	20	8.0 (1.5)	29
	OCF	6.0 (1.0)	3	6.3 (2.4)	4	6.1 (1.8)	7
	CF	5.9 (1.4)	10	7.6 (2.1)	7	6.6 (1.9)	17
Date first egg hatched	C1	47.8 (2.3)	9	48.7 (3.4)	20	48.4 (3.1)	29
	OCF	49.7 (1.5)	3	50.8 (6.7)	4	50.3 (4.9)	7
	CF	47.7 (3.5)	10	45.9 (4.0)	7	46.9 (3.7)	17
Number of eggs that hatched	C1	8.3 (1.0)	9	7.0 (1.3)	20	7.4 (1.4)	29
	OCF	7.7 (3.5)	3	6.8 (1.5)	4	7.1 (2.3)	7
	CF	5.8 (1.4)	10	6.3 (2.1)	7	6.0 (1.7)	17
Number of fledglings at day 15	C1	5.6 (2.7)	8	5.1 (1.8)	20	5.3 (2.1)	28
	OCF	7.0 (3.6)	3	6.0 (1.4)	2	6.6 (2.7)	5
	CF	4.3 (2.0)	8	5.3 (2.3)	7	4.7 (2.1)	15
Number that died after day 15 <sup>a</sup>	C1	0.0 (0.0)	8	0.2 (0.4)	20	0.1 (0.3)	28
	OCF	0.3 (0.6)	3	0.0 (0.0)	2	0.2 (0.4)	5
	CF	0.0 (0.0)	8	0.0 (0.0)	7	0.0 (0.0)	15
Number of young that fledged	C1	5.6 (2.7)	8	5.0 (1.9)	20	5.1 (2.1)	28
	OCF	6.7 (3.5)	3	6.0 (1.4)	2	6.4 (2.6)	5
	CF	4.3 (2.0)	8	5.3 (2.3)	7	4.7 (2.1)	15
	CF <sup>c</sup>	4.2 (1.9)	9	-	-	4.7 (2.1)	16
Mean body mass at day 15 <sup>b</sup>	C1	15.4 (1.0)	8	16.9 (2.0)	20	16.5 (1.9)	28
	OCF	11.6 (3.8)	3	14.6 (4.8)	2	12.8 (4.0)	5
	CF	17.0 (1.8)	8	16.1 (1.2)	7	16.6 (1.6)	15
	CF <sup>c</sup>	16.8 (1.8)	9	-	-	16.5 (1.5)	16
Reared young <sup>d</sup>	C1	1.9 (0.3)	13	2.0 (0.0)	21	2.0 (0.2)	34
	OCF	2.0 (0.0)	3	1.5 (0.6)	4	1.7 (0.5)	7
	CF	1.8 (0.4)	10	1.8 (0.4)	11	1.8 (0.4)	21
	CF <sup>c</sup>	1.8 (0.4)	11	-	-	1.8 (0.4)	22

<sup>a</sup> Full name: Number of fledglings that died after day 15 but before fledging.

<sup>b</sup> Full name: Mean body mass at day 15 of the young that fledged.

<sup>c</sup> One re-nesting attempt included: female, reared by blue tits.

<sup>d</sup> Two categories 1=no, 2=yes.

**Note:** For explanation of variables, see main text.



**Appendix 2b:** Great tit fitness data, separated by sex and rearing condition (C1 = reared by blue tits, OCF = reared by parents reared by great tits, CF = reared by great tits). First clutches only unless specified. Data from 2011.

Variable	Rearing condition	Female		Male		Total	
		Mean (SD)	n	Mean (SD)	n	Mean (SD)	n
Date first egg laid	C1	25.2 (1.8)	5	27.2 (3.9)	19	26.8 (3.6)	24
	OCF	27.7 (9.1)	3	26.0 (4.0)	7	26.5 (5.4)	10
	CF	27.0 (3.7)	5	25.4 (2.1)	8	26.0 (2.8)	13
Number of eggs laid	C1	10.4 (1.1)	5	9.0 (2.0)	19	9.3 (1.9)	24
	OCF	8.3 (3.1)	3	10.0 (1.2)	7	9.5 (1.9)	10
	CF	9.2 (0.8)	5	9.3 (1.8)	8	9.2 (1.5)	13
Date first egg hatched	C1	48.2 (3.3)	5	49.7 (3.3)	19	49.4 (3.3)	24
	OCF	49.0 (7.6)	3	49.0 (4.4)	7	49.0 (5.0)	10
	CF	49.2 (0.8)	5	48.0 (2.7)	8	48.5 (2.2)	13
Number of eggs that hatched	C1	9.6 (1.1)	5	7.6 (2.5)	18	8.0 (2.4)	23
	OCF	5.3 (3.5)	3	6.8 (2.0)	6	6.3 (2.5)	9
	CF	7.0 (1.4)	5	8.5 (2.1)	8	7.9 (2.0)	13
Number of fledglings at day 15	C1	7.2 (2.3)	5	7.0 (1.7)	16	7.1 (1.8)	21
	OCF	7.0 (2.8)	2	5.0 (3.1)	6	5.5 (3.0)	8
	CF	5.8 (2.5)	5	6.7 (1.9)	7	6.3 (2.1)	12
Number that died after day 15 <sup>a</sup>	C1	0.6 (1.3)	5	0.7 (1.5)	16	0.7 (1.5)	21
	OCF	0.0 (0.0)	2	0.2 (0.4)	6	0.1 (0.4)	8
	CF	0.0 (0.0)	5	0.3 (0.8)	7	0.2(0.6)	12
Number of young that fledged	C1	6.6 (2.4)	5	6.4 (2.1)	16	6.5 (2.1)	21
	C1 <sup>c</sup>	6.3 (2.3)	6	-	-	6.4 (2.1)	22
	OCF	7.0 (2.8)	2	4.8 (2.8)	6	5.4 (2.8)	8
	CF	5.8 (2.5)	5	6.4 (2.6)	7	6.2 (2.4)	12
Mean body mass at day 15 <sup>b</sup>	C1	10.1 (1.5)	5	11.1 (1.8)	16	10.8 (1.7)	21
	C1 <sup>c</sup>	10.1 (1.4)	6	-	-	10.8 (1.7)	22
	OCF	13.9 (5.4)	2	14.1 (3.4)	6	14.0 (3.5)	8
	CF	13.4 (3.4)	5	11.0 (0.9)	7	12.0 (2.5)	12
Reared young <sup>d</sup>	C1	2.0 (0.0)	5	1.9 (0.4)	20	1.9 (0.3)	25
	C1 <sup>c</sup>	2.0 (0.0)	6	-	-	1.9 (0.3)	22
	OCF	1.7 (0.6)	3	1.9 (0.4)	7	1.8 (0.4)	10
	CF	2.0 (0.0)	5	1.9 (0.4)	8	1.9 (0.3)	13

<sup>a</sup> Full name: Number of fledglings that died after day 15 but before fledging.

<sup>b</sup> Full name: Mean body mass at day 15 of the young that fledged.

<sup>c</sup> One re-nesting attempt included: female, reared by blue tits.

<sup>d</sup> Two categories 1=no, 2=yes.

**Note:** For explanation of variables, see main text.

**Appendix 3:** Statistics of the first measurement of great tits for the individual observers (here first measurement is the first measurement the observer in question did on the bird, i.e. the bird may have been measured before by another observer). Observer 4 and 5 excluded because of low sample size ( n = 4 and 2 respectively). Data from autumn 2010.

Variable	Observer 1		Observer 2		Observer 3	
	Statistic	n	Statistic	n	Statistic	n
Bite	59% <sup>1</sup>	41	58% <sup>1</sup>	72	54% <sup>1</sup>	13
Fear scream	26% <sup>1</sup>	39	38% <sup>1</sup>	72	62% <sup>1</sup>	13
Alarm call	70% <sup>1</sup>	40	70% <sup>1</sup>	71	75% <sup>1</sup>	12
Flight distance	64% <sup>1</sup>	22	78% <sup>1</sup>	40	75% <sup>1</sup>	12
Breathing rate	82.2 (14.7) <sup>2</sup>	40	76.06 (19.3) <sup>2</sup>	72	90.9 (17.8) <sup>2</sup>	13
Tonic immobility	165 (175) <sup>3</sup>	32	175 (180) <sup>3</sup>	70	180 (180) <sup>3</sup>	13
Wing length (mm)	76.1 (2.0) <sup>2</sup>	42	76.7 (1.9) <sup>2</sup>	72	75.4 (1.9) <sup>2</sup>	13
Tarsus length (mm)	22.5 (0.5) <sup>2</sup>	42	22.6 (0.6) <sup>2</sup>	72	23.2 (0.5) <sup>2</sup>	13
Body mass (g)	18.2 (0.8) <sup>2</sup>	41	18.9 (1.0) <sup>2</sup>	71	18.1 (1.3) <sup>2</sup>	13

<sup>1</sup> Per cent of individuals biting/screaming/calling/flying ≤10m.

<sup>2</sup> Mean (SD).

<sup>3</sup> Median (Range).

**Note:** For explanation of variables, see main text.

**Appendix 4a:** Comparison of anti-predator variables between a) female and male great tits, b) juvenile and adult great tits, and c) great tits reared by great tits (control) and great tits reared by blue tits (cross-fostered). Data from autumn 2010 and 2011.

Variable	Male	n	Female	n	Test-value*	p
Biting	69% <sup>1</sup>	153	67% <sup>1</sup>	90	$\chi^2 = 0.08$	0.78
Fear scream	39% <sup>1</sup>	153	47% <sup>1</sup>	88	$\chi^2 = 1.17$	0.28
Alarm call	64% <sup>1</sup>	152	70% <sup>1</sup>	90	$\chi^2 = 0.71$	0.40
Flight distance	63% <sup>1</sup>	127	63% <sup>1</sup>	70	$\chi^2 = 0.00$	1.00
Breathing rate	75.5 (1.2) <sup>2</sup>	152	74.35 (1.2) <sup>2</sup>	89	t = 0.54	0.59
Tonic immobility	180 (180) <sup>3</sup>	147	180 (180) <sup>3</sup>	88	z = -0.24	0.82

\*  $\chi^2$  values refer to chi-square test, t-value refers to unpaired t-test and z-value refers to Mann-Whitney U-test.  
<sup>1</sup> Per cent of individuals biting/screaming/calling/flying  $\leq 10$ m.      <sup>2</sup> Mean (SD).      <sup>3</sup> Median (range).

**Note:** For explanation of variables, see main text.

**b)**

Variable	Juvenile	n	Adult	n	Test-value*	p
Biting	66% <sup>1</sup>	131	71% <sup>1</sup>	112	$\chi^2 = 0.30$	0.58
Fear scream	45% <sup>1</sup>	130	37% <sup>1</sup>	111	$\chi^2 = 1.43$	0.23
Alarm call	70% <sup>1</sup>	130	62% <sup>1</sup>	112	$\chi^2 = 1.54$	0.22
Flight distance	53% <sup>1</sup>	99	72% <sup>1</sup>	98	$\chi^2 = 7.34$	<b>0.007</b>
Breathing rate	74.8 (1.2) <sup>2</sup>	130	74.7 (1.2) <sup>2</sup>	111	t = 0.05	0.96
Tonic immobility	180 (180) <sup>3</sup>	124	160 (180) <sup>3</sup>	111	z = -0.98	0.33

\*  $\chi^2$  values refer to chi-square test, t-value refers to unpaired t-test and z-value refers to Mann-Whitney U-test.  
<sup>1</sup> Per cent of individuals biting/screaming/calling/flying  $\leq 10$ m.      <sup>2</sup> Mean (SD).      <sup>3</sup> Median (range).

**Note:** For explanation of variables, see main text.

**c)**

Variable	Reared by great tits	n	Reared by blue tits	n	Test-value*	p
Biting	70% <sup>1</sup>	185	60% <sup>1</sup>	53	$\chi^2 = 1.25$	0.26
Fear scream	43% <sup>1</sup>	183	38% <sup>1</sup>	53	$\chi^2 = 0.23$	0.63
Alarm call	67% <sup>1</sup>	184	66% <sup>1</sup>	53	$\chi^2 = 0.00$	0.99
Flight distance	58% <sup>1</sup>	150	81% <sup>1</sup>	42	$\chi^2 = 6.5$	<b>0.011</b>
Breathing rate	74.9 (1.2) <sup>2</sup>	183	74.4 (1.2) <sup>2</sup>	53	t = 0.23	0.82
Tonic immobility	160 (180) <sup>3</sup>	177	180 (180) <sup>3</sup>	53	z = -2.34	<b>0.020</b>

\*  $\chi^2$  values refer to chi-square test, t-value refers to unpaired t-test and z-value refers to Mann-Whitney U-test.  
<sup>1</sup> Per cent of individuals biting/screaming/calling/flying  $\leq 10$ m.      <sup>2</sup> Mean (SD).      <sup>3</sup> Median (range).

**Note:** For explanation of variables, see main text.

**Appendix 5:** Repeatability between the years for the anti-predator variables of the 21 great tits caught both years. Data from 2010 and 2011.

Variable	2010	2011		n	$\chi^2$ -value	p
		No	Yes			
Biting	No	5	3	21	0.08	0.78
	Yes	6	7			
Fear scream	No	14	4	21	0.00	1.00
	Yes	2	1			
Alarm call	No	3	5	21	0.05	0.85
	Yes	3	10			
Flight distance <sup>1</sup>	≤10m	7	2	13	0.12	0.73
	>10m	2	2			

Variable	n	Test-statistic*	p
Breathing rate	21	$r = 0.43^1$	0.06
Tonic immobility	18	$r_s = 0.11^2$	0.66

\* r-value refers to Pearson correlation test and  $r_s$ -value refers to Spearman rank correlation tests.

<sup>1</sup>“No” represents values ≤10m in 2011 and “Yes” represents values >10m in 2011.

**Note:** For explanation of variables, see main text.

**Appendix 6a:** Comparison of great tit mean (SD) values for the morphological variables body mass (g), wing length (mm), and tarsus length (mm) within the anti-predator variables. Separate analyses for females and males. Data from autumn 2010.

Anti-predator variable	Morphological variable	Females				Males			
		n <sup>1</sup>	Mean (SD)	t-value*	p	n <sup>1</sup>	Mean(SD)	t-value*	p
Biting	Body mass	No 18	17.3 (0.6)	-0.90	0.38	No 25	18.5 (0.9)	0.93	0.36
		Yes 23	17.5 (0.8)			Yes 38	18.3 (0.9)		
	Wing length	No 18	74.8 (1.1)	-0.18	0.86	No 26	77.3 (1.3)	-0.74	0.47
		Yes 23	74.8 (1.2)			Yes 39	77.6 (1.8)		
Fear scream	Tarsus length	No 18	22.2 (0.6)	-1.03	0.31	No 26	22.8 (0.5)	0.16	0.87
		Yes 23	22.4 (0.6)			Yes 39	22.8 (0.5)		
	Body mass	No 23	17.3 (0.6)	-0.33	0.74	No 44	18.4 (0.9)	-0.64	0.95
		Yes 16	17.4 (0.9)			Yes 19	18.4 (1.0)		
Alarm call	Wing length	No 23	75.0 (1.2)	0.74	0.46	No 44	77.5 (1.8)	0.49	0.63
		Yes 16	74.8 (0.9)			Yes 21	77.3 (1.4)		
	Tarsus length	No 23	22.2 (0.7)	-1.20	0.24	No 44	22.8 (0.5)	0.53	0.60
		Yes 16	22.4 (0.5)			Yes 21	22.8 (0.4)		
Alarm call	Body mass	No 12	17.1 (0.7)	-1.52	0.14	No 16	18.2 (1.0)	-0.86	0.39
		Yes 29	17.5 (0.7)			Yes 46	18.5 (0.9)		
	Wing length	No 12	75.0 (1.3)	0.42	0.68	No 17	77.9 (1.2)	1.17	0.25
		Yes 29	74.8 (1.1)			Yes 47	77.3 (1.8)		
Tarsus length	No 12	22.5 (0.7)	1.64	0.11	No 17	22.7 (0.7)	-1.41	0.16	
	Yes 29	22.2 (0.6)			Yes 47	22.9 (0.4)			

\* Unpaired t-test.

<sup>1</sup> Number of birds that did not and did bite/scream/give alarm call respectively.

**Note:** For explanation of variables, see main text.

**Appendix 6b:** Relationship between great tit anti-predator variables and the morphological variables body mass (g), wing length (mm) and tarsus length (mm). Separate analyses for females and males. Data from autumn 2010.

Anti-predator variable	Morphological variable	Females			Males		
		n	Test-value*	p	n	Test-value*	p
Breathing rate	Body mass	40	r = 0.30	0.061	62	r = 0.14	0.29
	Wing length	40	r = -0.17	0.29	66	r = 0.22	0.077
	Tarsus length	40	r = -0.39	<b>0.012</b>	64	r = -0.07	0.57
Tonic immobility	Body mass	37	r <sub>s</sub> = 0.09	0.62	58	r <sub>s</sub> = -0.16	0.23
	Wing length	37	r <sub>s</sub> = 0.04	0.83	59	r <sub>s</sub> = -0.34	<b>0.008</b>
	Tarsus length	37	r <sub>s</sub> = -0.09	0.60	59	r <sub>s</sub> = -0.36	0.79

\* r-values refer to Pearson correlation test and r<sub>s</sub>-values refer to Spearman rank correlation test .

**Note:** For explanation of variables, see main text.

**Appendix 7a:** Comparison of blue tit mean (SD) values for the morphological variables body mass (g), wing length (mm), and tarsus length (mm) within the anti-predator variables. Separate analyses for females and males. Data from autumn 2010.

Anti-predator variable	Morphological variable	Females				Males			
		n <sup>1</sup>	Mean(SD)	t-value*	p	n <sup>1</sup>	Mean(SD)	t-value*	p
Biting	Body mass	No 4	10.7 (0.3)	-0.96	0.35	No 12	11.4 (0.5)	0.24	0.81
		Yes 13	11.0 (0.5)			Yes 44	11.4 (0.6)		
	Wing length	No 4	65.6 (1.5)	-0.94	0.36	No 12	67.9 (1.3)	-1.1	0.28
		Yes 14	66.4 (1.5)			Yes 44	68.4 (1.5)		
Fear scream	Tarsus length	No 4	19.1 (0.4)	-1.3	0.20	No 12	19.8 (0.7)	1.36	0.18
		Yes 14	19.5 (0.6)			Yes 44	19.5 (0.6)		
	Body mass	No 14	10.9 (0.3)	-0.05	0.96	No 44	11.4 (0.6)	0.47	0.64
		Yes 3	10.9 (0.9)			Yes 12	11.3 (0.4)		
Alarm call	Wing length	No 15	66.2 (1.7)	-0.10	0.92	No 44	68.1 (1.4)	-1.66	0.10
		Yes 3	66.3 (0.6)			Yes 12	68.9 (1.39)		
	Tarsus length	No 15	19.3 (0.4)	-2.8	<b>0.013</b>	No 44	19.6 (0.6)	0.39	0.70
		Yes 3	20.1 (6.0)			Yes 12	19.5 (0.5)		
	Body mass	No 7	11.1 (0.4)	1.71	0.11	No 39	11.3 (0.6)	-0.71	0.48
		Yes 10	10.8 (0.4)			Yes 17	11.5 (0.4)		
	Wing length	No 8	66.3 (1.6)	0.15	0.88	No 39	68.2 (1.5)	-0.97	0.34
		Yes 10	66.2 (1.5)			Yes 17	68.6 (1.3)		
Tarsus length	No 8	19.4 (0.6)	0.24	0.81	No 39	19.6 (0.7)	-0.04	0.97	
	Yes 10	19.4 (0.5)			Yes 17	19.6 (0.5)			

\* Unpaired t-test.

<sup>1</sup> Number of birds that did not and did bite/scream/give alarm call respectively.

**Note:** For explanation of variables, see main text.

**Appendix 7b:** Comparison/relationship between blue tit anti-predator variables and the morphological variables body mass (g), wing length (mm) and tarsus length (mm). Separate analyses for females and males. Data from autumn 2010.

Anti-predator variable	Morphological variable	Females			Males		
		n	Test-value*	p	n	Test-value*	p
Breathing rate	Body mass	17	r = -0.10	0.69	56	r = 0.01	0.97
	Wing length	18	r = -0.60	0.81	56	r = -0.12	0.37
	Tarsus length	18	r = -0.15	0.55	56	r = 0.11	0.43
Tonic immobility	Body mass	17	r <sub>s</sub> = 0.06	0.83	55	r <sub>s</sub> = 0.23	0.089
	Wing length	18	r <sub>s</sub> = 0.12	0.64	55	r <sub>s</sub> = 0.15	0.28
	Tarsus length	18	r <sub>s</sub> = 0.49	<b>0.041</b>	55	r <sub>s</sub> = 0.11	0.44

\* r-values refer to Pearson correlation test and r<sub>s</sub>-values refer to Spearman rank correlation test .

**Note:** For explanation of variables, see main text.

**Appendix 8:** Per cent survival during winter 2010/2011 of great tits and blue tits, in relation to sex, age and rearing condition respectively.

Species	Variable	N	% Survival	$\chi^2$ value	p
Great tits	Male	66	62	0.44	0.51
	Female	41	54		
	Juvenile	76	58	0.01	0.92
	Adult	31	61		
	Reared by blue tits	34	56	0.05	0.83
	Reared by great tits	73	60		
	Total	107	59		
Blue tits	Male	57	51	0.38	0.54
	Female	18	39		
	Juvenile	41	41	1.02	0.31
	Adult	34	56		
	Reared by great tits	23	30	3.15	0.076
	Reared by blue tits	52	56		
	Total	75	48		

**Appendix 9:** First row shows the expected relationship between the anti-predator variables and the shy-bold axis (see Methods), with + indicating a positive correlation and – a negative correlation (e.g. the higher tonic immobility a bird has, the shyer it is expected to be, hence a negative correlation). The gray area shows the expected correlation between the different anti-predator variables. The white area shows the actual trends, with bold symbols indicating trends that matched the direction of the expected trends.

	<b>Biting</b>	<b>Fear scream</b>	<b>Alarm call</b>	<b>Flight distance</b>	<b>Breathing rate</b>	<b>Tonic immobility</b>
<b>Shy-bold expectancy</b>	+	+	+	-	-	-
Biting		+	+	-	-	-
Fear scream	<b>+++</b>		+	-	-	-
Alarm call	-	+		-	-	-
Flight distance			- - -		+	+
Breathing rate				- -		+
Tonic immobility		+++		- -		

---/+++ p<0.05, --/++ p<0.10, -/+ 0.10≤ p <0.20.

**Note:** For explanation of variables see main text.